



Human smooth pursuit direction discrimination

Scott N.J. Watamaniuk^{a,*}, Stephen J. Heinen^b

^a *Wright State University, Psychology Department, Dayton, OH 45435, USA*

^b *The Smith-Kettlewell Eye Research Institute, 2232 Webster Street, San Francisco, CA 94115, USA*

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Abstract

The smooth pursuit system is usually studied using single moving objects as stimuli. However, the visual motion system can respond to stimuli that must be integrated spatially and temporally (Williams DG, Sekuler R. *Vision Res* 1984;24:55–62; Watamaniuk SNJ, Sekuler R, Williams DW. *Vision Res* 1989;29:47–59). For example, when each dot of a random-dot cinematogram (RDC) is assigned a new direction of motion each frame from a narrow distribution of directions, the whole field of dots appears to move in the average direction (Williams and Sekuler, 1984). We measured smooth pursuit eye movements generated in response to small (10 deg diameter) RDCs composed of 250 dynamic random dots. Smooth eye movements were assessed by analyzing only the first 130 ms of eye movements after pursuit initiation (open-loop period). Comparing smooth eye movements to RDCs and single spot targets, we find that both targets generate similar responses confirming that the signal supplied to the smooth pursuit system can result from a spatial integration of motion information. In addition, the change in directional precision of smooth eye movements to RDCs with different amounts of directional noise was similar to that found for psychophysical direction discrimination. These results imply that the motion processing system responsible for psychophysical performance may also provide input to the oculomotor system. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Most previous studies of smooth pursuit eye movements have measured pursuit to horizontally-moving single spot targets that contain both motion and position information. While motion is thought to be the dominant signal driving smooth pursuit (Rashbass, 1961), position information may influence pursuit responses (Seagraves & Goldberg, 1992). Another feature of traditional smooth pursuit research is that the measure of interest is gain, i.e. the speed of the eye divided by the speed of the target. Thus the typical study has been designed to determine how well the oculomotor system matches the speed of the moving target.

The present study was designed to determine not how well the speed of the eye matches the target but how well the direction of the eye matches the target. Since most previous studies have used only horizontally moving stimuli, few have been concerned with the directional precision of the smooth pursuit response. In fact,

any subject who consistently or even occasionally made pursuit movements in the direction opposite the target would likely have been excused from the experiment. A couple of studies have measured pursuit responses to obliquely moving targets. Kosnik, Fikre and Sekuler (1985) measured tracking eye movements to stimulus directions of upwards (90 deg) and three degrees to the left (93 deg) and right (87 deg) of upwards. They found that the pursuit movements were in the correct general direction although there was some error, usually within 2–8 deg. The purpose of their study however, was not to determine the directional precision of smooth pursuit movements but to show that when making psychophysical direction discrimination judgments that eye movements were not contributing systematically to the decision. Deno and Keller (1989) also measured pursuit movements to obliquely moving targets. They too found that eye movements were generally in the approximate direction of the target, but that was the extent of their analysis.

Measuring fine-grained direction discrimination psychophysically has developed over the last several years. Initially, researchers were concerned with the maximum

* Corresponding author. Fax: +1 937 7753347; e-mail: swatamaniuk@wright.edu.

displacements that allowed observers to discriminate leftward from rightward motion (Braddick, 1974). These experiments were designed to reveal characteristics of the putative underlying opponent direction mechanisms. Others were interested in evaluating the capacity and limits of human's ability to discriminate small changes in directions. For this task, it was important to devise a stimulus that did not permit judgments based upon information other than the direction of motion. If the stimulus was a single dot, the direction task could be done by either using directionally-tuned motion detectors or static orientation-tuned detectors. In fact, Westheimer and Wehrhahn (1994) found that for single spots, direction discrimination thresholds were equivalent to orientation discrimination thresholds for lines equal in length to the motion path. To obscure position cues, researchers began using small fields of moving dots, referred to as random-dot cinematograms (RDCs) (Ball & Sekuler, 1979; Sekuler, Ball, Tynan & Machamer, 1982). Many researchers have used RDCs in psychophysical tasks to evaluate the motion processing capacities of the human visual system (Williams & Sekuler, 1984; Snowden & Braddick, 1989; Watamaniuk, Sekuler & Williams, 1989; Cleary & Braddick, 1990; Watamaniuk & Duchon, 1992; Watamaniuk & Sekuler, 1992; Smith, Snowden & Milne, 1994; Hiris & Blake, 1996). With regards to direction discrimination, Watamaniuk et al. (1989) found that for RDCs in which all dots moved in the same direction, observers could reliably distinguish directions that differed by about 1 deg. Moreover, since each dot in the cinematogram could be controlled independently, it was possible to add directional noise to the stimulus to assess how well observers carried out the task with differing amounts of noise. Noise was added by assigning each dot in the stimulus a new direction of motion from a distribution of directions centered about some mean direction. Watamaniuk and colleagues have found that as the amount of directional noise increases, discrimination performance stays constant until the distribution from which the directions are chosen reaches a range of about 40–60 deg, after which performance declines (Watamaniuk et al., 1989; Watamaniuk, 1993).

RDCs have been used not only for psychophysical experiments of motion perception but also to study the characteristics of neurons in MT (Maunsell & Van Essen, 1983a,b; Albright, 1984; Mikami, Newsome & Wurtz, 1986a,b; Newsome, Britten & Movshon, 1989; Duffy & Wurtz, 1991a,b), an area dedicated to processing motion, and MST (Albright, 1984; Newsome et al., 1989; Salzman, Britten & Newsome, 1990; Duffy & Wurtz, 1991a,b; Britten, Shadlen, Newsome & Movshon, 1992; Salzman, Murasugi, Britten & Newsome, 1992; Britten, Shadlen, Newsome & Movshon, 1993; Murasugi, Salzman & Newsome, 1993; Salzman & Newsome, 1994; Zohary, Shadlen & Newsome, 1994), an anatomically subsequent area thought to convert the motion signals of MT into

commands to drive smooth pursuit (Komatsu & Wurtz, 1988a,b; Newsome, Wurtz & Komatsu, 1988). In addition, RDCs have even been used in the past to drive smooth pursuit (Tychsen & Lisberger, 1986). Most recently, Heinen and Watamaniuk (1998), using RDCs, have shown that the smooth pursuit system integrates motion information spatially to obtain a better motion signal and hence produce a stronger and more precise smooth pursuit response. The integration of motion information over space and time has been a fundamental finding in the psychophysical literature. It is this correspondence between the psychophysical and smooth pursuit performance that has prompted the present experiments. In this study, we systematically examine the human smooth pursuit system's ability to track different directions of motion with added directional noise and quantitatively compare pursuit performance to psychophysical performance for the same stimuli.

Previously, researchers have compared neuronal responses with both psychophysical (Mikami et al., 1986b; Newsome, Mikami & Wurtz, 1986; Newsome et al., 1989) and oculomotor responses (Newsome, Wurtz, Dürsteler & Mikami, 1985; Page, King, Merigan & Maunsell, 1994), but only one study has attempted to compare pursuit with psychophysical performance (Kowler & McKee, 1987). The lack of comparative behavioral studies is likely due to the methodological difficulties in obtaining equivalent measures. Oculomotor researchers usually measure the accuracy (gain) of smooth eye movements to target motion. Accuracy refers to how closely the measured response estimates the actual stimulus value (Bevington, 1969). Visual psychophysicists usually measure discrimination thresholds which depend upon the precision (variability) of the response to motion. Precision describes the reproducibility of a response from trial to trial (Bevington, 1969) and indicates how well a system can discriminate between two different stimuli (e.g. speeds). Although a few pursuit studies have reported the variability of pursuit gain, these data have never been critically analyzed or incorporated into theories of smooth eye movement control (Robinson, 1965; Carl & Gellman, 1987; Kowler & McKee, 1987).

By using an 'equivalent noise' paradigm (Barlow, 1957; Mumford & Schelbe, 1968; Pelli, 1990) to determine the noise within two systems, one may be able to determine if both system responses are limited by similar processes. In this paradigm, responses are measured for stimuli that have different amounts of added directional noise and plotted as a function of that noise. Equivalent noise curves typically have a flat portion where performance is not dependent upon stimulus noise, followed by a sloped portion where it is dependent upon stimulus noise. The 'knee-point' of the curve indicates the amount of stimulus noise that is equivalent to the internal noise in the system (Green & Swets, 1966; Geisler, 1989; Watamaniuk, 1993). If two systems are limited by a common stage of processing and have the same internal noise, their

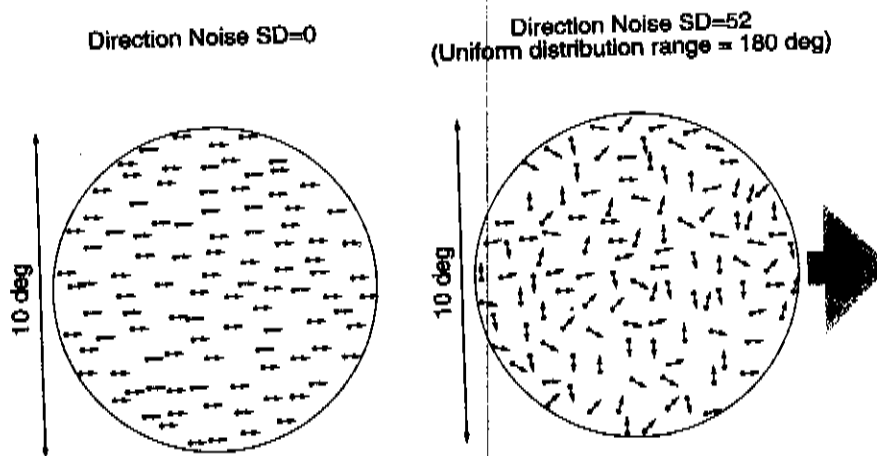


Fig. 1. A schematic representation of two RDC stimuli which have the same mean direction (0 deg-rightward) but different amounts of added directional noise. The RDC on the left has directional noise with an SD = 0 deg (no noise—all dots move in the same direction) while that on the right has directional noise with an SD = 52 deg (directions chosen from a uniform distribution spanning 180 deg).

equivalent noise curves should overlap.

Here, we show that the characteristics of human smooth eye movements to small RDCs are similar to those generated to single spot targets. We also present an analysis of how well the smooth pursuit response can distinguish different directions of motion, using RDCs. Throughout these studies, we have limited our analysis to the open-loop period which is defined as the first 130 ms after pursuit onset, consistent with previous research (Robinson, 1965; Michael & Melvill-Jones, 1966; Robinson, Gordon & Gordon, 1986). We chose this point of analysis because eye movements during this period are uncontaminated by oculomotor feedback (Lisberger & Westbrook, 1985). Finally, we compare smooth eye movement performance with psychophysical performance for RDCs with varying amounts of directional noise, to determine whether a common motion processing substrate might limit the precision of both responses.

2. Smooth eye movements to RDCs

Since RDCs containing directional noise have never been used as oculomotor stimuli, the first set of experiments was carried out to establish the characteristic oculomotor responses to such stimuli.

3. Methods

3.1. Observers

The two authors served as observers for all experiments. While both authors are experienced observers, SH has participated in substantially more eye movement experiments and SW has participated in more psychophysical experiments. Observers wore their corrective

lenses during psychophysical experiments. During eye movement recording, optics placed between the observers' eyes and the display monitor corrected for each observer's myopic vision.

3.2. Stimuli

Stimuli were RDCs presented on a Tektronix 604 monitor (P4 phosphor) at a rate of 50 Hz through a 10-deg diameter aperture (Fig. 1). Dots were 0.05 deg in diameter, had a density of 2.0 dots/deg², and moved at a speed of 8 deg/s. Dot luminance was 5.4 cd/m² with a background luminance of 0.05 cd/m² and the viewing distance was 57 cm. In each trial, the dots were randomly positioned for the first frame and then were assigned directions of motion randomly from a uniform distribution of directions. Stimulus directional noise was varied by changing the standard deviation of the direction distribution (Watamaniuk, 1993). As described in the introduction, the percept produced by an RDC is that of the whole field of dots moving in the mean direction. The perceived speed of the RDC movement depends upon both the speed of individual dot movements and the range of directions in a stimulus. Since the perceived direction of the RDC is in the mean direction of its underlying direction distribution, the dots, although moving at the same speed, do not contribute an equal speed signal to the resulting percept. One can estimate the speed of an RDC's motion by determining for each dot in the RDC the magnitude of its component vector in the mean direction, and then take the average magnitude of this vector across all dots (pilot data from our lab suggests that the perceived speed of RDCs like those used here is consistent with this computation). Thus although the dots in every display moved at 8 deg/s, the perceived movement of the RDC slowed down as the amount of directional noise increased. Direction of the RDC varied from trial to trial. Although pursuit trials

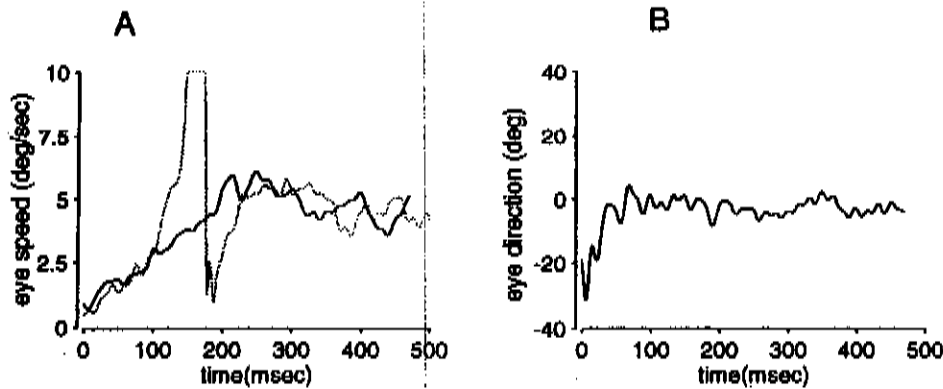


Fig. 2. Panel A. Eye speed as a function of time for individual trials for an observer (SW) tracking a single spot target moving to the right (dashed line) and an RDC with added directional noise ($SD = 52$ deg) with a mean direction to the right (solid line). Eye traces have not been desaccaded but have been clipped at 10 deg/s. Panel B. Eye direction as a function of time for an individual trial for an observer (SW) tracking an RDC with added directional noise ($SD = 52$ deg) with a mean direction to the right (0 deg). All eye traces have been aligned on pursuit initiation.

had a duration of 800 ms, all analyses were carried out over a 20 ms bin centered at 130 ms after pursuit initiation.

3.3. Measuring and evaluating eye movements

Subjects viewed the display with their right eye while the left eye was patched. Horizontal and vertical eye position were measured with a Generation V dual-Purkinje-image eyetracker.¹ Subject's eye position was calibrated to tracker output before each session by having the subject fixate several times at each of four 5-deg-ecentric cardinal positions and at the center while offsets and gains were adjusted. The eye position signal was sampled at 500 Hz by a PC.

Eye velocity signals were obtained by analog differentiation of eye position signals and filtered to remove 60 Hz noise (2 pole Butterworth filter, cutoff = 50 Hz). Eye records were desaccaded in the usual way using an eye acceleration threshold (Winterson & Steinman, 1978; Keller & Kahn, 1986; Wyatt & Pola, 1987; Seagraves & Goldberg, 1992; Krauzlis & Lisberger, 1994). The records were then filtered using a single-pole Butterworth filter (cutoff = 25 Hz) to remove any corners caused by the desaccading algorithm.² Records contaminated by eye blinks were not included in the analyses.

Latency of the eye movement was determined from the eye velocity traces by visual inspection. Since anticipatory smooth eye movements are difficult to eliminate, even with the most rigorous randomization of trial

parameters (Kowler & Steinman, 1981; Kowler, 1989), records where evidence of anticipation was present were rejected. For this study, we adopted a particularly stringent criteria for rejection of trials. In the past we have found, as have others, that randomization of pursuit between opposite directions (e.g. left and right) is a powerful way to minimize anticipation and this is our usual technique. However, in this study we had to use a small range of directions in order to compute direction discrimination thresholds and the potential for anticipation was high. Thus we rigorously examined each eye trace and employed a strict criterion for rejection; if eye speed was 2 deg/s or higher before 100 ms after target motion onset, the trial was rejected. Eye velocity and acceleration were assessed for successive time intervals starting from pursuit onset until the end of the trial. Each point stored was the average of data collected over a 20 ms time interval. There was no overlap between bins for successive points. Horizontal and vertical eye velocity and acceleration were kept separate to allow pursuit direction analysis. The direction of the eye velocity vector was computed by transforming individual horizontal and vertical velocity components to polar coordinates.

4. Results and discussion

Fig. 2A shows a typical eye speed record to an RDC with directional noise (uniform distribution spanning 180 deg thus having an $SD = 52$ deg and a computed speed in the mean direction of 5.1 deg/s) overlaid on one to a single spot target moving at the same speed (5.1 deg/s) and direction (0 deg-rightward). Neither trace has been desaccaded. Notice that the initial acceleration (slope), time to reach steady state, and steady state behavior are similar. The most noticeable difference is the absence of a catch-up saccade in the RDC trace, which was a consistent feature even in naive observers. The lack of such saccades is due to the fact that RDCs do not contain

¹ In tests of our instrument with an artificial eye, the overall noise of the system was less than 1 min arc.

² Although these filters are non-causal, it should be noted that any smoothing process causes distortion of a record, and hence can affect the determination of a time-based event (e.g. latency). Therefore, filter parameters were chosen carefully to keep such distortion at a minimum, while still allowing a reasonable assessment of eye velocity and acceleration.

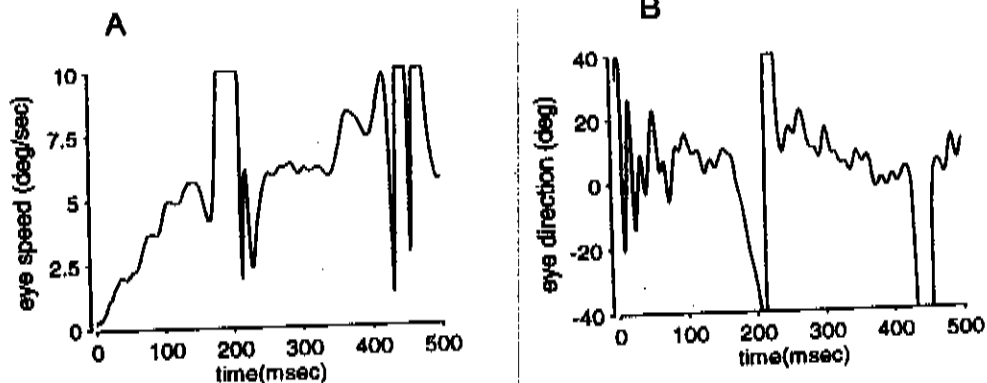


Fig. 3. Panel A. Eye speed as a function of time for an individual trial for an observer (SW) tracking a single spot target with added directional noise ($SD = 52$ deg) with a mean direction to the right. Eye trace has not been desaccaded but has been clipped at 10 deg/s. Panel B. Eye direction for an individual trial for an observer (SW) tracking a single spot target with added directional noise ($SD = 52$ deg) with a mean direction to the right (0 deg). Eye trace has not been desaccaded and has been clipped at ± 40 deg. All eye traces have been aligned on pursuit initiation.

consistent position cues, the signal for saccade generation (Rashbass, 1961). Fig. 2B shows the direction of the eye movement to the RDC over the course of the stimulus presentation. Within about 100 ms after pursuit initiation, the direction of the eye closely matched that of the direction of the RDC.

Since RDCs contain many moving dots, one may expect that the observer may simply follow which ever dot happens to be closest to the center of the fovea at the start of the trial. Fig. 3 shows both eye speed and eye direction to a single dot with added directional noise ($SD = 52$ deg). This is the same amount of directional noise that was present in the RDC used for generating the data in Fig. 2. Notice, however, that these traces do not resemble those in Fig. 2. When tracking the single, directionally-noisy moving dot, eye speed shows erratic behavior and is interrupted by several saccades (Fig. 3A). Eye direction also shows erratic behavior because the direction of the spot is selected randomly each frame from a wide direction distribution and the observer is doing his best to track it (Fig. 3B). Obviously, the smooth pursuit responses in Fig. 2, which were generated to an RDC with the same amount of directional noise, are not due to the observer following a single dot. Rather, the motion processing system integrates the motion information over the display to obtain a coherent motion signal (Williams & Sekuler, 1984; Watamaniuk, Sekuler & Williams, 1989). It is to this motion signal that the smooth eye movement system responds (also see Heinen & Watamaniuk, 1998).

Further support for this claim is obtained by looking at the angular speed of the eye during the initiation phase. Fig. 4 shows average eye speed during pursuit initiation to RDCs with different amounts of directional noise (SD s of 0, 26, and 52 deg). Since the perceived speed of the RDC slows as the amount of directional noise increases (see Section 3), one would expect the speed of pursuit to also decrease as the amount of directional noise increases. Notice that by the end of the open-loop

period, 130–150 ms after pursuit initiation, average eye speed has reached three distinctly different speeds ranked correctly according to the calculated mean speed of the RDCs, which are indicated by the labeled horizontal dotted lines.

As a final comparison, we looked at smooth eye movements to RDCs without directional noise ($SD = 0$) and single spot targets moving at different speeds. Fig. 5A and B show average eye speed traces to single spots and small RDCs moving at five different speeds during the first 150 ms of pursuit. The two plots show similar performance. The notable differences are that the RDCs generated eye speeds that were, (1) more widely separated

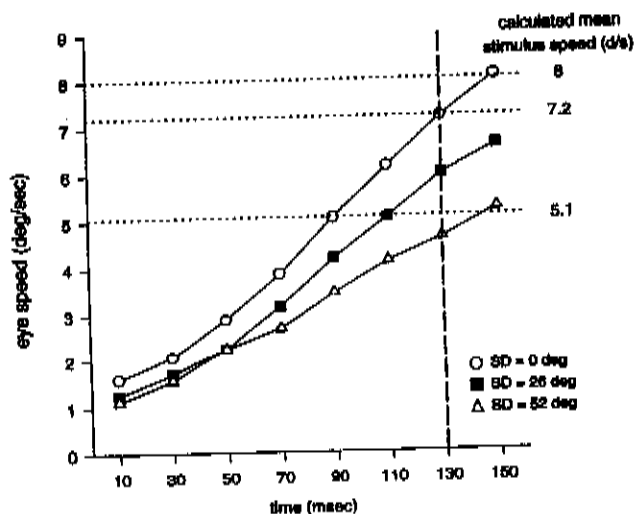


Fig. 4. Eye speed as a function of time for RDCs with differing amounts of added directional noise ($SD = 0, 26$ and 52 deg) for a single observer (SW). Points represent average eye speed computed over 20 ms bins centered on the plotted time coordinates. Although the individual dots in the RDC all were displaced the same distance in their respective directions from frame-to-frame, the average vector in the mean direction decreases as the amount of directional noise increases. The computed magnitude of the vector in the mean direction is indicated beside each curve. All eye traces have been aligned on pursuit initiation.

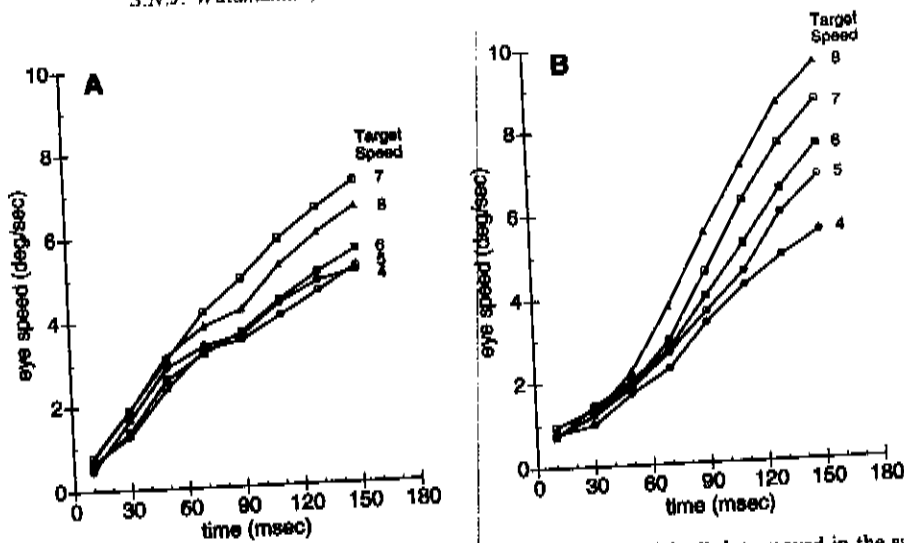


Fig. 5. Eye speed as a function of time for pursuit to single spots (panel A) and RDCs in which all dots moved in the same direction—no added directional noise (panel B). Data are shown for stimuli moving at five different speeds as indicated beside curves. Points represent average eye speed computed over 20 ms bins centered on the plotted time coordinates. Data are for a single observer (SW).

for the various target speeds, and (2) showed higher gains at the end of the open-loop period (average gain: SW-RDCs = 1.41, single spot = 1.16; SH-RDCs = 1.48, single spot = 1.01). One likely reason why RDCs produced pursuit with higher open-loop gains is that the RDCs have no consistent position cues. When following a single spot, there is typically a catch-up saccade close to midway through the open-loop period that brings the fovea to the target. Thus the pursuit system can accelerate more slowly and thus have a lower gain during the open-loop period because the saccade does part of the work of getting the fovea to the target. Since RDCs have no consistent position cues, a catch-up saccade cannot be generated and the pursuit system alone is responsible for 'catching up' to the target. Therefore, the pursuit system accelerates at a faster rate, resulting in a higher open-loop gain. This higher open-loop gain does not seem to give RDCs any particular advantage for use as pursuit targets. However, the fact that pursuit responses to RDCs showed a better separation for different speeds suggests that responses to RDCs are more precise at least for this range of speeds. However, these differences do not persist into steady state (250–500 ms after pursuit onset) where the gains for both stimulus types become equivalent (average steady-state gain for single spots, 1.03 ± 0.027 ; average steady-state gain for RDCs, 0.97 ± 0.05). These data are consistent with our previous findings regarding the improvement in the pursuit response to stimuli with larger spatial extents (Heinen & Watamaniuk, 1998).

The above data show that smooth eye movements generated to small RDCs are similar to those generated to traditional single spots with some notable exceptions. Two of these differences may make RDCs an attractive choice of stimuli for smooth eye movement researchers interested in the open-loop period; the more precise

pursuit response as evidenced by a better separation for different speeds and the marked absence of catch-up saccades (see Fig. 2A).

5. Direction discrimination

The next series of experiments was designed to measure direction discrimination thresholds, under several levels of directional noise, for the smooth eye movement system and compare them with psychophysically determined thresholds. To this end, we adopted the same strategy as Kowler and McKee (1987) to carry out this comparison. In their study of smooth pursuit speed discrimination, Kowler and McKee adapted signal detection theory (Swets, 1964; Green & Swets, 1966), the fundamental basis of most psychophysical studies, to the oculomotor domain. Signal detection theory posits that when an observer must discriminate between two stimuli within a trial of which only one contains the signal, the internal responses to the 'noise' and 'signal + noise' can be conceptualized as Gaussian-shaped likelihood distributions on an axis of the stimulus dimension of interest (see Fig. 6). The ability of an observer to detect the signal

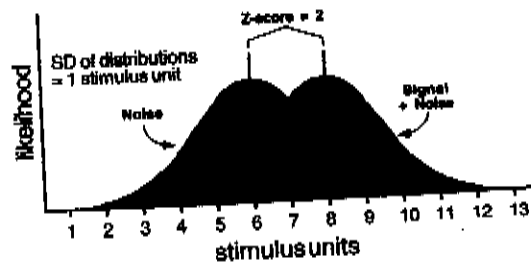


Fig. 6. Theoretical likelihood distributions underlying psychophysical decisions about the presence of a signal illustrating how a z-score is computed.

depends upon both the width (standard deviation) and the distance between the means of the 'noise' and 'signal + noise' distributions. The z -score transformation standardizes detectability measures by expressing them as a function of the standard deviation of the hypothetical likelihood distributions. The z -score is computed using the equation

$$Z = \frac{(M_N - M_{SN})}{SD_{SN}} \quad (1)$$

where Z is the evaluated z -score, M_N is the mean of the 'noise' distribution, M_{SN} is the mean of the 'signal + noise' distribution, and SD_{SN} is the standard deviation of the 'signal + noise' distribution. In discrimination tasks, where the observer must detect the difference between a standard and test stimulus, the standard is considered as 'noise' and the test as 'signal + noise'.

In a typical psychophysical experiment, the likelihood distributions of possible internal responses to the stimuli are not known. However, for the oculomotor system, one can measure eye movements to the same stimuli many times and create distributions of responses to each stimulus. One can then use the statistics of these distributions to compute a z -score (Kowler & McKee, 1987).

6. Methods

6.1. Stimuli

Stimulus characteristics were essentially the same as those described for the previous experiments. However, for this series of experiments, there were eight different levels of directional noise corresponding to uniform distributions spanning ranges of 0, 20, 40, 60, 80, 100, 120 and 160 deg. These levels are referred to by their standard deviations of 0, 5.8, 11.5, 17.3, 23.1, 28.9, 34.6 and 46.2 deg. Again, in each trial, the dots were randomly positioned for the first frame and then assigned directions of motion randomly from a distribution of directions. The direction of the RDC varied from trial to trial. Analyses of the smooth pursuit responses were again carried out over a 20 ms bin centered at 130 ms after pursuit initiation.

6.2. Procedure

In order to illustrate the similarity between the computation of the psychophysical and smooth pursuit direction discrimination thresholds, we first describe the more familiar procedure for determining the psychophysical thresholds, and then that used to determine oculomotor thresholds.

6.2.1. Psychophysical direction discrimination

The method of single stimuli (McKee, 1981) was used

to obtain psychophysical direction discrimination data. Five different directions of motion (6, 3, 0, -3, -6 deg) centered around rightward (0 deg) were used. We will refer to the mean direction of the set (0 deg) as the standard stimulus and the other four directions as test stimuli. The observer saw a single stimulus each trial and judged whether the direction of that stimulus was clockwise or counterclockwise from the standard (the mean direction of the set). To equate the amount of stimulus information being used for pursuit during the open-loop period (Robinson, 1965; Robinson et al., 1986) with the psychophysical response, psychophysical trials had a duration of 140 ms. Data were summarized as the proportion of trials in which the observer judged a given stimulus to be more clockwise than the standard. The data were then plotted as a function of target direction and fitted with a cumulative normal by means of probit analysis (Finney, 1964). Discrimination thresholds along with standard errors of the threshold were estimated from the fitted function. The direction discrimination threshold was defined as the difference in direction that produced a change in the response level from 50% 'greater' to 75% 'greater'. This difference threshold is equal to a z -score of 0.675 (McKee, Silverman & Nakayama, 1986).

6.2.2. Oculomotor direction discrimination

Smooth pursuit eye movements were recorded for the same random dot stimuli as used for the psychophysical tasks. We computed a z -score for each of the test stimuli in the following way. First, we created frequency distributions of eye directions for each of the five different direction stimuli. These distributions of eye directions were determined by measuring the direction of the eye, over a 20 ms bin centered 130 ms after initiation of pursuit, for many trials. Each eye movement recording provided one measure of eye direction. We then applied Eq. (1) using the parameters from these distributions of eye directions; M_N was the mean direction of the distribution of eye movements for the center stimulus of a set or standard; M_{SN} was the mean direction of the eye movement distribution for the test stimulus; and SD_{SN} was the standard deviation of the eye movement distribution for the test stimulus. Specifically, we had an average of 20 eye movement recordings for each of the five directions. To calculate z -scores, a histogram of the 20 eye directions was constructed for each stimulus and the mean and standard deviation of the distributions evaluated. Fig. 7 shows typical eye-direction frequency distributions for a test and standard stimulus for an RDC with directional noise. The parameters for the standard and a test stimulus were entered into the z -score formula to obtain a z -score for that test stimulus. A z -score was calculated for each test stimulus. Tables of the standard normal distribution were then used to determine the proportion of the distribution that was located below

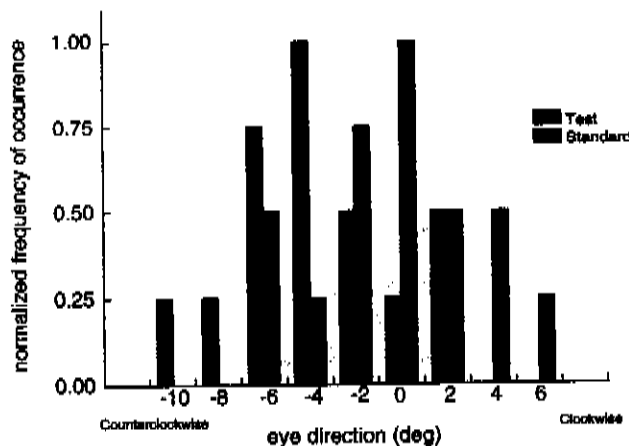


Fig. 7. Typical eye-direction frequency distributions, for observer SW, for a test stimulus with a direction 8 deg clockwise and standard stimulus with a direction of 0 deg for an RDC with directional noise ($SD = 28.9$ deg). Eye directions have been grouped into bins spanning 2 deg with the lower value of the bin being used as the axis labels. Notice that there is some bias in the direction of the eye such that the distribution for the standard has a mean direction of about 3 deg counter-clockwise while that for the test stimulus has a mean of about 1 deg clockwise.

each z -score. These proportions are analogous to the proportion of 'greater' judgments obtained in a psychophysical experiment and can be plotted as a function of target direction, creating an 'oculometric' function (Kowler & McKee, 1987). Then, as with the psychophysical data, the oculomotor data were analyzed with probit analysis (Finney, 1964) to evaluate the difference threshold.

7. Results and discussion

Fig. 8 shows psychophysical direction discrimination thresholds for single spot targets moving at 8 deg/s and

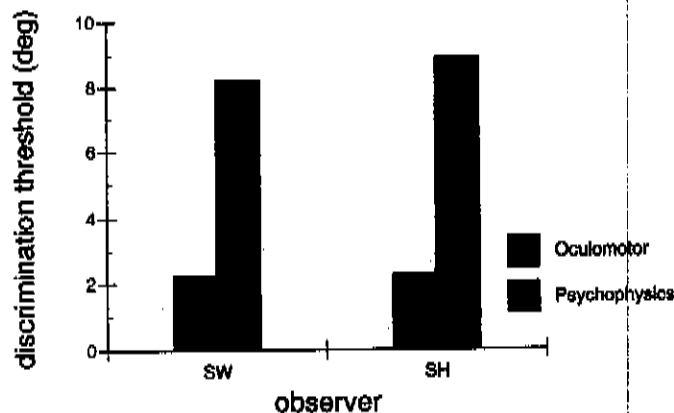


Fig. 8. Psychophysical and oculomotor direction discrimination thresholds plotted for two observers for single spot targets. The standard error of the means for the psychophysical thresholds were 0.27 deg for both observers while that for the oculomotor thresholds were 6.8 deg for SW and 8.3 deg for SH.

oculomotor direction discrimination thresholds for the same condition. Each psychophysical threshold is the result of 240 trials (48 trials per direction per noise condition). Each oculomotor discrimination threshold was computed from an average of 100 eye movement trials (approx. 20 trials per direction per noise condition). This graph makes three important points. First, for both observers the psychophysical thresholds are substantially lower than oculomotor thresholds. In typical psychophysical direction discrimination studies, the movements of the eyes are not monitored but observers are instructed to fixate a constantly-visible stationary spot. An often raised issue is that perhaps psychophysical direction discrimination performance was benefiting from eye movements; the data in Fig. 8 show that smooth pursuit eye movements are not likely to be responsible for psychophysical performance. Second, the thresholds for the two observers are quantitatively similar suggesting that performance on these tasks is likely due to basic motion processing rather than any cognitive strategy. And third, notice that the thresholds for smooth pursuit are on the order of 8-9 deg. One implicit assumption of previous smooth pursuit studies has been that the eye moves in the appropriate direction of the target, thus only measuring the horizontal component for leftward/rightward moving targets is sufficient. These data show that the eye is not following the single moving spot as precisely as has been assumed.

Fig. 9 shows psychophysical and oculomotor direction discrimination thresholds for RDCs with varying amounts of added directional noise. The open data points are discrimination thresholds for the single spot stimuli taken from Fig. 8. Each psychophysical threshold is the result of 150-270 trials (30-54 trials per direction per noise condition). All but one of the oculomotor data points are averages of two thresholds computed from two sets of data taken on each observer approximately 10 months apart. Thus each oculomotor discrimination threshold was computed from an average of 200 eye movement trials (approx. 40 trials per direction per noise condition).

In order to determine if the higher thresholds for the pursuit system were due to there being more internal noise in that system, we fit both the smooth pursuit and psychophysical data with a simple function of the form,

$$\text{Threshold} = k * \sqrt{(N_i^2 + N_s^2)}. \quad (2)$$

In this formulation, direction discrimination threshold is assumed to be determined by noise intrinsic to the motion system which acts like directional noise, N_i , that is added to the directional noise in the stimulus, N_s . There is also a multiplicative factor, k , that shifts the function vertically and will depend on things such as the level of performance defining threshold. This model is fundamentally equivalent to a model proposed by

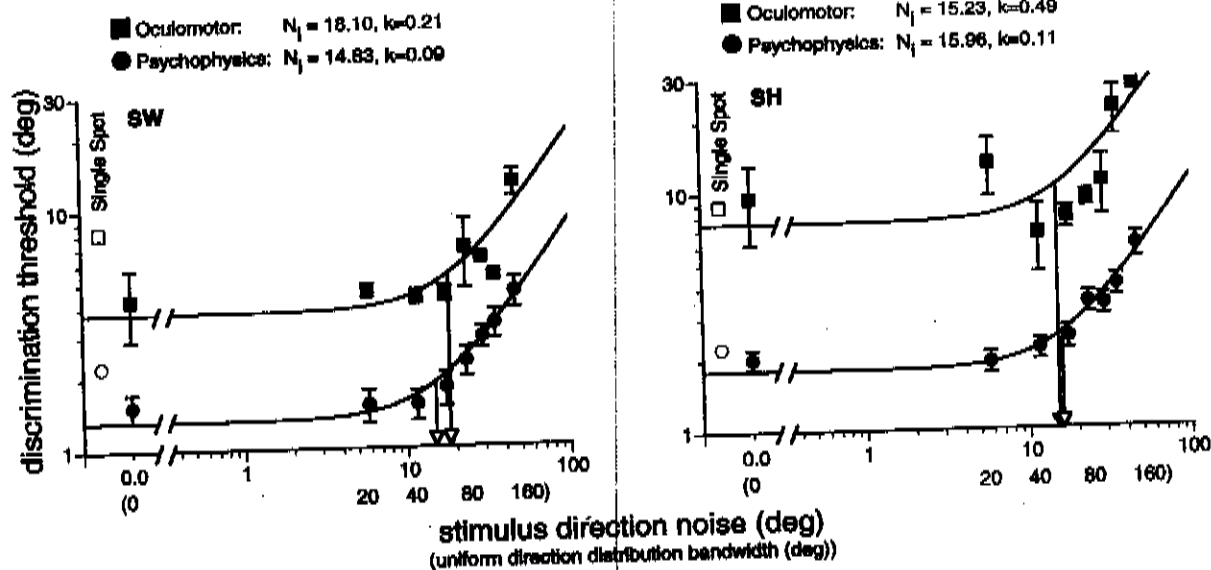


Fig. 9. Psychophysical and oculomotor direction discrimination thresholds plotted as a function of added directional noise for two observers (SW and SH). Solid curves are best fits of a model of the form shown in Eq. (2). Values for the two free parameters of the model are provided above each plot for the psychophysical and oculomotor data. Error bars represent standard errors of the mean. No error bar has been plotted for the oculomotor datum at the highest noise level for subject SH because only one of the two sets of data collected for that condition resulted in the determination of a threshold—the other data set was too variable to allow a threshold to be estimated. Discrimination thresholds for single spot stimuli are also included on the far left of each plot for comparison (open symbols). Arrows extending from the curves indicate the values of N_i .

Watt and Morgan (1984) and later used by Watt and Hess (1987) and Levi and Klein (1990) to estimate equivalent blur in spatial vision. If the smooth pursuit system had an additional independent source of internal noise, we would expect its variance to add to the variance of the internal noise already present in the system. However, if the best fitting functions for the psychophysical and smooth pursuit data differ only in k , then this implies that the smooth pursuit system does not have an additional independent source of internal noise but rather introduces a different gain. The best fitting functions and the parameter values for N_i and k also appear in Fig. 9.

There are several points to note from these graphs. First, the oculomotor thresholds are always higher than psychophysical thresholds. Again, this suggests that observers are not using their eye movements as a basis for making their psychophysical judgments about direction. Second, a single spot produces similar discrimination performance as an RDC in which all dots move in the same direction (stimulus noise = 0). However, the variability in the threshold is higher for the single spot (refer to Fig. 8). Third, both oculomotor and psychophysical thresholds increase as the directional noise increases. Fourth, although the oculomotor thresholds are higher, best fitting functions for the psychophysical and oculomotor data look quite similar. In fact, the parameter N_i changes little and the direction of the change is not systematic across the two observers; oculomotor N_i is higher for observer SW but lower for observer SH. The value of k appears to be the param-

ter that captures the difference between the psychophysical and oculomotor threshold values. This suggests that the oculomotor thresholds are higher because of a difference in gain. The data do not support the idea that the oculomotor system has a higher internal noise level than that present in the visual motion processing system.

8. General discussion

In the first experiment, we showed that observers can use smooth pursuit to follow RDCs well, and that these stimuli are an effective probe of spatial summation in the smooth pursuit system. When the direction of motion of all dots is the same, the eye movements are qualitatively similar to that seen during pursuit of a single spot, except that there is a prominent absence of saccades while tracking the RDCs. When the motion of each individual dot is assigned randomly, from frame-to-frame, from a distribution of directions spanning 180 deg or less, the eyes follow the vector which specifies the mean direction and speed of the field of dots. In the second experiment, we looked at the effect of adding directional noise to the stimulus on both pursuit and perception. We then applied equivalent noise analysis to our data and determined that the pursuit responses and the psychophysical responses showed approximately the same amount of internal noise, no new source of internal noise was added to the motion signal by the pursuit system.

8.1. Using moving random dot fields to assess pursuit

RDC's have been used previously to investigate spatial integration by the visual system (Ball & Sekuler, 1979; Williams & Sekuler, 1984; Watamaniuk et al., 1989; Watamaniuk & Duchon, 1992; Watamaniuk & Sekuler, 1992). Heinen and Watamaniuk (1998) have used RDCs to show that the smooth pursuit system utilized spatial integration as well. Other random-dot displays exist, such as correlated-motion displays in which a proportion of dots are designated signal dots and move in the same direction while the remaining dots are repositioned randomly each frame. The RDCs used in the present study afford greater flexibility and control than correlated-motion displays. Each individual element of an RDC can be manipulated independently from frame-to-frame and provides a much more deterministic assay of motion processing.

Another benefit of RDCs is that they provide a signal that is free from contamination from consistent position cues (Ball & Sekuler, 1979). Although it is true that the individual elements of the array move, since the dots are identical to each other, there is no unique feature that can be linked to a specific spatial location. Data from Experiment 1 provide empirical evidence to support this claim. We showed that tracking a single-dot presented alone from a random dot array with directional noise was very different than tracking the field (Fig. 3). Another piece of evidence is the virtual absence of saccades that are normally used to correct for position error when pursuing a single spot.

Thus RDCs appear to be an especially useful stimulus for studying the pursuit system, since there has been a controversy in the literature concerning the importance of position as a contributor to the pursuit response. The initial observation that position did not contribute to the pursuit response was advanced based on results obtained with the step-ramp paradigm (Rashbass, 1961). When the target was 'stepped' away from the center, and then 'ramped' back across the center and into the periphery, the eyes were found to move initially towards the ramp (a position change plus a motion), and not towards the step (a pure position change). However, more recently it has been shown that certain step sizes will elicit a smooth eye movement towards the pure position change (Pola & Wyatt, 1980). RDCs allow us to study the response of the pursuit system to functionally 'pure' motion.

8.2. Pursuit or OKN?

One issue raised by using RDCs as stimuli for the smooth pursuit system is that these stimuli may also excite the optokinetic system. However, there has never been a clear distinction between smooth pursuit and OKN in the literature. One variable that has been thought important is the size of the field. Most OKN

experiments have utilized full-field stimuli; in comparison, our 10 deg RDCs are much smaller. In fact, objects that we normally pursue in the world can be quite a bit larger than the 1 deg or less target that is used in laboratory experiments. For example, a person who is six feet tall would subtend almost 7 deg of visual angle at a distance of 50 feet and a compact car would subtend about 8.5 by 2.5 deg of visual angle from a distance of 100 feet. Even at the physiological level the distinction between pursuit and OKN is blurred. The neuronal substrate for pursuit and OKN initiation are thought to be the same (Robinson, 1981). Neurons in both cortical (MT and MST) and cerebellar (foculus and vermis) limbs of the pursuit system respond to large field moving stimuli (Miles & Fuller, 1975; Lisberger & Fuchs, 1978; Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986; Suzuki & Keller, 1988a,b; Duffy & Wurtz, 1991a). Possibly the only defining characteristic of OKN is that it developed to stabilize an image on the retina during self-motion. Smooth pursuit has probably arisen from the neuronal substrate which generates OKN. This idea is supported by the overlapping pathways in the brain which generate each movement, as well as a nasal-temporal asymmetry present in both movements (Atkinson & Braddick, 1981; Schor, Narayan & Westall, 1982; Boothe, Dobson & Teller, 1985) that seems to benefit OKN, by stabilizing the world on the retina when a lateral-eyed animal rotates toward an object, but not pursuit. Therefore it seems reasonable that the smooth pursuit system is capable of integrating information over a retinal area larger than the fovea.

8.3. Intrinsic directional noise in the pursuit system

Intrinsic noise is an inherent characteristic of biological systems. The effect of noise on a movement control system is to increase the variability of the output. The variability of the response directly determines how precise the movement can be. Despite the importance of knowing the character and sources of noise in movement systems, the concept of noise in the pursuit system has been given little attention in the literature. Only a few investigators have quantified variability in the pursuit response (Robinson, 1965; Carl & Gellman, 1987; Kowler & McKee, 1987). We have verified that the pursuit system has intrinsic noise, and shown that the noise is largely a function of noise in the visual motion processing system. Since the breakpoints of the psychophysically and oculometrically derived equivalent noise curves are similar, the oculomotor system apparently does not introduce a new independent noise source (Geisler, 1989; Levi & Klein, 1990; Pelli, 1990). However, the oculomotor curve is shifted vertically, implying that the oculomotor system multiplies the noise that the visual system passes to it. Where is this gain? It is possible that when the motion signals in the visual system are selected

to be acted upon, both the signal and the noise are amplified in the process of generating the response.

Current models of smooth pursuit do not incorporate noise (Robinson et al., 1986; Krauzlis & Lisberger, 1994). There are several possible problems associated with this oversight. One problem is that while the models will be able to predict the average response of the system, they will fail to describe the variability inherent in the pursuit system and hence the precision of its response. Building a model that is robust in the presence of noise to ensure that the output remains stable requires the use of perhaps different algorithms. Some mathematical functions, such as differentiation, are poor choices because they will amplify any noise in the input and thus would likely not be chosen to build a robust model. Finally, comparing current smooth pursuit models with motion processing models is difficult because motion processing models have been developed around measures of precision while smooth pursuit models have not. More studies of the effects of noise on pursuit performance should allow for the development of a more realistic model of the smooth pursuit system.

To summarize, the present data show that RDCs are potent stimuli for driving smooth pursuit eye movements. While smooth pursuit to RDCs is similar to that to single spot targets, the response to RDCs have higher gain and show better separation for the stimulus speeds tested. Moreover, observers can smoothly pursue RDCs that contain added directional noise. This further supports Heinen and Watamaniuk (1998) previous results showing that the motion signal driving pursuit can result from spatial integration. Finally, the similarity between pursuit and psychophysically measured direction discrimination suggests that both responses may be limited by a common stage of motion processing.

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