Pursuit eye movements to second-order motion targets

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We studied smooth-pursuit eye movements elicited by first- and second-order motion stimuli. Stimuli were random dot fields whose contrast was modulated by a Gaussian window with a space constant of 0.5°. For the first-order stimuli, the random dots simply moved across the screen at the same speed as the window; for the second-order stimuli the window moved across stationary or randomly flickering dots. Additional stimuli which combined first- and second-order motion cues were used to determine the degree and type of interaction found between the two types of motion stimuli. Measurements were made at slow (1°/s) and moderate (6°/s) target speeds. At a velocity of 1°/s the initiation, transition, and steady-state phases of smooth pursuit in response to second-order motion targets are severely affected when compared with the smooth pursuit of first-order motion targets. At a velocity of 6°/s there is a small but significant deficit in steady-state pursuit of second-order motion targets but not much effect on pursuit initiation. © 2001 Optical Society of America

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1. INTRODUCTION

Primates use smooth-pursuit eye movements to track attended moving visual targets, thereby stabilizing the target image on or near the fovea. The visual signals that drive smooth pursuit are known to convey information about visual image motion to the motor system. The neural pathway underlying smooth-pursuit eye movements includes retino-cortical-ponto-cerebellar connections before the generation of the motor commands in the oculo-motor plant. The cortical signals in this pathway arise from a specific visual motion-processing pathway that includes the middle temporal and medial superior temporal extra-striate visual areas[1,2] and from the frontal eye fields[3–5] and supplementary frontal eye fields.[6,7] The effectiveness with which different visual signals elicit smooth pursuit may therefore provide insight into the functional organization of this part of the cortical visual processing network. Furthermore, a comparison of perceptual motion judgments and pursuit eye movement performance may give us insight into whether the signals that drive perception are also available to the pursuit system.[8–18]

Psychophysical evidence indicates that stimulus configurations that do not have a primary luminance cue for motion can elicit the perception of movement and judgments of velocity (see Refs. 19 and 20 for reviews). One particular class of second-order motion stimuli, originally described by Chubb and Sperling,[21] has been widely used in recent years to study the processes involved in visual motion analysis. In this stimulus there is an equal amount of first-order motion energy in opposite directions; hence this class of stimuli is called drift-balanced

by Chubb and Sperling. There are other types of second-order stimuli that can give rise to a percept of object motion. One of these, which is particularly interesting for our purposes in the study of pursuit, has a moving object defined by motion of texture elements, which move in the direction opposite to that of the motion of the object. This is called a theta stimulus.[22]

The majority of experiments on pursuit have used luminance-based motion stimuli that stimulate first-order, or Fourier, motion detectors.[23–25] When the stimulus is a first-order motion target, there is quite a close correspondence between pursuit performance and perceptual performance at low speeds (1–2°/s).[15] Pursuit of second-order motion targets has, to our knowledge, been studied in two series of experiments.[26,27] For both first- and second-order motion targets of moderate to fast speeds (6–9°/s), Butzer *et al.*[26] reported that smooth-pursuit eye movements were initiated and maintained in the direction of object motion. Initially, pursuit eye movements in response to second-order targets show low gain,[27] but during the steady-state phase, pursuit shows a gain slightly greater than 1.[26] In contrast, Harris and Smith[28] found that large-field second-order motion gratings moving at speeds between 3 and 20°/s did not elicit optokinetic nystagmus.

Since psychophysical studies indicate that there are some quite distinct differences in the processing of slow and moderate velocities, we have studied pursuit to targets moving at either 1°/s or 6°/s. Our general aims were to investigate the responses of different stages of pursuit eye movements to the two classes of motion stimuli, first and second order, at slow and moderate speeds. In ad-

dition, we investigated the interaction between the two classes. To accomplish these aims we used three classes of targets:

1. Those that have a net motion energy and that would stimulate primarily first-order motion detectors.

2. Those that have no net first-order motion energy (drift-balanced stimuli) and would not preferentially stimulate a subset of the first-order motion detectors. The two stimulus configurations used were a window moving over either stationary texture elements or dynamically flickering texture elements. Neither stimulus has net first-order motion energy. The static texture would provide a powerful fixation cue in conjunction with second-order motion energy, whereas the dynamic target would give the same second-order motion energy but no fixation cue.

3. Those that have both first- and second-order motion energy. In this class is the theta-motion stimulus described above and another stimulus type that we devised (first-order+) to further study the interaction between first- and second-order processing. The object in the first-order+ stimulus is defined by texture velocity at twice the velocity of the object. With these stimuli we wished to test whether the primary drive for pursuit is due to the first-order motion, defined by the motion of the texture elements, or the second-order motion, defined by the object motion.

Using a modified step-ramp paradigm,[29] we measured smooth-pursuit eye movement performance in the period up to 120 ms after the onset of pursuit, while the pursuit mechanism is in the open-loop mode,[30,31] and during the later stages of pursuit, in which the motion signal and internal feedback interact to give a steady-state response.

We also studied the effect of changing the contrast of the first- and second-order targets on smooth-pursuit responses. This is important as a control for first-order artifacts in the second-order stimuli. There is always the possibility of introducing first-order motion cues as a result of nonlinearities in the visual system or in the equipment, and the strength of these cues will scale with contrast. If pursuit were driven by motion energy from first-order artifacts in the second-order stimuli, then it would be expected that the measures of pursuit performance would scale with contrast in a way similar to the scaling of first-order stimuli with contrast.

Some of these results have been presented in abstract form.[32]

2. METHODS

A. Equipment
Stimuli were displayed on a Barco RGB monitor (CCID 7351B) by a CRS (Cambridge Research Systems) VSG 2/3 graphics board with a refresh rate of 60 Hz noninterlaced. Each gun of the CRT was linearized by a look-up table to give 12-bit intensity resolution. A Photo Research Model 703-PC spectroradiometer was used to calibrate the display screen. The display was $17° \times 12°$ at the viewing distance of 117 cm and had a mean luminance of 57 cd m^{-2}. Each pixel subtended 1 arc min. Subjects were seated with their heads stabilized by a bite bar. They viewed the display binocularly through natural pupils. Stimulus display and data collection were controlled by a personal computer.

B. Subjects
Four subjects participated in the study: one of the authors (MH), who was experienced, and three naïve subjects, NH, JZ (the effects of stimulus types), and BS (the effects of contrast). All procedures were approved by the New York University Human Subjects Committee.

C. Visual Stimuli
Small Gaussian vignetted patches of texture were used as stimuli. The texture stimuli were black and white random-noise pixel blocks and were displayed on a neutral gray background. Each pixel block subtended 8 $\times$ 8 arc min. The space constant of the Gaussian was 0.5° for all experiments (Fig. 1).

A diagrammatic representation of the movement of our standard first- and second-order motion targets is shown in Figs. 1(a) and 1(b), respectively. If the onset of motion occurs at t_0 and then at times t_1 through t_3, the stimulus envelope has moved the same distance for both first- and the second-order targets. In the case of the first-order target the static texture within the window also moves to the right at the same speed as the envelope, whereas in the static second-order motion case the texture appears to move toward the left relative to the envelope, which moves to the right.

We investigated five types of motion stimuli (Fig. 2). In all cases the stimulus envelope was the Gaussian window, which moved at a constant speed. A space–time diagram indicating the motion targets is shown in Fig. 2. For our standard first-order motion target the random texture and the Gaussian envelope move in the same direction at the same speed (Fig. 2, bar A). Our standard second-order motion target was the Gaussian envelope moving over a static-texture background (Fig. 2, bar B). The stationary texture elements are visible during the passage of the window; thus for the slow-moving window the individual texture elements are visible for ~1 s. For the window moving at 6°/s the individual elements are visible for less than 200 ms and are not reported as stationary elements by the observers. We used a dynamic version of this second-order motion target, where the Gaussian envelope moves across a random-texture background that is replaced on every frame (Fig. 2, bar D). For the dynamic targets the texture elements have the same appearance for both 1°/s and 6°/s conditions, yet the differences between the two speed conditions remain (see Section 3). We used two more stimuli for which the motion of the texture and the envelope were different. For theta motion[22] the Gaussian window moves across a textured background that is moving at the same speed as the envelope but in the opposite direction (Fig. 2, bar C). In the first-order+ condition the Gaussian window moves across a random textured background that is moving in the same direction as the envelope but at twice the speed (Fig. 2, bar E). The modulation was always around a mid-gray background illumination that covered the $17° \times 12°$ screen.
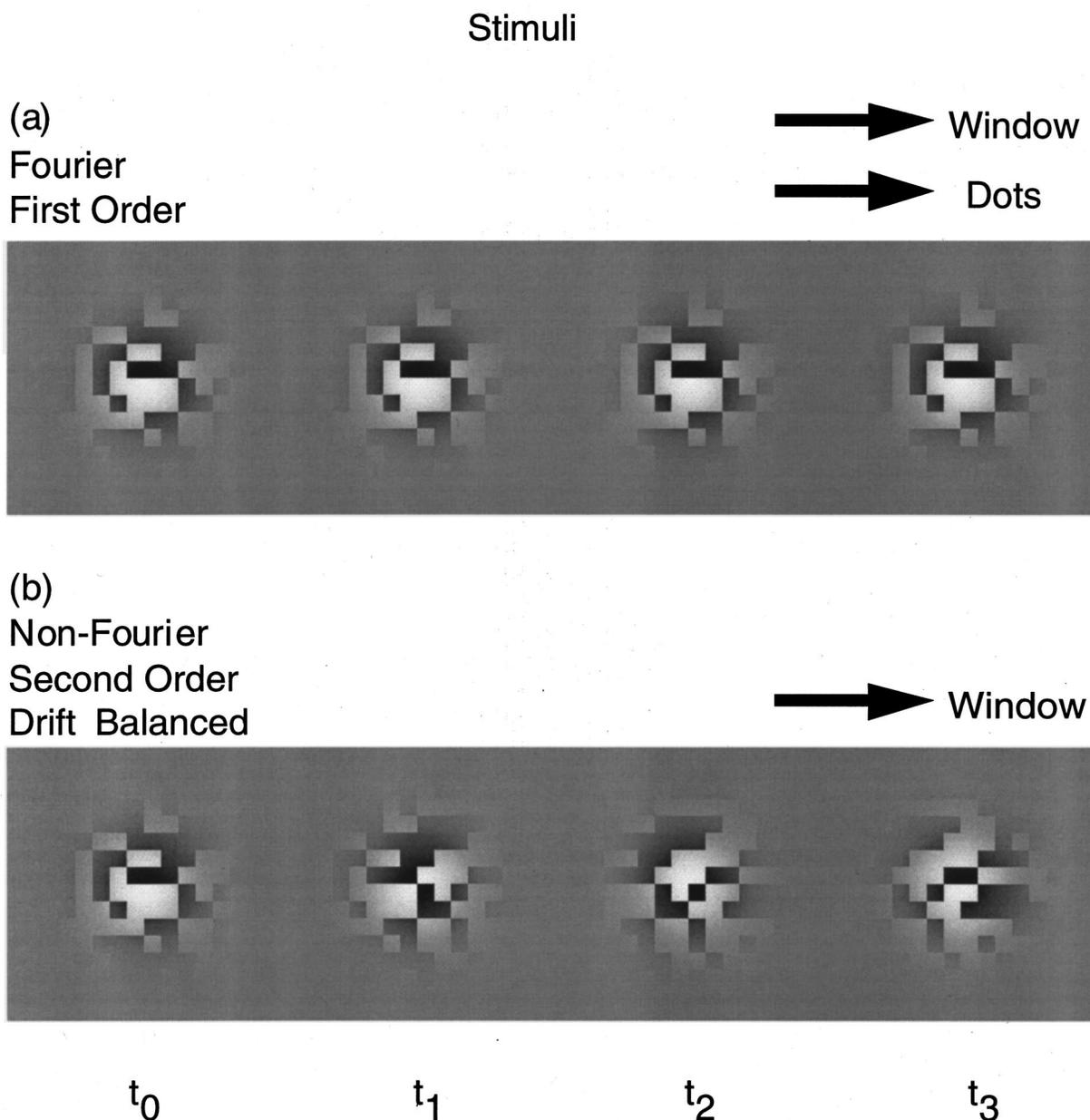
Stimuli

Fig. 1.   Halftone of a random-texture patch moving across the display.   (a) First-order (Fourier) stimulus.   At different points in time ($t_0 \ldots t_3$) the same random dots are located within the Gaussian window as both the window and the dots move to the right.   (b) Second-order, static-noise, drift-balanced (non-Fourier) stimulus.   At different points in time different dots are located within the window, which moves to the right on top of a static, stationary, random-noise field.

D.   Eye Movement Recording
The position of the right eye was measured with a double-Purkinje-image infrared eyetracker[33] (Fourward Technologies—Generation V).   Viewing was binocular with natural pupils, and each eye's view was through a 45° angled glass plate with greater than 90% transmittance.   The observer's head was kept steady by a bite bar. The analog outputs of the horizontal and the vertical eye positions were sampled with an analog-to-digital converter at 500 Hz at 12-bit precision and stored on disk for later analysis.   The initiation of sampling was synchronized with the display of the visual stimulus.   Details of the eye movement monitoring and data collection are essentially the same as those described by Ringach et al.[34]

E.   Procedure
Each session consisted of between 32 and 120 trials, depending on the subject and the type of experiment. Within the trials of each session we included all the stimulus conditions (stimulus types, speeds, and directions), randomly mixed.   One or two sessions were run each day; the only difference between sessions was that the order of trials was randomized.   Before and after each session we did a calibration of the relationship between horizontal eye position and eye tracker output signal, which was used later in the analysis of the trials from that session.   We used a step-ramp paradigm similar to that introduced by Rashbass.[29]   At the start of each trial, a small black central fixation spot appeared on the gray

background. After an unpredictable interval between 0.5 and 1 s, the pursuit target appeared to the left or the right of fixation; its contrast was modulated at 2 Hz during this period. At some time during the interval of 0.5 to 1 s, the fixation spot disappeared and the envelope of the target began to move to the left or to the right at a constant speed. In all experiments the speed was either 1°/s or 6°/s. All target movements were along the horizontal meridian. According to convention we call the trials where the stimulus moves across the fixation point "toward" trials and those where the stimulus moves away from fixation "away" trials. Total stimulus movement duration was 5 s for the 1°/s target condition and 1.8 s for the 6°/s target condition in the toward trials. Observers were instructed to maintain fixation on the central black spot until the target started to move and then follow the moving target with their eyes as rapidly and accurately as possible. It was made clear to the sub-

jects that the target object was always the Gaussian envelope or window, and this was what they were instructed to follow. They were also asked to avoid anticipatory slowing as the target approached the edge of the screen.

For one set of experiments with 6°/s object motion we needed a longer excursion to get an improved estimate of the steady-state velocity. In this experimental paradigm the fixation spot first appeared at the center of the screen for 1 s, and then it jumped horizontally to the left or right to a location 2.6° from the edge of the screen. The subject was required to fixate at this new position. The target then appeared between the fixation point and the edge of the screen. At this stage the paradigm was the same as outlined for all other trials except that there was only toward movement. Using this method we obtained ~14° of horizontal movement for the 6°/s targets and were able to obtain estimates of steady-state responses that were not
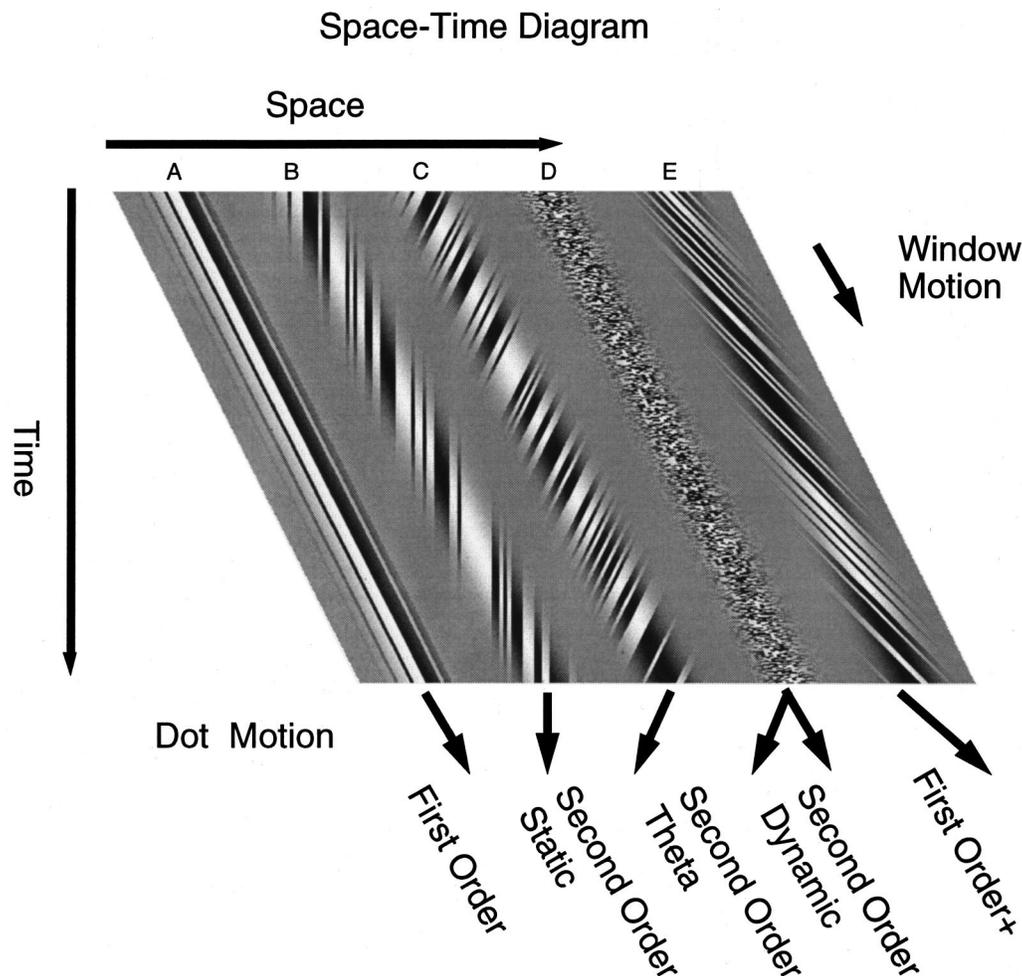
Space-Time Diagram

Fig. 2. Space–time diagram illustrating the five different types of motion stimuli we used. A horizontal slice through the random-noise pattern is shown on the x axis. The y axis indicates time. (a) First-order, Fourier motion: random dots and Gaussian window move in the same direction at the same speed. (b) Second-order, static-noise, non-Fourier, drift-balanced motion: the window moves across a static random-noise background. (c) Second-order, theta motion: the window moves across a random-noise background that moves at the same speed but in the opposite direction. This stimulus is perceived to move rightward, even though most of its Fourier energy is in the leftward direction. (d) Second-order, dynamic-noise, non-Fourier, drift-balanced motion: the window moves across a dynamic-random-noise background. (e) First-order+stimulus: the random dots move to the right at twice the speed of the window. The solid arrow under each strip shows the dominant direction vector of first-order motion energy. The arrow to the right of the diagram marked "window motion" is the second-order-motion direction vector and is the same for all five conditions.

so much influenced by anticipatory slowing (see Section 3).

F. Analysis

Traces for individual trials were stored on disk for off-line analysis. We recorded position traces for 500 ms before the onset of stimulus movement and for 500 ms after the cessation of stimulus motion. For the 6°/s stimulus conditions the position traces were initially filtered by a 130-point finite-impulse-response filter with a cutoff at 60 Hz. The position signal was differentiated to produce a velocity trace, which was then smoothed by the same finite-impulse-response 60-Hz low-pass filter. For the 1°/s traces we used a filter with a more gradual high-frequency roll-off, a Gaussian, with a time constant of 20 ms (corresponding to 50 Hz). We chose the filters such that they would attenuate the higher frequencies but not alter the parameters that we extracted from the traces, especially the initial peak velocity. We detected saccades in each trace by compiling a histogram of the instantaneous velocities for each trial and then computing the limits for detection of velocities above and below the dominant velocity distribution. This method leads to a more conservative criterion than does a fixed-velocity or fixed-acceleration cutoff, which are frequently used in saccade-detection algorithms. It also leads to a criterion that is tailored for the different stimulus speeds; i.e., the cutoff is much lower for the slow stimuli (mean 2.4°/s) than for the fast stimuli (mean 12.2°/s), depending not only on the mean pursuit velocity but also on its variance. By using this more conservative method we could detect all large saccades and the majority of microsaccades, while the inclusion of ±3 standard deviations of the velocity distribution virtually excluded false positives. That the algorithm removed all saccades was confirmed by visual inspection of each trace. A period of 16 ms before and a period of 70 ms after a saccade were also excluded from further analysis, as were pursuit segments in between saccades that were shorter than 50 ms. Saccades produce an overshoot in the recorded trace with use of the Purkinje-image eye tracker owing to the movement of the lens with rapid accelerations, which overshoots eye position.[35] In the analysis of pursuit, we excluded the saccade, including the overshoot, so this artifact does not influence our results.

The onset of pursuit was detected with a method similar to that used by Carl and Gellman.[36] After the onset of stimulus motion, we looked for the first 40-ms period in which the eye velocity over the whole 40-ms period was greater than a critical value. The critical value was computed as the mean plus 1.96 times the standard deviation of the eye velocities during fixation. We fitted a straight line to the velocity trace for a 64-ms interval after onset, beginning at the onset of the 40-ms period. The intercept of this regression line with the time axis was defined as the latency. Neither this method nor any other method that we tried worked well for the eye velocity traces generated in response to 1°/s object motion, where the exact point of initiation is often poorly defined. For this reason we have not presented a detailed analysis of the latency for the slow traces. Rather, we have relied on the latency obtained from the average traces. Further, with averag-

ing, it is customary to use the initiation of pursuit as the point of alignment for the velocity traces. We followed this procedure only for the 6°/s traces. Owing to the imprecision of the initiation for 1°/s traces we chose to align the averages for the 1°/s traces with the onset of stimulus motion.

We analyzed acceleration during the first 120 ms following the onset of the eye movement from the velocity traces according to the methods outlined by Lisberger and Westbrook.[30] Acceleration on an individual trial basis was analyzed only for the 6°/s object motion condition: We estimated acceleration from each velocity trace during four 30-ms time segments after the onset of movement (1–30 through 91–120 ms) and fitted a linear regression to each segment. Any traces with a saccade during the acceleration phase were not included in the analysis of the acceleration phase of pursuit. The eye acceleration period in the trials with 1°/s object motion is not well defined on individual trials, and consequently analysis over segments during the first 120 ms is not meaningful. We averaged individual traces for the 1°/s stimulus condition with the traces aligned to the stimulus onset in order to obtain estimates of acceleration.[36] The profile of the averaged eye velocity in response to the 1°/s object motion can be seen in Fig. 5(a) below.

Any traces where the algorithm returned a value of latency that was less than 50 ms were not included in the analysis, as we assumed the subject was making anticipatory eye movements.[37–40] We also excluded traces from the analysis where there was a saccade to the target position before the onset of motion, thus eliminating trials where the subject made a saccade to the stationary target before it started to move.

Steady-state velocity was estimated during the period 1.5–2.5 s after the onset of motion for the targets moving at 1°/s and for the period 750–1250 ms for the targets moving at 6°/s. The periods corresponding to a saccade were omitted from the data used for calculating the average velocity. For the 1°/s stimuli it is clear from the inspection of the traces for all subjects that the initial overshoot in velocity that often accompanies the onset of pursuit is complete by 1.5 s, and there is little or no anticipatory slowing before 2.5 s. On the other hand, there is clear anticipatory slowing for targets moving at 6°/s, which is discussed further in Section 3 along with an additional set of experiments in which we arranged for the target to move across nearly the whole width of the screen (14 deg) so that there was enough time to reach the steady-state velocity. The total duration for the 1°/s condition was 5 s, and for 6°/s it was 1.8 s for the toward trials, which was extended to 2.33 s for some experiments (see Section 3).

For each trial we inspected the eye position and eye velocity traces, along with the stimulus time course, all of which were displayed graphically on the computer screen. Sections of the eye movement traces that were designated to be fixation, pursuit, or saccadic episodes were displayed in different colors. The latency, peak, and steady-state positions and values were also displayed. Traces that did not conform to the criteria outlined above or where the lock of the eye tracker was lost during an individual trial were excluded from further analysis. For the

three subjects in the main series of experiments (JZ, NH, and MH) the total number of trials in the toward direction was 380, 416, and 780, respectively. The number of trials that met the criteria was 218, 304, and 698, respectively, corresponding to an average number of trials per data point in Figs. 6–9 (below) of 22, 30, and 68 for each subject (JZ, NH, and MH). In the contrast experiments (Fig. 10 below) the total number of toward trials in the 1°/s condition was 364 for MH and 338 for BS. The number of trials that met the criteria were 305 and 226 for MH and BS, respectively; this corresponded to an average number of trials per data point in Figs. 10(b) and 10(c) (below) of 28 and 21, respectively for each subject. For the 6°/s condition [Fig. 10(a) below] the total number trials was 332, of which 227 met the criteria, resulting in 38 trials per data point.

3. RESULTS

A. Individual Eye Position and Velocity Traces

Figure 3(a) shows a representative eye movement trace for observer MH recorded during the pursuit of a standard first-order Gabor patch moving at 1°/s. The contrast of the texture elements was 37.5%, which was greater than ten times the contrast required for the identification of the direction of motion of the same patch. The target appears as a stationary Gabor patch with the

contrast of the texture modulated at 2 Hz. This is shown by the dashed stimulus-position trace below the eye position trace. The subject is fixating a small spot in the center of the screen at this stage. The target then begins to move at a constant velocity toward the fixation spot, and after approximately 170 ms, the characteristic pursuit latency for this type of target, the subject initiates a pursuit movement that captures the approximate center of the target and holds it in the center of gaze using smooth pursuit interspersed with small saccades. In the velocity profile for this suprathreshold target there is an initial acceleration followed by a relatively constant velocity for the smooth-pursuit segments. The saccades are shown by the abrupt changes in velocity; these were automatically detected and removed from the traces before the pursuit analysis.

Figure 3(b) shows the eye position and velocity traces for a single trial in which the stimulus was a first-order target moving at 6°/s. In the position trace it can be seen that the observer holds steady fixation during the period that the target is stationary, and then when the target begins to move, the subject captures the target as it moves toward fixation and is able to pursue it at a velocity close to the target velocity.

The position and velocity traces for two individual trials of subject MH tracking second-order targets (second-order static condition, Fig. 2, bar B) are shown in Fig. 4. The traces in Fig. 4(a) show pursuit in response to an ob-
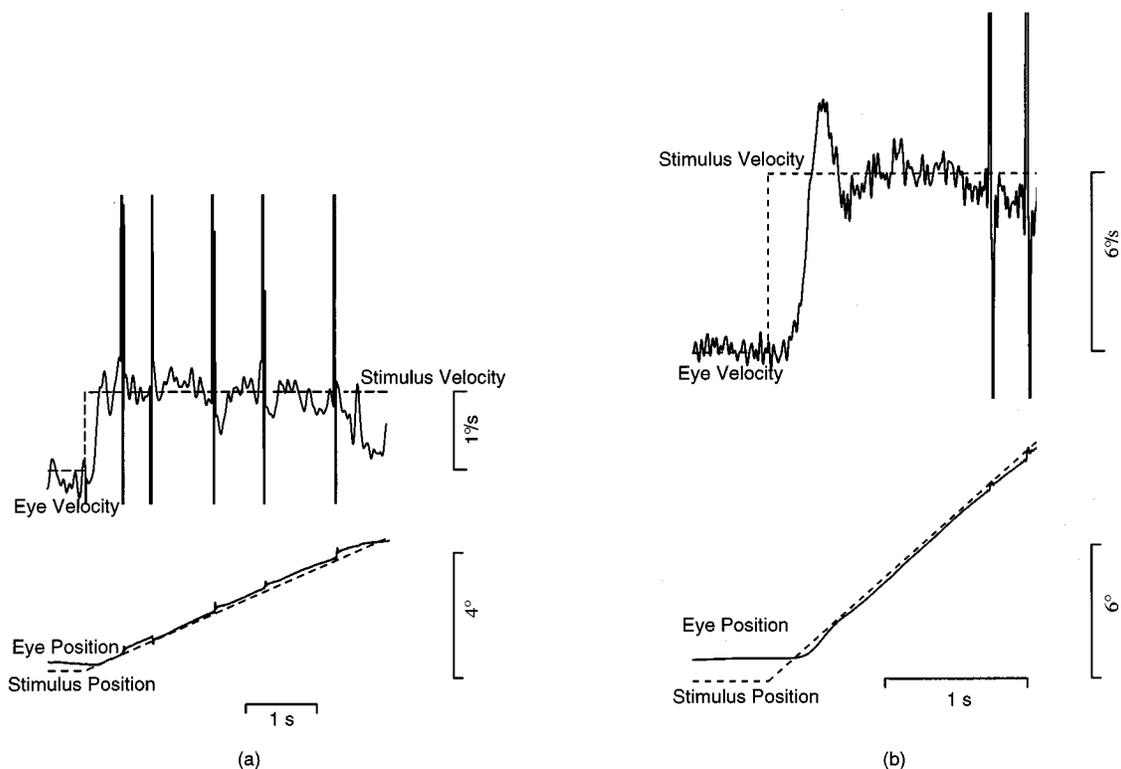
Fig. 3. Example traces of pursuit to first-order motion stimuli. All individual pursuit trials are for subject MH. Contrast was 37.5% for all stimuli. The lower traces show the stimulus position and eye position before and during stimulus motion. The upper trace shows stimulus velocity and eye velocity. The saccades in the velocity traces are truncated, but the full extent of the saccades is shown in the position traces. (a) 1°/s object motion stimulus. In general, there is consistent initiation reaching a peak velocity of just greater than 1°/s, and then pursuit proceeds during the steady-state phase with a gain close to 1. Note that there are a number of small corrective saccades. (b) 6°/s object motion stimulus. After the latency there is a clear acceleration phase with a velocity overshoot followed by a steady-state region with a velocity close to 1.
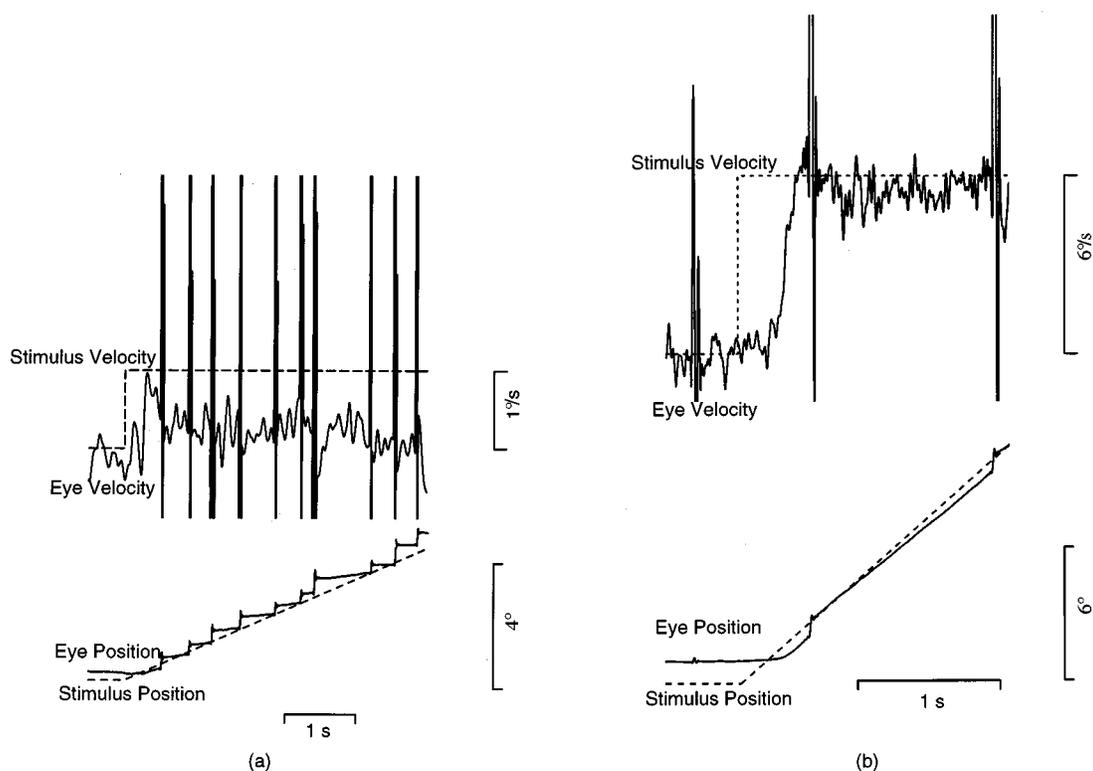
Fig. 4.   Example traces of pursuit to second-order non-Fourier motion stimuli.   All details are the same as given in Fig. 3.   (a) 1°/s object motion stimulus.   (b) 6°/s object motion stimulus.

ject moving with a velocity of 1°/s. There is a clear initiation followed by a number of segments of pursuit that have low-velocity gain. Frequent saccades are used to maintain the center of gaze close to the center of the target. Comparison with the trace shown in Fig. 3(a) makes it clear that the pursuit is seriously compromised for the second-order object. When the second-order object moves at 6°/s the initiation of pursuit is rapid, and subsequent pursuit velocity is well matched to the stimulus velocity [Fig. 4(b)]. In Subsection 3.B the responses are quantitatively assessed at each stage of pursuit across the different stimulus conditions.

B.   Average Eye Velocity
For each target velocity we averaged the eye velocity traces of all the toward trials where the pursuit response was not initiated with a saccade. For averaging the eye velocity in the 1°/s stimulus condition all the traces were aligned at the stimulus onset, whereas for the 6°/s stimulus condition the traces were aligned with the onset of pursuit. It should be noted that the alignment was done for averaging only in the 6°/s condition; for trial-by-trial latency analysis (Fig. 7 below) the individual traces were aligned to stimulus onset.

1.   Speed 1°/s
For a target velocity of 1°/s the average pursuit response to the standard first-order target shows an initial acceleration followed by an overshoot in eye velocity beyond the target velocity until the eye movement settles to a steady-state velocity, which is, on average, just below the

target velocity. When the texture moves in the same direction as the envelope but at twice the speed (first-order+) there is initially an overshoot in velocity that approaches the velocity of the texture followed by a steady-state velocity that is greater than that of the standard first-order target. The overshoot is seen in many of the individual traces but is masked in the average trace because it is asynchronous from trial to trial. For the static second-order motion target there is an initial response or peak velocity that undershoots that of the target. The subsequent steady-state eye velocity is substantially lower than the target velocity [Fig. 5(a); the dashed line shows the target velocity]. The other second-order targets also show the same trend across the three subjects. When the random texture is changed on each frame, the dynamic second-order condition, the initial eye velocity lies between the first-order and the second-order static conditions, and the steady-state eye velocity gain is greater than for the static condition. Nonetheless, pursuit gain is still severely disrupted, with an average gain of approximately 0.5. When the first-order motion of the texture is in the direction opposite to that of the motion of the envelope (theta motion), then the initiation of pursuit to the envelope is slowed substantially and the average eye velocity is lower than for the second-order static condition. In fact, on some trials the first-order motion of the texture dominates at the very earliest time, and the movement is in the direction opposite to that of the window. This is seen as a diphasic episode at the beginning of the averaged theta trace in Fig. 5. The initial response on individual trials did not fall into two distinct response types, one in the direction of the first-order texture mo-

tion and another in the direction of the second-order motion, rather there was a continuum of responses.

2. Speed 6°/s

When the target speed is 6°/s the differences in the averaged eye velocity traces [Fig. 5(b)] in response to first- and second-order motion targets are small. In the initiation phase of pursuit there are small but significant differences in latency and acceleration, but these differences across the different stimulus conditions are much smaller than those seen in response to the same stimuli moving at 1°/s. The peak and average eye velocities show a small but significant reduction in gain, of ~15%, for second-order targets compared with that of first-order targets.

C. Pursuit Phases

Pursuit eye movement responses can be divided into a number of phases.[41] We will consider measures of the eye movements that characterize three phases: (1) The initiation phase, which is predominantly open loop, depending primarily on the visual motion signals[42] especially for the fast speed. Measures that characterize the initiation phase are pursuit latency and eye acceleration during the first 120 ms after the beginning of pursuit. The period chosen as open loop depends on the average latency for pursuit initiation, the initial target velocity, the primate species (monkey or human), and the type of pursuit target.[30,36,43] Consideration of these factors suggests that 120 ms is an appropriate choice for our experimental conditions. (2) A transition phase that is thought to be influenced by both the initial visual motion signals

driving the open-loop phase and the first internal feedback signals. The transition phase can be partly characterized by the maximum eye velocity reached just after initiation. (3) The steady-state phase during which the pursuit eye movement is closed loop. It depends on a number of factors including velocity and position error signals.

1. Initiation

The initiation of pursuit depends on a number of stimulus features. For example, eye acceleration to small spots depends on both the target velocity and its contrast.[30] Here we wished to determine whether the stimulus type played a role in influencing the initiation phase. Therefore we kept the contrast of the texture elements constant at 37.5%, greater than ten times threshold for the identification of the direction of motion, and compared the eye acceleration between stimulus types. An analysis of the acceleration for individual traces when the stimulus object moved at 1°/s proved to be complicated because of the problems defining the pursuit latency (see next paragraph). Hence we are not presenting acceleration results for the 1°/s stimulus condition. The average eye acceleration for the five different stimulus types with the object moving at 6°/s is shown in Fig. 6. We found small differences between stimulus types during the initial acceleration period for subject MH, where there were sufficient trials to perform meaningful analysis. Pursuit initiation was analyzed in 30-ms intervals for the first 120 ms after pursuit onset (see Section 2). When these inter-
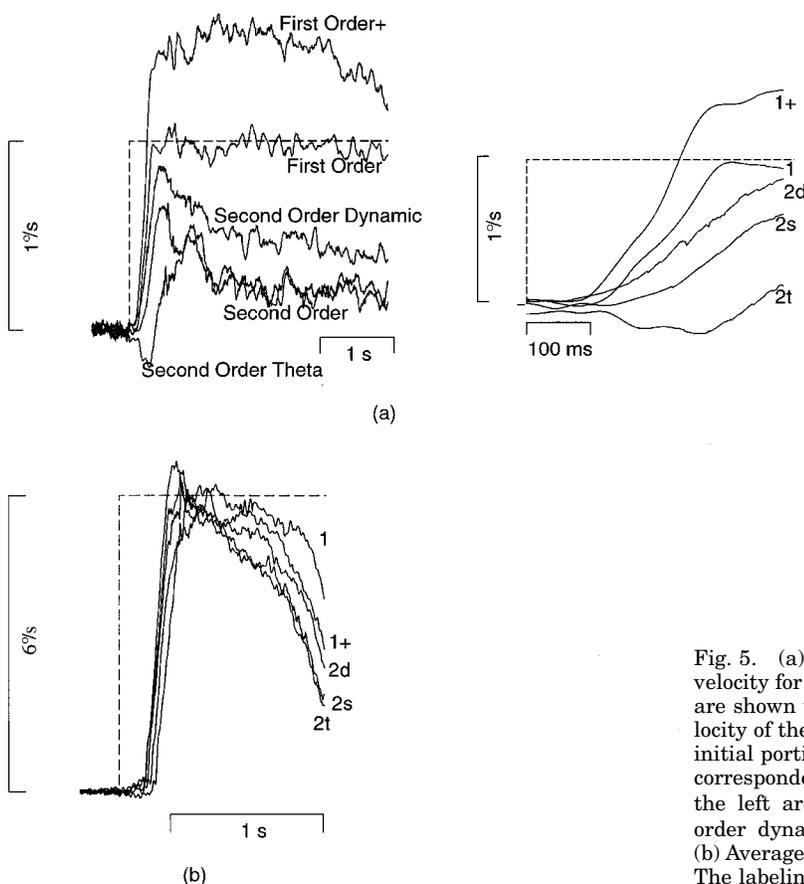
Fig. 5. (a) averaged eye velocity traces in response to 1°/s target velocity for all five motion stimuli that are shown in Fig. 1. Data are shown for one observer, MH. The dashed line shows the velocity of the stimulus envelope. The insets on the right show the initial portion of the response with an expanded time scale. The correspondence of the labels on the right-hand graphs to those on the left are 1+ = first-order+; 1 = first-order; 2d = second-order dynamic; 2s = second-order; 2t = second-order theta. (b) Averaged eye velocity traces in response to 6°/s target velocity. The labeling convention is the same as for (a).
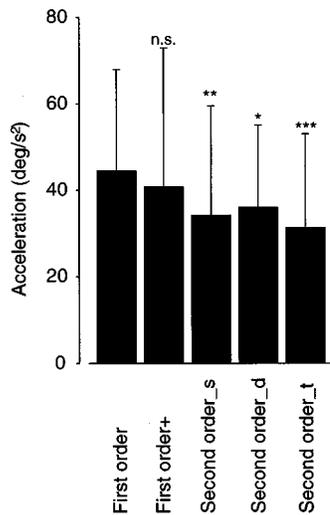
Fig. 6. Mean eye acceleration traces to 6°/s object motion stimuli for one observer, MH. The eye acceleration was averaged for all the 30-ms periods up to 120 ms after the initiation of pursuit. The height of the histogram bars is the mean, and the error bars are one standard deviation of the mean. The significance of the results of Student's t test between the first-order condition and other conditions are given above the error bars. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; n.s. (not significant), $p > 0.05$.

vals were grouped together there was a 17% reduction in average acceleration for the static second-order motion condition compared with that of the first-order stimulus condition. A reduction of ~9% was found for the dynamic condition and a 25% reduction for the theta condition.

For the 1°/s condition the latency on individual trials is often difficult to define either by visual inspection or by using an algorithm such as that used for the traces from the 6°/s condition. For this reason we chose to take the estimate of visual latency from the averaged responses. In the averaged velocity traces in Fig. 5(a) there is a substantial increase in latency for the second-order condition compared with that of the first-order condition. Latency of pursuit initiation for the 1°/s stimulus condition was defined as the point where an eye velocity of 0.2°/s is reached. The latency difference between the traces from pursuit of the standard first-order target and the second-order static targets were 50, 63, and 90 ms for JZ, NH, and MH respectively. Figure 7 shows the average latency of pursuit initiation for the five stimulus types in the 6°/s condition based on analysis of individual trials. The average latency for the two first-order stimulus types is between 150 and 175 ms across the three observers. There is a small increase in average latency for the static and the dynamic second-order patterns for all three subjects. The latency of pursuit initiation for the theta condition is always above 200 ms for all three observers. It should be noted that the latency for initiation for the theta condition is for pursuit in the direction of second-order motion. Clearly, in the theta condition there is most often an initial pursuit acceleration in the direction of the first-order target motion with a shorter latency than the pursuit acceleration to the second-order stimulus motion.

2. Transition

The peak eye velocity that is reached during smooth pursuit of 1°/s targets is most often greater than the target velocity. The overshoot of eye velocity following the initiation stage is seen clearly in some of the average traces [Figs. 5(a) and 5(b)]. The peak velocity in the transition phase of the response is thought to be influenced by both the pure motion signal that dominates the open-loop response and the complex interaction of stimulus-driven responses and feedback that dominate the steady-state response of pursuit. We wished to determine whether there was a difference in the average and range of the peaks reached during the different stimulus conditions. Studying the peak velocities of pursuit of the different targets may be especially important for ascertaining the interaction between the pure motion signal and the signals derived during pursuit initiation. Furthermore, we noted that there was a tendency for the first segments of pursuit to approach a velocity that was closer to target velocity than later segments. This is likely to be reflected
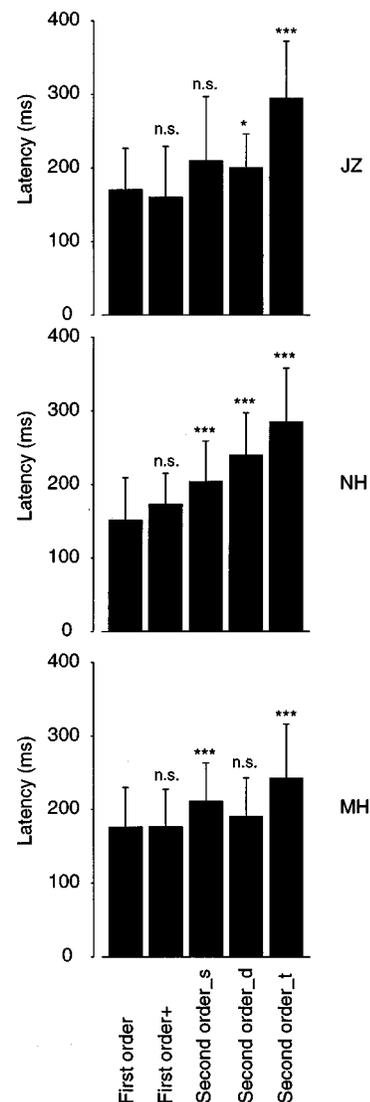
Fig. 7. Latencies of smooth pursuit for three observers to the five different types of motion stimuli moving at 6°/s. All else is as for Fig. 6.
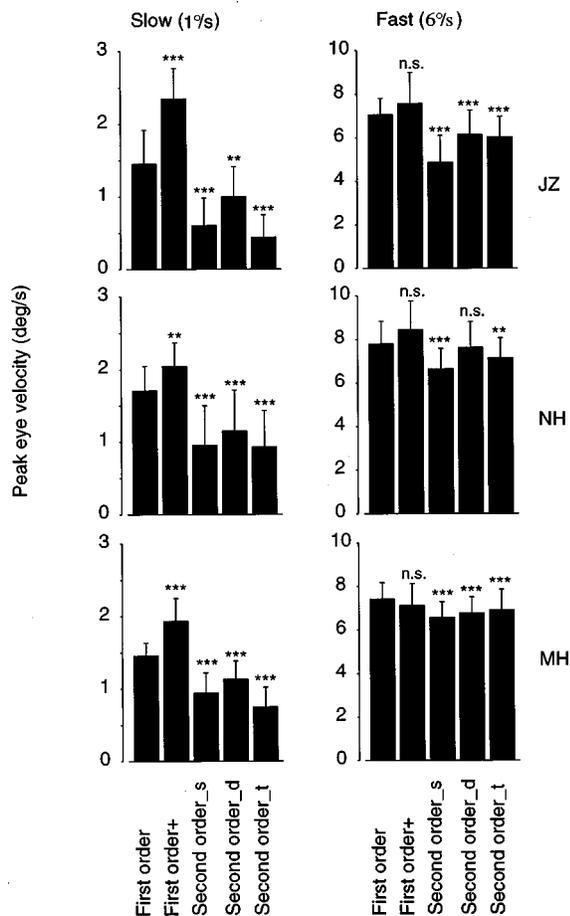
Fig. 8. Peak eye velocity for three observers to the five different types of motion stimuli.   The left column shows data for 1°/s target velocity, and the right column shows the data for 6°/s target velocity.   All else is as for Fig. 6.

effect is seen for JZ, with a reduction of the order of 50% for the static and theta conditions and of ~30% for the dynamic condition.   Smaller effects in the same direction are seen for the other two observers.   There is a significant and consistent increase in peak velocity for the first-order+ condition.   These results suggest that the peak eye velocity is influenced by the interaction of the first-order and second-order motion signals early in the processing of the motion information for the targets moving at 1°/s.

For the targets moving at 6°/s there is a small difference between the first- and second-order conditions for observer JZ (Fig. 8 top right), particularly for the static condition, and a small reduction in the average peak velocity for the other two observers (Fig. 8 right column, middle and bottom).   This difference between the first- and second-order static conditions is significant ($p < 0.001$) for all three observers.   Interestingly, the first-order+ stimulus, which showed a large interaction between first- and second-order motion signals at 1°/s, does not influence the peak velocity much when the speed of the envelope is moving at 6°/s.   The difference between the first-order and first-order+ conditions is not significant for any of the three observers at the 5% level of significance.

3. Steady State
Beyond the transition state the pursuit eye movements are in a closed-loop condition, where the eye velocity and

in the peak velocity.   Determining the peak velocity from the average traces [Figs. 5(a) and 5(b)] gives an indication of the peaks reached on individual trials, but it is a reliable indication of the individual peaks only when the time course of the individual trials is similar.   If the time course of the initiation and transition phases differs from trial to trial, then the peak eye velocity obtained from the average trace may not reflect the peaks found on individual trials.   We determined the peak velocities reached on a trial-by-trial basis.   Even for the 1°/s condition, where the pursuit latency is not well captured, it is still possible to obtain an accurate, reliable, and meaningful estimate of the peak velocity.   The summary of the distribution of the peak eye velocity on an individual trial basis is given for the two target velocities in Fig. 8.

There are small but consistent effects of the stimulus condition on the peak velocity for the targets that moved at 1°/s.   In the standard first-order motion condition all three observers show an overshoot amounting to 25–50% of the target velocity.   For all three subjects the overshoot in the first-order+ condition goes beyond that for the first-order condition.

For the second-order targets there is a reliable reduction in average peak velocity for all three observers compared with that of the first-order condition.   The greatest

Fig. 9.   Steady-state eye velocity for three observers to the five different types of motion stimuli.   All else is as for Fig. 6.

position can be corrected by an error signal. In our experiments it is in the steady-state condition that we found the most pronounced differences among the different stimulus conditions. For the stimuli that had envelopes moving at 1°/s it is quite clear that the eye velocity reaches a steady state at ~1.5 s after stimulus onset. Thereafter the average eye velocity fluctuates near a constant value over the next 1–2 s [Figs. 3(a) and 3(b) and Fig. 5(a)]. We chose the period between 1.5 and 2.5 s for calculation of the steady-state eye velocity.

For the stimulus objects moving at 1°/s the steady-state gain for the first-order target is ~0.9, which is typical for a relatively high-contrast stimulus. There is a significant reduction in the steady-state velocity gain when the observers are pursuing the static, dynamic, or theta targets and a significant increase in gain when subjects view the first-order+ target (Fig. 9, left column).

The steady-state velocity gain in response to second-order targets is between 20 and 50% of the first-order gain, whereas the initiation and transition phases showed only relatively minor effects on latency and peak velocity. One possible explanation would be that expectation and memory effects contribute to these phases. Therefore we inserted two further control conditions in the slow trials. These were conventional first-order stimuli that moved at 2° or 3°/s. If there is an effect of expectation or memory on initiation and transition, then it should affect the relatively few 2°/s and 3°/s targets. In other words, we needed to discover whether having most of the trials at 1°/s would tend to make the initial pursuit velocity less than the target velocity for the unexpected 2° or 3°/s targets—a reduction in gain due to expectation.[15,36] We found no indication of reduced peak velocity or steady-state gain for these conditions.

When the stimulus objects moved at 6°/s there was a reduction in gain for all conditions (Fig. 9) that was highly significant for all conditions except the Fourier+ stimulus condition for twq of the three observers (JZ and NH). There were some individual differences in the magnitude of the effects, but the trends in the results were consistent across observers. The relative reductions in gain, however, are considerably smaller than for the 1°/s stimulus condition 50–95% of the first-order gain. It is particularly interesting to note that there is a small reduction in gain for the Fourier+ condition, which contrasts with the increase in gain shown by all three observers for the 1°/s stimulus condition.

For the targets moving at 6°/s there is no period when subjects showed a constant velocity for all the conditions. There was a significant amount of anticipatory slowing in all cases, as can be seen in the decline of the average velocity responses in Fig. 5(b) before the stimulus stops at the edge of the screen. For one observer (MH) we ran an additional set of experiments with longer ramps to get a better estimate of the steady-state period for the targets moving at 6°/s (data not shown). In these experiments the fixation point was repositioned after 1 s to the left or right to within 2.6° of the edge of the display. The target appeared always eccentric to the new fixation point and moved toward the fixation and the center of the screen. With 14° ramps the observer reached higher steady-state velocities before anticipatory slowing as the target approached the edge of the screen. Although there may be concerns that eccentric fixation would affect the pursuit eye movements, comparison of the results for the initiation and the transition phase of the eye movement response with central fixation and with eccentric fixation did not show any differences. In the steady-state condition there was a small improvement in the gain for all conditions in the experiment with the longer target ramps, suggesting that the anticipatory slowing does have an effect on the absolute level of gain. However, the differences across conditions remained almost identical for the two excursion lengths. These experiments indicate that there is a small but often significant difference in the steady-state response across stimulus conditions. The fact that the differences are so small can be seen as quite remarkable because the observer is capable of using the second-order motion information over and above the first-order motion information to drive pursuit. However, there is a rather conspicuous difference in the dynamics of the responses to first- and second-order targets. In particular, during the steady-state phase there is a systematic slowing for the second-order stimulus condition that is not seen in the eye velocity responses to first-order targets.

Another possible explanation for the relatively poor performance for second-order targets could be a reduction of the effective contrast. We devised a second series of experiments to explore this possibility.

D. Effect of Contrast

Contrast provides a control for first-order artifacts in the second-order stimulus. If it is the case that responses are due solely to a first-order motion artifact, then we should expect to see a large difference in the responses to high- and low-contrast conditions for the second-order motion targets. In particular, the response to the high-contrast second-order stimulus condition should resemble the response to the low-contrast first-order stimulus condition. We used a range of contrasts from just above threshold to 75% contrast. For the first-order 1°/s condition this corresponded to a 1.5-log-unit range of contrasts, while the range was 1.2 log units for the other stimulus conditions.

For the 1°/s condition there is a significant reduction in gain for the second-order condition that is independent of contrast. The mean average eye velocity gain for the 1°/s first-order targets rises from just below 0.8 for observer MH and 0.7 for observer BS at the lowest contrast, where the target and motion are just detectable, to ~0.9 at 4% contrast and then remains constant across remaining contrasts [Figs. 10(b) and 10(c), solid squares]. The gain for the second-order static targets remains at ~0.25 for observer MH and 0.4 for observer BS across all contrasts [Fig. 10(b), open squares]. It seems as if there is little or no first-order artifact in our second-order stimulus. The responses to the lowest-contrast first-order target do not resemble any of the responses to the second-order static target at any of the contrast levels.

For stimuli that moved at 6°/s we used the long excursion condition for both the first-order and the second-order motion targets. In the steady-state response for

the 6°/s condition [Fig. 10(a)] it is apparent that there is a lower gain for all the second-order targets, while the gain approaches unity across all contrasts for the first-order condition. There is no significant difference between contrasts for either the first-order or the second-order conditions when compared within condition.

4. DISCUSSION

Compared with first-order motion stimuli, slow-moving second-order motion targets (1°/s object motion) elicit weak pursuit eye movements. Most of the foveation of second-order targets moving with 1°/s object motion is due to saccades [see e.g., Fig. 4(a)]. For static- and dynamic-noise texture elements, the steady-state pursuit gain was, on average, 0.28 and 0.46, respectively, compared with 0.95 for the first-order motion object (Fig. 9). Theta motion, where the first-order component moved in the direction opposite to that of the object motion, results in the lowest average gain, 0.23. However, the theta-motion condition does not show a steady-state eye move-

Fig. 10. Steady-state eye velocity as a function of contrast for first-order and second-order static targets. (a) Observer MH, stimuli moving at 6°/s; (b) observer MH, stimuli moving at 1°/s; (c) observer BS, stimuli moving at 1°/s. Solid squares, first-order motion target; open squares, second-order motion targets.

ment in the direction opposite to that of the object motion as would be expected from a pure first-order motion detector. In the first-order+ condition, where the object is defined by texture motion at 2°/s, there is a significant interaction between the first- and second-order motion signals. The eye velocity gain with respect to the object motion is 1.37 across the subjects, which is both greater than the object motion alone (1°/s) and less than the pure first-order motion signal (2°/s). In this condition the traces often show segments with smooth pursuit where the velocity is higher than the object velocity, and these segments are interrupted by "negative" saccades, which are saccades in the direction opposite to that of the object motion. The eye is ahead of the object owing to the faster pursuit linked to the texture, and it makes a correction, much like a catch-up saccade in the normal pursuit–saccade sequence seen in foveation of first-order motion targets. The segmentation of the eye movement response into pursuit and saccades can be very informative about the nature of interactions between the pursuit and saccadic systems[44] and deserves a more thorough investigation in our experimental conditions.

The results for moderate-velocity targets (6°/s) are different, at least in magnitude. The steady-state gain of the object motion was much closer to that obtained for the comparable first-order motion target (Fig. 9, right column). The average gain for the static, dynamic, and theta conditions was 0.71, 0.85, and 0.77, respectively, across the three observers compared with a value of 0.99 for the first-order motion target.

A. Comparison with Other Studies
Butzer et al.[26] investigated pursuit to targets moving at 4 and 9°/s. Under both of these conditions the gain of pursuit was close to 1 for both first- and second-order stimuli during the steady-state phase. Pursuit after an initial saccade was impoverished for second-order targets especially at 9°/s. A later study on pursuit initiation[27] reported that the gain during initiation to second-order stimuli was reduced. Our results show that at 6°/s, a velocity in between the two velocities used by Butzer et al.,[26] acceleration is mildly compromised (Fig. 6) and the latency is longer for second-order object motion (Fig. 7). Inspection of the average traces for the theta motion condition show that the initial pursuit is an acceleration component in the direction of the first-order motion, opposite to that of the second-order motion; therefore two competing responses are interacting, which may account for the lower acceleration seen for theta motion.

Harris and Smith[28] showed that second-order stimuli do not elicit optokinetic nystagmus (OKN). However, as pointed out by Butzer et al.,[26] there are at least three important differences between OKN and pursuit: For OKN there are different neural subsystems, different stimulus quality, and no foveal viewing. Even though the range of speeds for the OKN stimuli used by Harris and Smith[28] was between 3° and 20°/s, which spans our moderate-speed condition, the other differences between pursuit and OKN must play the critical role in producing a moderate gain for pursuit and almost zero gain for OKN.

Our results for slowly moving stimuli agree with psychophysical results by Seiffert and Cavanagh,[45] who found that positional displacement was the main cue for determining the speed of slowly moving second-order stimuli. For first-order motion there is good evidence for velocity-tuned detectors.[46]

B. Motion at 6°/s

Experiments comparing the initiation of pursuit with and without stationary textured backgrounds have shown that there can be a delay in the initiation phase of pursuit for first-order motion in a step-ramp paradigm[47] in the presence of a textured background, even when the background is not directly in the motion path of the dot. So there is accumulating evidence that even the initiation phase of pursuit can be modulated under a variety of stimulus conditions (Fig. 6). In our theta condition it is not until 50–100 ms after the initial first-order response that the second-order motion dominates the pursuit eye movement. Thus it might be the case that initiation to second-order motion is slowed by the first-order motion component. This seems to be the case in our experiments.

During the steady-state phase of pursuit there was a small but consistent reduction in gain for the 6°/s pure second-order targets compared with a gain of almost 1 for the first-order condition. Also, the theta-motion stimulus shows a clear domination of the smooth pursuit by second-order motion, and it is not maintained by a succession of saccades as would be expected if the first-order signal dominated and the foveation of the object was maintained solely by saccades. The dominance of the second-order motion is consistent with the findings of Butzer et al.[26] even though the exact level of gain is lower under our stimulus conditions. The first-order+ condition that had a 12°/s carrier inside a 6°/s window did show a gain of almost 1 for the second-order object motion. Yee et al.[48] reported that pursuit gain for a small spot was greater than 1 when an optokinetic surround moved at a greater velocity than but in the same direction as the target. In this case negative saccades were used by the observers to keep the pursued target foveated. In our 6°/s first-order+ condition we did not observe a gain higher than 1 or negative saccades. Collewijn and Tamminga[49,50] reported that a stationary textured background produced a small reduction in the smooth-pursuit gain for small foveal targets. With voluntary selection of a moving field on a stationary background the reduction in gain by the background is eliminated.[51] We find a similar result for all our second-order conditions for targets moving at 6°/s (Fig. 9). However, in Collewijn and Tamminga's experiments, smooth-pursuit gain to an imaginary centroid of two vertical line segments 5° eccentric from fixation in triangular motion at 6°/s over a stationary textured background was reduced by a much larger amount than for foveal targets, from approximately 0.9 to 0.6. Collewijn and Tamminga[50] argue that the difference between the two conditions is due to a dominance of the foveal retinal representation of the stationary background. This is closest to our second-order static condition, which does show the largest gain reduction in both peak eye velocity (Fig. 8) and steady-state eye velocity (Fig. 9).

The effects of contrast can be highly instructive. If there is a similarity in the form of response as a function of contrast for two stimulus types, it is consistent with a single underlying process. The observations that for 6°/s targets both first- and second-order motion show very similar dependencies on contrast (Fig. 10) indicates that a similar process may underlie the generation of the motion signal that is driving pursuit. How the signals from these two motion stimuli combine and interact is not clear. Simple explanations for the results of the 6°/s stimulus such as motion averaging between first- and second-order motion signals with equal weighting are ruled out by the results of Butzer et al.[26] and our own study. Other rules that allow for unequal weighting of first- and second-order signals could account for the results, but the weights for the theta-motion condition or the first-order+ condition would need to be quite different. An alternative explanation whereby the first-order motion provides motion energy that increases the gain of the second-order system irrespective of the speed does not seem to fit the data, because in this case we would expect to see the first-order+ and theta-motion conditions result in the same gain, and they do not. Further experiments are needed for us to understand how the signals generated by these motion stimuli combine.

C. Motion at 1°/s

Kowler et al.[52] found that a static background did not impair the smooth pursuit of small slow-moving bright dots and that a slow-moving dot-field did not impair fixation. Performance in either condition was dependent on instructions to the observer. Collewijn and Tamminga[49] found a modest reduction in smooth-pursuit gain of a foveal spot on a structured background, and, in a later study, Collewijn and Tamminga[50] found a more pronounced effect if the pursuit target was defined by peripheral stimulus elements. In our experiments the observers were instructed to follow the window, and the window was defined by the second-order motion characteristics that are in foveal vision. The initiation phase and the steady-state phase of pursuit were both clearly compromised for the second-order targets. Although there was an initial response, as seen in the average traces (Fig. 5), the average acceleration was poor and the peak speed seldom overshot the stimulus speed, which is characteristic of the response to first-order motion. So as far as we are able to measure it, the initial open-loop phase of the response to slow-moving second-order motion is more compromised than for the faster-moving objects. During the steady-state the gain is low compared with that seen for first-order motion, and it does not improve with contrast (Fig. 10). The first-order+ condition results in a significantly higher gain than the first-order condition even though the observers have been instructed to concentrate on and follow the motion of the object. This suggests that the first-order motion dominates in the 1°/s condition and cannot be overcome by instructions. One simple explanation is that there is only a very weak second-order motion signal generated by slow-moving second-order targets that is available to pursuit.

The static texture condition shows a lower gain than the dynamic texture condition for all three observers [Fig.

8(a)].   The static condition might include a fixation signal that is acting to reduce the gain of the second-order motion signal, whereas in the dynamic texture condition this potential fixation cue is not present, and consequently the gain is higher.   The low gain of pursuit is compensated by frequent catch-up saccades [Fig. 4(a)].   This compensation for low pursuit gain by saccades was also reported by Collewijn and Tamminga[49] for pursuit of a dot on a textured background, and together their composite pursuit–saccade gain is approximately 1, as it is in our experiments.

D.   Relationship to Perception

There is accumulating evidence that motion defined in a number of ways; i.e., by luminance, second- or higher-order correlations, color, or contrast can lead to similar neural signals and consequent perceptual judgments. This phenomenon has been termed form–cue invariance by Albright.[53]   Psychophysically, this type of form–cue-invariant perception seems to hold only for moderate to high velocities of motion.[54]   Similarly, for pursuit eye movements at velocities of 4°/s or greater, second-order targets approximate their first-order counterparts in generating smooth pursuit.   For the perception of second-order motion targets we found that the perceived velocity of fast-moving targets was only mildly dependent on contrast, because first- and second-order motion targets took the same form.[54]   The same trend is found for pursuit, which suggests that a common motion mechanism is handling the perceptual and pursuit performance of both first- and second-order motion stimuli.[55]   Perceptually the contrast dependency of slow-moving first- and second-order motion targets is different.   The perceived speed of second-order motion is strongly dependent on contrast,[54,56] and this dependency is much greater than that seen for first-order motion stimuli.[57,58]   In the case of slow-moving second-order stimuli there seems to be a dissociation between perception and pursuit performance: At all contrasts, smooth pursuit of slow-moving targets is compromised, the gain is low, and there is no improvement with increasing contrast.   One conclusion from these results is that the neural pathway involved in making perceptual judgments of the low speed of second-order motion stimuli does not provide a visual signal for driving pursuit eye movements.

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