

A MODEL OF VOLUNTARY CONTROL OF SMOOTH PURSUIT EYE MOVEMENTS

by

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SYNOPSIS

Smooth pursuit eye movements (SP) are involuntary movements in the sense that SP cannot be elicited volitionally if there is no moving visual stimulus. Meanwhile, if there is an object changing position, the eyes can track at any speed below that of the object. When several moving objects are given with different speeds and directions, the eyes can choose and track one of the objects, showing that SP are voluntarily controlled.

This paper describes a model which uniformly explains the above inconsistent characteristics of SP. The basic assumption of the model is that the SP system is composed of two units engaged in eye movements toward the opposite directions to each other and their gains can be controlled voluntarily. This model shows good agreement with the results reported in several papers associated with voluntariness and involuntariness of SP.

1. INTRODUCTION

Smooth pursuit eye movement (SP, for short), as is well known, appears when the eyes are viewing moving objects or patterns. The most fundamental characteristic of SP is that (1) in ordinary situations SP does not appear if there is no moving visual target. Even if one tries to move the eyes smoothly in the absence of a moving target, only saccadic eye movements (SC, for short) will be elicited, but SP will not occur. In this sense SP can be considered as an involuntary movement.

However, SP also has a voluntary characteristic:

- (2) given a point object moving at a constant speed, one can move his eyes smoothly with an arbitrary speed not faster than the target speed (Steinmann et al., 1969).

When the subject is instructed to move his eyes at half of the target speed, for example, he can move the eyes by SP at approximately half of the object speed. SP is a voluntary movement in the sense that the tracking speed can be changed intentionally.

Steinmann et al. also pointed out that

- (3) the speed of SP never exceeds that of the object.

It implies the involuntariness of SP; even if one tries to move the eyes twice as fast as the object speed, it results in more occurrence of SC, but the speed of the SP component never exceeds that of the object.

A possible explanation to the above involuntariness of SP, (1) and (3), is such that SP is caused by excitation in some direction-selective neurons on the retina (or higher-level visual systems) generated only when the object image is slipping on the retina (we shall refer to it as retinal slip). According to this explanation, the reason of why SP does not occur in the absence of a moving object is that there is no retinal slip when there is no moving object. On the other hand if there is some moving object, the excitation of the

direction-selective neurons by retinal slip will rotate the eyes in the same direction as the target.

However, a question arises (Young, 1971): when the eye is tracking a moving object, the image of the background (which usually exists except for special cases such as experiments in a darkroom) slips on the retina toward the opposite direction of the object and is expected to have an effect of suppressing SP. Actually, however,

(4) the retinal slip of the background image rarely prevents SP for the moving target. This means that a certain selecting function must work for a plural number of stimuli on the retina.

An answer easily imagined to this question is one based upon the difference between the foveal vision and the peripheral one. When one is fixating an object, its retinal image is usually nearby the central fovea and it will be natural to think that the retinal slip in the central fovea causes a larger nerve excitation than that in the peripheral area. It is probable in consideration of the difference between the visibilities in the central fovea and the peripheral area. In addition, the cerebral visual area, which corresponds topologically continuously with the retinas, has a larger area for the central fovea than for the peripheral area. It might suggest that nerve stimuli in the central fovea has a more dominant effect on SP than that in the peripheral area.

Another possible explanation is one related to accommodation. Since the background objects are usually located at positions farther from the eyes than the target, the retinal image of the background will be out of focus. Because the contrast of the retinal images of the background objects is low, the neuronal excitation by them might be smaller than by the retinal slip of the target.

Although the existence of the above mechanisms cannot be denied, there is a series of experiments inexplicable by them. Ter Braak and Bouis (1970) and Ter Braak (1972) showed that

(5) given an ambivalent moving pattern (a pattern that can be regarded as moving either to the right or to the left), SP appears either to the right or to the left and its direction is volitionally alterable.

Fig. 1 depicts two examples of ambivalent stimuli. Fig. 1a shows two spirals drawn in opposite directions on a drum. When the drum is rotated, one spiral appears to move to

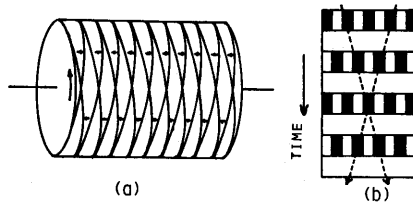


Fig. 1 Ambivalent optokinetic stimuli. (a) Two spirals drawn in opposite directions on a rotating drum. (b) Two patterns of vertical stripes displayed alternately with a spatial disparity of 180° (1/2 stripe).

the right and the other to the left. In Fig. 1b two black-and-white patterns (one is shifted a stripe from the other) are alternately displayed with a frequency of about 10 Hz. When viewing a moving pattern of this kind, the eye moves smoothly either to the right or to the left with intentional controllability of the direction.

Moreover, Wald and Morgan (1978) indicated that

(6) when viewing a dynamic visual noise (such as a TV screen with no broadcasting), one can move the eye smoothly and freely.

The selectivity of direction of SP for moving stimuli in (5) or (6) cannot be attributed to the

difference between the central fovea and the peripheral area of to the difference of distances of the target and the background.

As is described so far, the SP system has both voluntary and involuntary characteristics. To elucidate the mechanism of SP, therefore, it is significant to construct a model capable of explaining the above-mentioned characteristics in a uniform manner. This paper is a trial to build such a model.

2. NEW MODEL OF THE SMOOTH PURSUIT SYSTEM

For a single object the model of the SP system can be illustrated quite generally as in Fig. 2a. Since the SP system can be considered as a kind of velocity servomechanism to

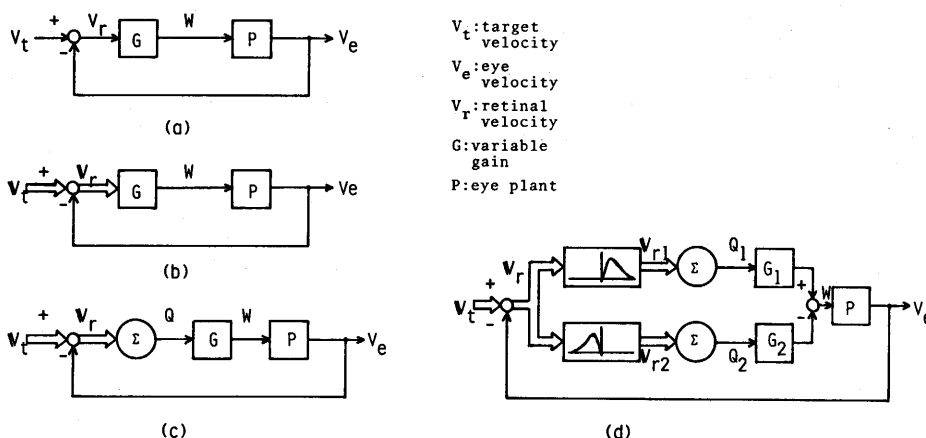


Fig. 2 Models of the smooth pursuit system. (a) Model for a single input. (b) Model for a multiple input. (c) Multi-input model in which the input to the eye plant are given by the algebraic sum of retinal slips of visual stimuli. (d) Multi-input model in which retinal slips are divided two parts according to their directions (left and right) and totalled respectively. The two sums are differently weighed and applied to the eye plant.

match the angular velocity of the eyeball to the velocity of the object, we consider the velocities (not positions) of the object and the eye as input and output of the system, respectively. If the target is a single point moving in a darkroom or a pattern uniformly moving in the visual field, as in the conventional models proposed previously, the target velocity, V_t , is a scalar variable; we only deal with horizontal (or vertical) eye movements to avoid unnecessarily complicated discussion. Moreover, we will not discuss dynamic characteristics at all, for our interest is only in the fundamental properties concerning the voluntariness and involuntariness of SP described in the last section. Besides, we assume that the transfer function of the eyeball-muscle system (eye plant in the figure; P) equals one; if P is a proportional element, it is always possible to let $P=1$ by slight modification of G .

Let us have the following fundamental assumption for the model.

“The gain of the forward path of the SP system, G (or $G \cdot P$) is voluntarily controllable.” We think that degree of “will” or “effort” of tracking the object can be represented by the magnitude of G . According this assumption we can uniformly interpret the first three experimental results described in the last section as follows.

Since the gain of the whole feedback system is $G/(1+G)$, the velocity of the eye, V_e , is $V_t G/(1+G)$. If G is large enough, the speed of the eye becomes almost the same as that

of the target. Therefore, if there is a moving object one can track it by SP with the same velocity as that of the target by adding to the magnitude of G , but if there is no moving target one cannot produce SP at all, for $V_e=0$ as long as $V_t=0$.

We can also explain why one can move the eye at an arbitrary speed below the object speed but not at higher speed; $V_e (=V_t G/(1+G))$ can be altered from zero to V_t by changing the magnitude of G , but it never exceeds V_t because $G/(1+G)$ is always less than one however large G may be.

Thus the hypothesis of the gain control successfully explains some of the fundamental characteristics of SP, (1), (2) and (3), at least for the case of tracking a single object without background objects.

Let us expand this idea of gain control to the case of general stimuli which includes more than one object with different directions or speeds.

The first problem that arises when considering general stimuli is how to express visual stimuli. In the model of Fig. 2a, the speed of the object is expressed by the input, but other factors of the object such as size, shape, brightness, etc. are not incorporated in the input at all. Such factors, however, must cause some effects onto the nerve nets on the retinas (or higher-level visual systems). In the model they will be expressed as difference of the magnitude of G .

If applying such an expression to general stimuli, it may lead to an inconvenience. Let an object is moving against the background at a constant speed. Then the stimulus to the retina might differ according to the relative location of the target object to background objects, even for the same object speed. As the object incidentally passes in a part of the background with the same brightness and color, for example, the image of the object on the retina will vanish momentarily and its retinal slip will disappear. It is difficult to express such a situation by our model, which uses the object speed as the input.

In spite of the above inconvenience we shall use the model that describes the object speed as input, because our purpose is to discuss the fundamental characteristics concerning the voluntariness of SP.

If there are n stimuli with different speeds, we think that the input of the SP system is a vector that has n components. For example when an object is moving against the background at a constant speed, we consider a constant vector $V_t = [0, V_t]$ as input of the system; 0 indicates the speed of the background and V_t that of the target. In the case of an ambivalent stimulus, let $V_t = [-V_t, V_t]$. For the dynamic noise we consider a vector that has innumerable components with a variety of values.

Using this expression of inputs, the SP system for more than one stimulus with different speeds can be illustrated as Fig. 2b. The retinal slip, or relative velocities of the objects to the eye, is also described by a vector $V_r = V_t - V_e \cdot \mathbf{I}$ ($\mathbf{I} = [1, \dots, 1]$).

Now the problem is the process through which vector V_r is transformed to scalar input W to the eyeball-muscle system.

One idea is that all the components of V_r are summed as in Fig. 2c. If it is the case, however, the sum of the input for symmetric stimuli such as in Fig. 1 will be zero, not producing any SP. Thus the author would like to propose the model of Fig. 2d.

The retinal slips are detected by two kind of direction-selective neurons that detect the retinal slip either to the right or to the left. By them the vector V_r is divided to the retinal slips to the left and to the right, V_{r1} and V_{r2} . The components of V_{r1} or V_{r2} are summed individually, giving scalar variables, Q_1 and Q_2 . They are summed with some weights, G_1 and G_2 , and are transferred to the eyeball-muscle system (eye plant in the figure). Then the following hypothesis is assumed.

“The magnitudes of G_1 and G_2 are voluntarily and independently alterable.”

This hypothesis enables voluntary selection of the object. Let us assume, according to

Collewijn (1972), that the output of direction-selective cells for elements of V_{r1} and V_{r2} has a limiter characteristic as is shown in Fig. 2d. The sensitivity of the limiter is high for small retinal slip, and decreases drastically as the slip becomes larger. It may greatly differ according to the shape, brightness, or other factors of the stimuli, for the same retinal slip. Although the limiter characteristic is not necessarily essential in the following discussion, it plays a role of enhancing the selectivity of the target object.

Let us consider an moving object with a constant speed V_t . The corresponding retinal slip, V_{r1} and V_{r2} , will be expressed as a function of V_e as in Fig. 3a and b. Since they have an effect of moving the eye to opposite directions to each other, we shall illustrate them as in Fig. 3c from now on. For a single object, V_{r1} and V_{r2} equal directly to Q_1 and Q_2 . If there are two stimuli with different speeds (V_t and V_t' , $V_t' > V_t$), Q_1 and Q_2 become as shown in Fig. 3d. The input to the eye plant is

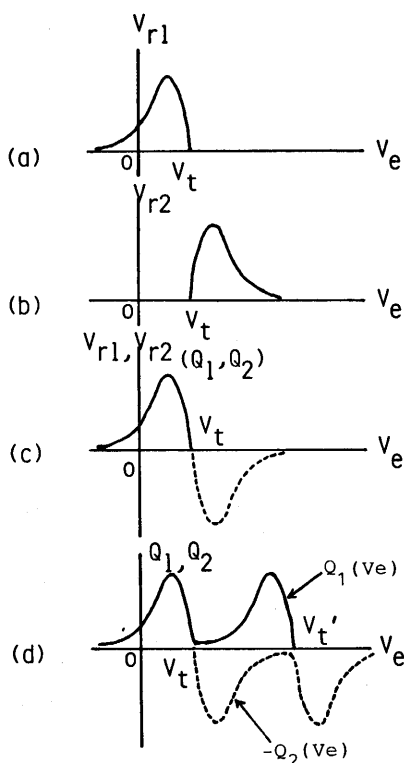


Fig. 3 Outputs of direction-selective units and their sums as functions of eye velocity.

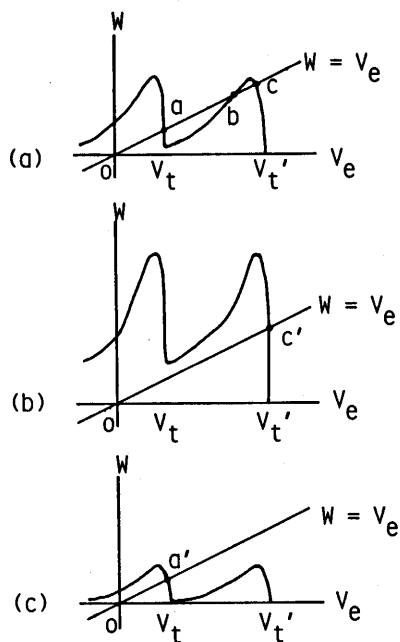


Fig. 4 Voluntary selection of a visual target from two objects with different speeds.

$$W(V_e) = G_1 \cdot Q_1(V_e) - G_2 \cdot Q_2(V_e).$$

When $W(V_e)$ is larger than the present eyeball speed (to the right), V_e , the eye speed will increase, and when W is smaller the eye speed will decrease.

The tracking speed in the steady state is given as the intersection point of the curve of $W(V_e)$ and the straight line

$$W(V_e) = V_e.$$

If $G_2 = 0$ and G_1 is large enough, the intersection points are a, b and c in Fig. 4a. a and c are stable equilibrium points and b is an unstable equilibrium point.

The change of the target object can be explained as follows. Let the eye be tracking the object moving at speed V_t . This state corresponds to point a. As G_1 becomes larger, $W(V_e)$ turns like Fig. 4b and the stable equilibrium point will vanish. In this state the eyeball speed increases approaching c' . Once entering this state the eye keeps moving at approximately the same speed as V_t' even if G is brought back to the original value, for point c is also a stable equilibrium point. Transition from V_t' to V_t goes the opposite way. Lessen G_1 (and bring it back), then the eyeball speed will become V_t (Fig. 4c). The essence in these discussions is that G_1 is changed with keeping $G_2=0$.

The idea successfully explains the fundamental characteristics (1) to (6) of SP stated in the previous section:

A. The case of tracking a single object moving in the darkroom.

The shape of $W(V_e)$ will be altered with variable G_1 as in Fig. 5, where the term $-G_2 \cdot Q_2(V_e)$ is omitted. As G_1 grows large, V_e becomes nearly equal to V_t . A smaller G_1 results in a smaller V_e . Also this figure suggests that V_e never exceeds V_t however large G_1 may be.

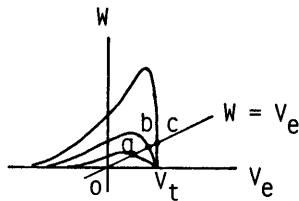


Fig. 5 Voluntary control of speed when tracking a single object.

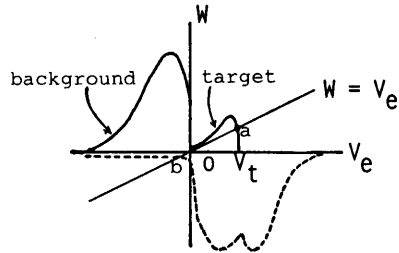


Fig. 6 Tracking of a moving object in the visible background.

B. The case where the object is moving against the background.

$G_1 \cdot Q_1(V_e)$ and $G_2 \cdot Q_2(V_e)$ will be as in Fig. 6. The difference between effects on the retinal excitation by the target and that by the background is expressed as the difference of the heights of peaks in this figure. When $G_2=0$ and G_1 is large enough, the eye is tracking at a speed much the same as V_t . When G_1 is small or G_2 is relatively large compared with G_1 , only the origin is the steady state, i.e., the eye is fixed to the background.

C. The case of ambivalent optokinetic stimuli

$G_1 \cdot Q_1(V_e)$ and $-G_2 \cdot Q_2(V_e)$ in this case will be as in Fig. 7. When G_1 is large enough

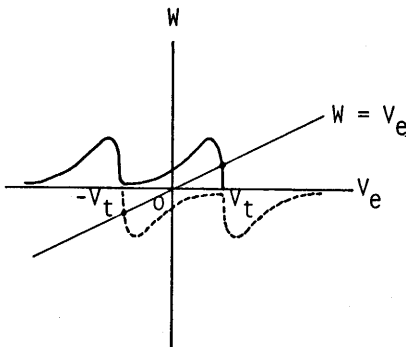


Fig. 7 Smooth pursuit movements elicited by an ambivalent stimulus.

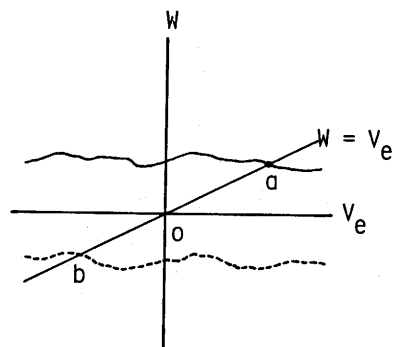


Fig. 8 Smooth pursuit movements elicited by visual dynamic noise.

and $G_2 = 0$ the eyeball moves to the right at a speed much the same as V_t and moves to the left when G_2 is large enough and $G_1 = 0$.

D. The case of dynamic visual noise

Visual noise of a TV screen or the like can be regarded as numberless stimuli with a variety of speeds. In this case $G_1 \cdot Q_1(V_e)$ and $-G_2 \cdot Q_2(V_e)$ will have a relatively flat shape as in Fig. 8. In such a case, changing G_1 and G_2 permits free SP of arbitrary directions and speeds.

3. DISCUSSION

The model described in the last section has successfully explained the characteristics of the voluntary control of SP. A couple of supplements are given in the following.

Since we consider the object speed as the input of the model, the following two stimuli give the same input to the model as long as their speeds are the same: a small point moving in a darkroom and a large pattern that covers the whole visual field. However, the latter stimulus will have a larger effect on stimulating the SP system. The difference between them is expressed in the model as the difference of the sensitivity of the limiter element. Then the following situation can occur. When the whole visual field is moving, it becomes difficult to suppress SP by lessening G_1 or G_2 , for the total gain cannot be small because of the large gain of the limiter element. This is well known from the experiment on optokinetic nystagmus (Young, 1971).

Robinson (1976) pointed out the role of efferent copy signal in the SP system. In terms of control theory it can be interpreted as a positive feedback added to the forward path of the model as is illustrated in Fig. 9. This minor loop becomes an integrator as the loop gain $G \cdot G'$ ($G_1 \cdot G_1'$ or $G_2 \cdot G_2'$) becomes close to one, and its time constant is determined by delays existing in the loop. In this state the eyeball speed V_e completely equals to the object speed V_t (under steady state). It is described in the last section that a very large gain is needed so that the eyeball moves at the same speed as the object, but

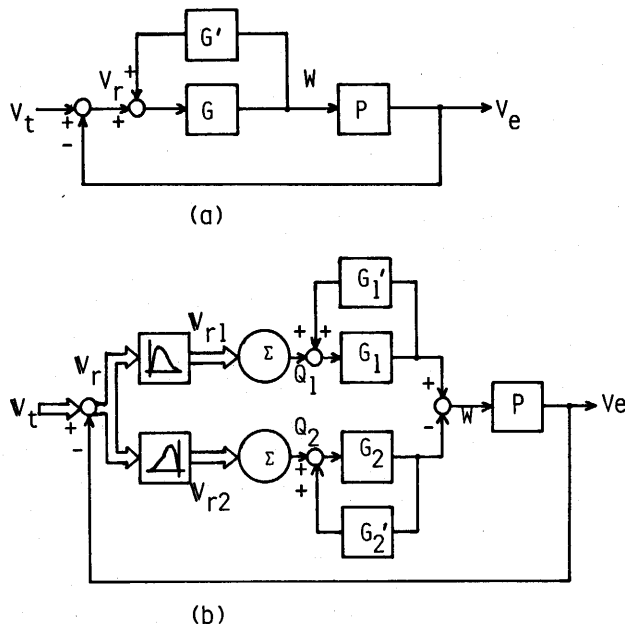


Fig. 9 Models of the smooth pursuit system including efference copy.

we can say in other words that an integral characteristic is necessary to move the eye with the same speed as the target; static gain of an integrator is infinite.

Our model is quite quantitative and speculative. A somewhat more quantitative model is shown in the appendix. Since the physiological location of the SP system is not identified yet, collation in a microscopic sense with the actual human organs is impossible, but macroscopic explanation is successful.

ACKNOWLEDGMENTS:

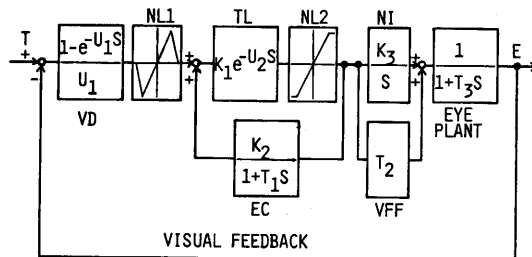
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Appendix A Quantitative Model of the SP System

Fig. A shows a quantitative model of SP system based on the idea of gain control. The



U1 = .33sec T1 = .05sec K1 = .1
 U2 = .01sec T2 = 1.2sec K3 = 1.2
 T3 = .1sec

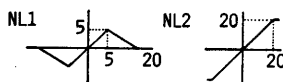


Fig. A A quantitative model of the SO system.

A Model of Voluntary Control of Smooth Pursuit Eye Movements

sensitivity of the efferent copy signal path, K_2 , is assumed to be voluntarily controllable. Because the units producing SP toward the right and to the left are not separated, this is the model which explains the phenomena (1) to (3) in the first section. Details of the model can be seen in Miyazaki (1981).

Responses of the model to a ramp input are shown in Fig. Ba with variable K_2 . If gain K_2 is large the eye moves almost as fast as the object and at a fractional speed of it as K_2 becomes smaller. Fig. Bb shows actual eye movements when a couple of subjects were instructed to move the eye once, a quarter, a half, three quarters, and twice as fast as the object speed (Steinmall et al., 1969), suggesting the voluntary change of speed.

It is well known that the frequency response of SP has the characteristic that the phase delay is much smaller than expected from the gain diagram by control theory when the target is periodic (sinusoidal movement, for example). Although this phenomenon has been conventionally explained as the predictive function of the SP system, the author suggested that the explanation by prediction is false (Matsuoka, 1982). Fig. C (—○—) indicates the frequency response of the model under the hypothesis that K_2 varies according to the frequency of the sine wave. It coincides with that of the experimental result (the shaded portion of the figure).

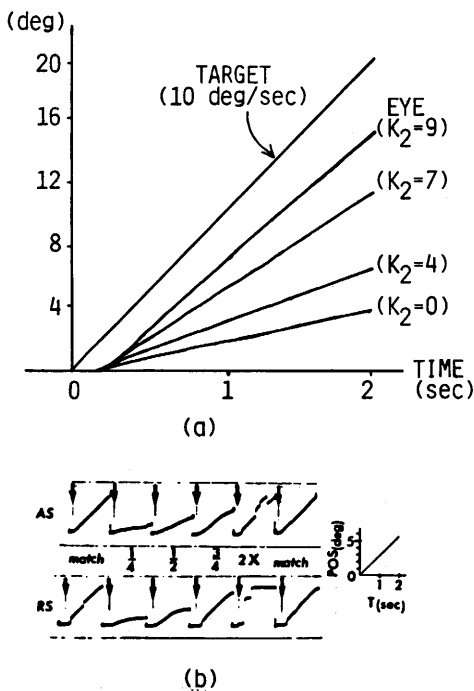


Fig. B Ramp responses. (a) the model; (b) experimental records.

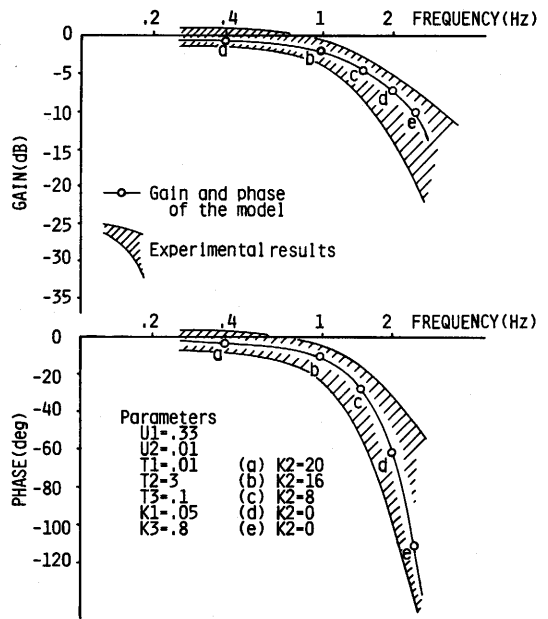


Fig. C Frequency response. (—○—) model; (///) experimental result.