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Initiation of smooth-pursuit eye movements by real and illusory contours

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Abstract

It is well established that elementary motion detectors are only able to code for the movement of a contour perpendicular to its orientation. This shortcoming explains why the initial direction of smooth-pursuit eye movements is directed orthogonal to the orientation of a moving contour independent of its veridical direction of motion. Here, we replicated this finding and asked whether this directional error can be reduced by subjects' prediction of upcoming target moving direction and whether this directional error also occurs during tracking of an illusory contour. Our results show that prediction did not abolish the directional error, it was only slightly reduced. On the other hand, the directional error was considerably diminished during pursuit initiation towards illusory contours and most likely reflected the amount of real stimulation defining the specific illusory contour. We conclude that pursuit initiation is driven by raw retinal image motion signals, which are not yet processed for figure completion.

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1. Introduction

Smooth-pursuit eye movements (SPEM) act to stabilise the image of a moving target on the retina (for a review see [Krauzlis, 2004](#)). This definition implies that these voluntarily directed eye movements crucially depend on the presence of retinal image motion. However, the results of numerous experiments suggest that this is not a strict rule. Opening the feed-back loop of the pursuit control system by retinal stabilisation (e.g. monkey: [Morris & Lisberger, 1987](#)) or transient blanking (human: [Masson & Stone, 2002](#)) of the moving target does not severely disrupt SPEM. Human subjects can use auditory ([Hashiba, Matsuoka, Baba, & Watanabe, 1996](#)), somatosensory ([Hashiba et al., 1996](#)) and efference copy ([Steinbach, 1969](#)) signals to perform SPEM, although pursuit gain is clearly reduced and saccade frequency is increased compared to pursuit

of a visual target ([Berryhill, Chiu, & Hughes, 2006](#); [Hashiba et al., 1996](#)). Moreover, humans ([Barnes, Schmid, & Jarrett, 2002](#); [Kowler & Steinman, 1979](#)) and monkeys ([Badler & Heinen, 2006](#); [Ilg, 2003](#)) are able to generate anticipatory SPEM in the expectation of a moving target. Surprisingly, only marginal differences in the ability to perform anticipatory pursuit exist between man and monkey ([Freyberg & Ilg, 2007](#)). With respect to prediction or anticipation, two different aspects have to be dissociated. First, although the onset of motion might be predictive, this does not provide information to generate the eye movement response. The target trajectory remains unsettled. Of course subjects can predict in this condition, but the correctness of their prediction is at chance level. Only if knowledge about the direction and speed of the appearing target is available, correct anticipatory movements are possible. Finally, it has been shown that SPEM can be directed towards an imaginary target (monkey: [Ilg & Thier, 1999](#) and human: [Mack, Fendrich, & Wong, 1982](#); [Steinbach, 1976](#); [Wyatt, Pola, Fortune, & Posner, 1994](#)). Taken

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together, these findings suggest that subjects pursue a perceptual rather than a retinal stimulus.

1.1. Need for speed during pursuit initiation

If a target starts to move suddenly, pursuit initiation has to be as fast as possible, since the retinal position error increases steadily with time. Initial eye acceleration, taken as a measure for the strength of pursuit initiation, increases with target speed and is adjusted to the target's moving direction when a single target is tracked (human: Tychsen & Lisberger, 1986 and monkey: Lisberger & Westbrook, 1985). When two targets—one pursuit target and one distractor—are being presented, the initiation of pre-saccadic SPEM, unlike steady-state pursuit, is not adjusted to the target's moving direction, but is well described by a vector average of all local motion signals (Kahlon & Lisberger, 1999; Recanzone & Wurtz, 1999). In contrast, during steady-state pursuit, i.e. after the initial saccade, a winner-takes-all process takes over and eye velocity is matched to the veridical moving direction and speed of one single target (Recanzone & Wurtz, 1999) irrespective of the order of motion. However, in every case, the eyes lag behind the target during pursuit initiation. As we have shown earlier, pursuit initiation is dominated by first-order motion signals (Lindner & Ilg, 2000) defined by local changes in luminance. These signals are also the adequate stimulus for the ocular following response (OFR), which acts to stabilise the retinal image mostly during translational self-movement. This kind of optokinetic response can be elicited in humans at ultra-short latencies (approx. 80 ms Gellman, Carl, & Miles, 1990) by brief unexpected movements of the visual scene and is directed towards the stimulus' moving direction. Latencies of the OFR systematically decrease with stimulus speed. The magnitude of the response depends on the temporal frequency, showing band-pass characteristics with a peak at 16 Hz. When a missing fundamental stimulus (Sheliga, Kodaka, Fitzgibbon, & Miles, 2006) is used to elicit an OFR, the response is directed towards the principal first-order component (3rd harmonic) of the stimulus. Thus, the OFR, like pursuit initiation, is dominated by first-order motion.

When computing global motion signals from local motion signals, the visual system suffers from the aperture problem, i.e. any local motion detector can measure movement of a contour, which extends the detector's field of view, only perpendicular to its orientation (Wallach, 1935; Wuerger, Shapley, & Rubin, 1996). A behavioural correlate of the aperture problem can be observed during the initiation of SPEM: A tracking direction error occurs when a moving contour tilted with respect to its moving direction is presented (Born, Pack, Ponce, & Yi, 2006; Masson & Stone, 2002). This error is gradually reduced over a time period of approx. 300 ms and is absent during steady-state pursuit. With respect to simple bar stimuli, the directional error is a function of stimulus orientation, speed, contrast, length and eccentricity. For example, a

35°-long central white bar on a black background tilted 45° with respect to direction of motion moving at 15°/s may elicit an initial tracking direction error of around 45° (Wallace, Stone, & Masson, 2005). The directional error scales with bar length (Born et al., 2006). The number of motion detectors activated by the 1D motion signal increases with bar length. The 2D motion signal originates from the line endings, which are independent of the length. Therefore, the initial directional error approximates a limit (orthogonal to the bar orientation) with increasing bar length.

Parallel to the temporal development of the initial tracking error, the neuronal response of single-units recorded from the middle temporal area (MT) of rhesus monkeys reveal a very similar development of their directional tuning to tilted moving contours (Pack & Born, 2001). MT is an important area for the generation of pursuit eye movements (for a review see Krauzlis, 2004). The initial response of MT neurons is directed towards the component of motion perpendicular to a contour's orientation. Over a period of approx. 60 ms the responses gradually shift to encode the true direction, regardless of orientation. The initial tracking error as well as the temporal development of MT responses inspired a computational model for motion integration by Bayerl and Neumann (2004). This model is able to solve the aperture problem by an iterative process, i.e. over time, resembling the reciprocal connections between areas V1 and MT in the rhesus monkey (Ungerleider & Desimone, 1986).

1.2. Illusory figures and Gestalt perception

Illusory contours (IC) have drawn increased scientific interest over the last years and are important to the understanding and modelling of the visual system (for a review see Purghé & Coren, 1992; Spillmann & Dresch, 1995). They have also been referred to as subjective contours, phenomenal contours, cognitive contours, anomalous contours, quasiperceptive contours, virtual contours, contours without gradients and apparent contours (Seghier & Vuilleumier, 2006). Two important mechanisms creating ICs are: (i) collinear contour induction (*edge-type*, e.g. Kanizsa-type figures or the stimuli *I1*, *I2* and *I3* in this study, see Fig. 2), (ii) contour induction perpendicular to line-endings (*line-type*, e.g. Ehrenstein-illusions or the stimuli *I4* and *I5* in this study, see Fig. 2). The ratio between real and illusory contour is defined as the support ratio. Obviously, the perception of the illusory contour critically depends on this support ratio (Leshner & Mingolla, 1993). In summary, illusory contours can be perceived in the absence of real physical continuity.

The first single-unit experiments in monkeys investigating the representation of ICs were performed by Peterhans and von der Heydt (1989). They discovered neurons in monkey visual area V2 that increased firing rate when an IC was moved across their receptive fields (RFs). They concluded that V2 neurons can detect illusory, physically

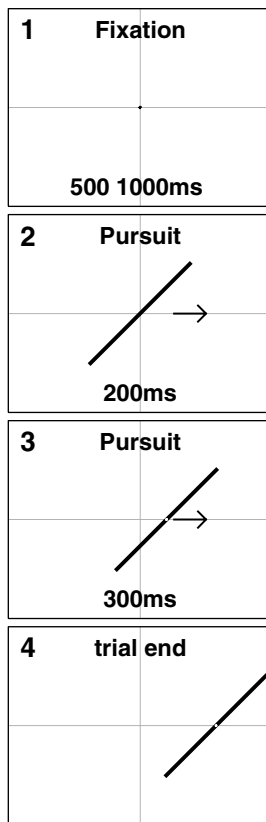


Fig. 1. Sketch of temporal development of our pursuit paradigm. Subjects were instructed to fixate as precisely as possible throughout the entire fixation period which was randomised between 500 and 1000 ms. The pursuit target appeared in the centre of the screen and moved at either $12^\circ/s$ (horizontal) or $16^\circ/s$ (diagonal). A red (here white) dot appeared in the centre of the pursuit target 200 ms after target motion onset. After 500 ms, the target disappeared and the end of trial was reached.

icant response of V1 neurons was reported (Lee and Nguyen, 2001).

1.3. Motivation of the present study

We asked whether the directional error during pursuit initiation is affected by subjects' prediction of the moving direction and whether the error is also present during pursuit of illusory contours.

2. Methods

Horizontal and vertical eye movements were obtained from four female and two male human subjects aged 24–27 years. All experiments were performed with the understanding and consent of each subject. All subjects had normal vision and were naïve to the paradigm. Eye positions were recorded using infrared oculography (IRIS Skalar), low-pass filtered (corner frequency 100 Hz), and digitised at a temporal resolution of 1 kHz. Horizontal eye position was recorded from the right eye and vertical eye position was recorded from the left eye. This is different to studies using the search coil technique in which horizontal and vertical movements of a single eye are recorded. Correct calibration of horizontal and vertical eye positions signals was assured by saccade trials towards targets presented 10° to the right/left and 5° up/down from the centre. Saccade latencies in these saccade trials were not significantly different for horizontal (right/left) and vertical (up/down) saccades. Consequently, there is no reason to assume that the binocular recording technique might introduce different latencies for horizontal and vertical eye movements.

2.1. Visual stimulation and experimental paradigm

The subjects faced a $19''$ CRT-screen at a viewing distance of 57 cm, resulting in maximal display area of 36.5° horizontally and 27° vertically. Spatial resolution was 44 pixels/deg in both horizontal and vertical directions corresponding to 1600×1200 pixels total screen resolution. The refresh rate of the display was 104.5 Hz. Each trial started with a randomised fixation period lasting between 500 and 1000 ms, during which a central red dot (diameter 0.17°) had to be fixated (see Fig. 1).

Next, a pursuit target moving in one of either two or six possible directions was shown for 500 ms. Nine different stimuli were tested using real ($R0 + R1$, $R2$, $R3$), illusory ($I1$, $I2$, $I3$, $I4$ and $I5$) or imaginary contours ($I6$)¹. The luminance of the bars and lines was 92 cd/m^2 . Background luminance was below the range of our luminance meter (Minolta) for all stimuli but one. In the $R3$ stimulus, background luminance was 29 cd/m^2 and luminance of the bar was 30 cd/m^2 , resulting in a contrast of 1.7%. The pursuit target was either a real contour ($R0 + R1$, $R2$ and $R3$), *edge-type* illusory contour ($I1$, $I2$ and $I3$), 20° in length and 0.5° in width, or *line-type* illusory contour ($I4$ and $I5$), also 20° in length. The latter were made up of phase shifted abutting line gratings with a spatial frequency of either 4 or 2 cpd. The $I6$ stimulus consisted only of the ends of the real bar. This condition can also be interpreted as pursuit of two para-foveal targets.

Horizontal moving directions were possible with all stimuli. Additionally, four diagonal moving directions deviating 45° from the horizontal axis were possible with $R0 + R1$. The diagonal moving directions are referred to as $R0$ and the horizontal moving directions are referred to as $R1$. In all other stimuli, the target moved exclusively horizontally. We informed our subjects about possible target trajectories before each experimental session. Speed of the horizontally moving targets was 12 and $16^\circ/s$

¹ $R0 + R1$, real contour using six possible moving directions; $R2$, real contour using only left and rightward moving directions; $R3$, same as $R2$ but using contrast of 1.7%; $I1$, illusory contour of the *edge-type* with a support ratio of 97.5%; $I2$ and $I3$, same as $I1$ but support ratios of 95% and 50%; $I4$, illusory contour of the *line-type* with a spatial frequency of 4 cpd; $I5$, same as $I4$ but only 2 cpd; $I6$, ends of the real bar only.

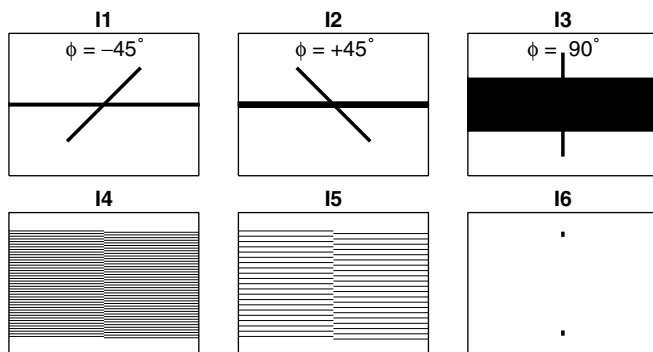


Fig. 2. All illusory stimuli are shown. Each single stimulus is illustrated by a snapshot at target motion onset. The three possible orientations ($\phi = -45^\circ$, $\phi = +45^\circ$, $\phi = 90^\circ$) relative to horizontal moving direction are shown for the *edge-type* stimuli ($I1$, $I2$ & $I3$). In the *line-type* illusory contours ($I4$ & $I5$), the contour was moved by lengthening and shortening of lines forming phase shifted abutting gratings. The $I6$ stimulus used only the ends of the real bar. Positive values of the directional error reflect a deviation of the eye movement towards a direction perpendicular to the contour's orientation (see Supplementary material, Videos 2 and 3). Illustrations are drawn to scale (width: 36.5° height: 27°) and black and white are inverted.

absent contours. Importantly, the authors did not find these responses in neurons recorded from V1. However, with respect to the Kanizsa-type figures, a weak but signif-

for the diagonally moving targets, constrained by the spatio-temporal properties of our video system. In all stimuli, three orientations of the target with respect to the moving direction were possible: $\varphi = 45^\circ$, -45° and 90° . The $\varphi = 90^\circ$ condition is also referred to as the *not-tilted* contour and both 45° conditions are referred to as the *tilted* contours. For all stimuli, a red dot (diameter 0.17°) appeared in the centre of the contour 200 ms after the onset of its motion. Gain of the horizontal and vertical eye movement recordings as well as the crosstalk between both channels were controlled by introducing calibration trials (white dots, diameter 0.17°) at the same positions as the aforementioned calibration targets. This resulted in $18 + 4$ trial types in *RO + RI* and $6 + 4$ trial types in the remaining stimuli. Each condition was presented 25 times in one experimental session lasting approx. 15 min. Each subject participated in at least 16 sessions.

2.2. Data analysis

About 23% of all recorded trials were excluded from the analysis mainly due to artefacts caused by eye blinks. Consequently, approx. 2300 trials recorded from each of six subjects were used for the analysis. The entire data analysis was performed on single trials. Horizontal and vertical eye velocity, acceleration and jerk (expressed as first, second and third derivative in time of eye position) were calculated by differentiation of the eye position data. Eye position profiles were low-pass filtered at 40 Hz, eye velocity profiles at 10 Hz (Butterworth, first order). Absolute eye velocity was computed according to the following formula:

$$V_{\text{abs}} = \text{sqrt}(v_{\text{hor}}^2 + v_{\text{vert}}^2)$$

Absolute eye jerk was computed from horizontal and vertical jerk in the same way. The applied saccade detector was optimised in order to detect the initial saccades during pursuit initiation characterised by rather small amplitudes ($1\text{--}2^\circ$). In detail, saccade onset was detected when the absolute eye jerk exceeded $80,000^\circ/\text{s}^3$. The maximal saccade duration was set to 65 ms. From this moment in time, saccade offset was determined backwards in time as the absolute eye jerk reached $35,000^\circ/\text{s}^3$. The figure in our [Supplementary material](#) shows the main sequence obtained during a single experimental session. Saccades were removed from the velocity profile including a safety period of an additional 20 ms before and 10 ms after the detected saccade interval. The velocity profile was linearly interpolated during this time segment.

2.3. Pursuit onset latency and initial acceleration

Pursuit onset was detected in the absolute velocity profile of each single trial using a sliding window technique (length of window: 100 ms). As soon as the standard deviation of the absolute velocity within this window reached $1.5 / \text{s}^2$, a linear regression of eye velocity for 50 ms was calculated. The slope of this regression was taken as initial eye acceleration. Pursuit onset latency was obtained from the intersection point of the regression line with the baseline. Earliest eye motion onset was set to 80 ms since shorter latencies could not be expected for pursuit of small targets moving slowly ($12\text{--}16^\circ/\text{s}$).

2.4. Initial saccade latency

The first saccade detected following target motion onset was labelled as initial saccade, and its latency with respect to target motion onset was determined.

2.5. Steady-state gain

The steady-state gain, i.e. de-saccaded eye velocity divided by target speed during maintained pursuit, is an indicator for pursuit quality and was determined during a time interval between the offset of the initial saccade and the end of measurement.

2.6. Directional tracking error

Horizontal and vertical velocity profiles of single trials were used to determine the direction of eye movement across 10 ms time bins. Subsequently, the temporal development of circular mean and median direction, circular variance and probability of uniformity was determined across all trials of a given condition and subject (see Fisher, 1995 for further details). The circular mean represents the vector sum of unit vectors each representing a single trial. The vector's direction is the circular mean. The circular variance is expressed as one minus the vector's length divided by the number of trials. Therefore, the circular variance spans a range between zero and one. A circular variance of zero means that the eye movements in all trials were in the same direction; a circular variance of one indicates that there was not a single bias in eye movement direction. According to Fisher (1995), the circular variance should be smaller than 0.18 in order to signal a robust direction.

In order to obtain the peak direction error expressed as the direction maximally deviating from target moving direction, (i) the probability of uniform distribution had to be smaller than 1%, (ii) a reasonable threshold had to be fulfilled for saccadic intrusion ($<5\%$), (iii) mean absolute eye velocity had to be $>2^\circ/\text{s}$ and (iv) the deviation between circular mean and circular median had to be $<5^\circ$. The peak direction errors usually occurred during the 1st or 2nd 10 ms time bin after pursuit onset. A positive directional error indicated eye movement towards the direction perpendicular to the contour.³

2.7. Statistics

To compare mean pursuit onset latency, initial acceleration, saccade latency and steady state gain, we used three-factorial ANOVAs and post-hoc Scheffé tests (matlab functions: `anovan` and `multcompare`). The three factors were type of stimulus, subject, and contour orientation. Statistical testing of directional data was performed either for the comparisons of circular means against a specified direction or for the comparisons of two circular means (Fisher, 1995).

3. Results

We report here the influence of real and illusory contours on smooth-pursuit eye movements. First, the classic pursuit parameters such as pursuit onset latency, initial acceleration, saccade latency, and steady-state gain are presented. Second, special emphasis is placed on the direction of eye movements during pursuit initiation.

3.1. Pursuit onset latency

Mean pursuit onset latencies for each stimulus and all orientations (φ) ranged from 105 to 167 ms as shown in [Fig. 3](#). Since we did not observe directional asymmetries, we pooled leftward and rightward target movements. Although the data revealed a high inter-subject variability, a general tendency towards longer latencies for ICs was present. A three-factorial ANOVA with the factors orientation, subject and stimulus revealed significant main effects and interactions ($p < 0.001$) on pursuit onset latency. The *R3* stimulus yielded the highest pursuit latencies (167 ms), verifying the dependency of pursuit latency on stimulus contrast. More importantly, the breakdown in orientations (*dark grey or red*: $\varphi = -45^\circ$, *grey or green*: $\varphi = 90^\circ$,

² This value was determined empirically (basically three standard deviations; for robustness, we did not apply an adaptive threshold).

³ See [Supplementary material](#), Video 1.

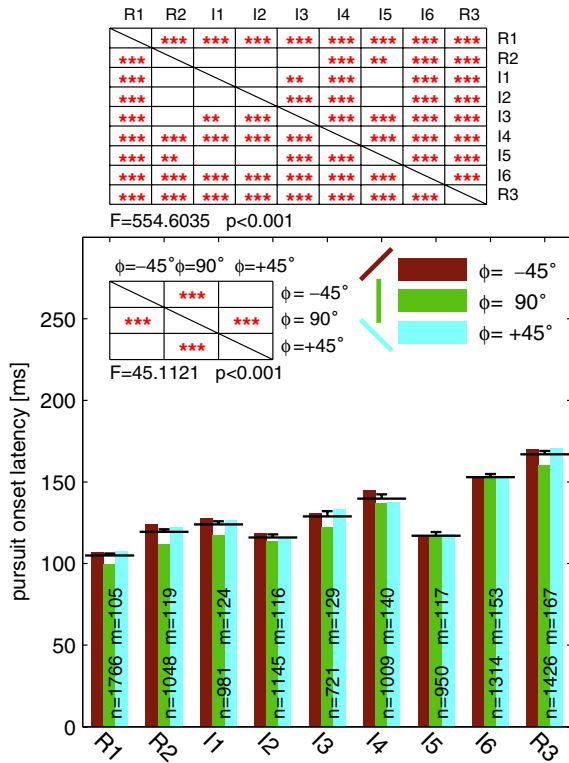


Fig. 3. Pursuit onset latencies: means for the three relative orientations ϕ as specified together with the total mean (m) and 95% confidence interval (black horizontal lines and error bars) for each stimulus are shown. The number of trials (n) and total mean (m) are also given in numbers for each stimulus. A statistical analysis of the pursuit onset latencies was performed by three-factorial ANOVA with the factors orientation, subject, and stimulus. The influence of each factor was significant ($p < 0.001$). The resulting post-hoc Scheffé tables are shown for the factors orientation and stimulus. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

light grey or blue: $\phi = +45^\circ$), revealed longer latencies for tilted ($\phi = -45^\circ$, $\phi = +45^\circ$) than for not-tilted contours ($\phi = 90^\circ$), as documented by the result of the orientation post-hoc table. This effect was more pronounced for the RCs as compared to ICs.

3.2. Initial eye acceleration

Mean pre-saccadic eye acceleration during pursuit initiation for each stimulus and all orientations scattered between 86 and $101^\circ/s^2$ as shown in Fig. 4. Acceleration values were quite similar across the entire range of stimuli used. A three-factorial ANOVA (orientation, subject, and stimulus) revealed significant main effects of all three factors ($p < 0.001$). The lowest acceleration value ($86^\circ/s^2$) was found in the I6 stimulus and the highest value ($101^\circ/s^2$) in R1. The significant main effect of orientation was most likely caused by the results obtained with the R1 stimulus. Note that the post-hoc test revealed only a significant difference between the $\phi = -45^\circ$ and $\phi = 90^\circ$ condition ($p < 0.05$). Overall, orientation had only a minor influence on initial eye acceleration.

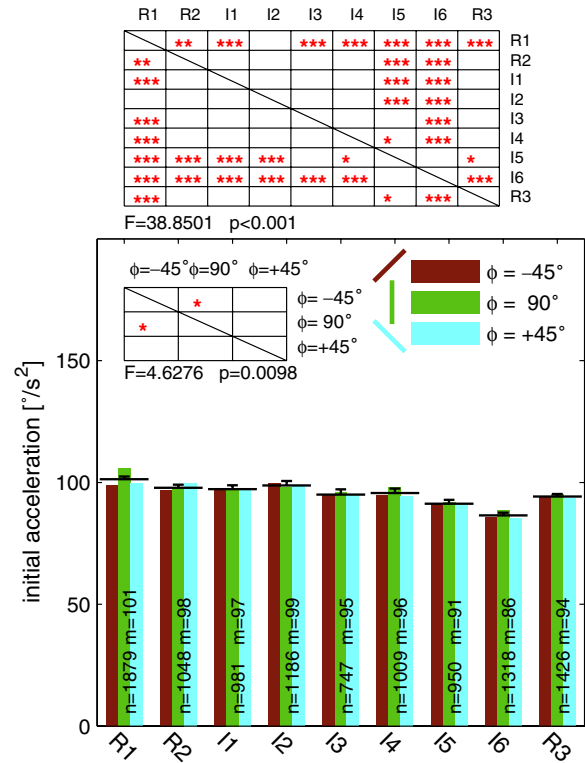


Fig. 4. Initial eye acceleration: Labelling and statistical analysis as explained in Fig. 3.

3.3. Initial saccade latency

Mean initial saccade latencies for each stimulus and all orientations varied between 204 and 298 ms as shown in Fig. 5. Since typical initiation of pursuit consists in pre-saccadic acceleration followed by the initial saccade, these latencies were much higher compared to pursuit onset latencies. High inter-subject variability and a general tendency towards longer latencies for ICs were evident, similar to the pursuit onset latencies. The variability between the stimuli was much higher compared to pursuit onset latencies, i.e. initial saccade latency of every stimulus was significantly different from almost any other. A three-factorial ANOVA (orientation, subject, and stimulus) revealed significant main effects and interactions ($p < 0.001$). The high latency values in R3 (274 ms) verified the dependency of saccade latency on stimulus contrast. The breakdown in orientations revealed longer latencies for tilted contours, which was true for the entire range of stimuli used, similar as for pursuit onset latencies.

3.4. Steady-state gain

Mean steady-state gain for each stimulus and all orientations was close to unity as shown in Fig. 6. There was a significant main effect (three-factorial ANOVA) of the factors stimulus ($p < 0.001$) and subject ($p < 0.001$) but no effect of orientation ($p = 0.24$). In addition, the interactions between orientation and the other factors were not

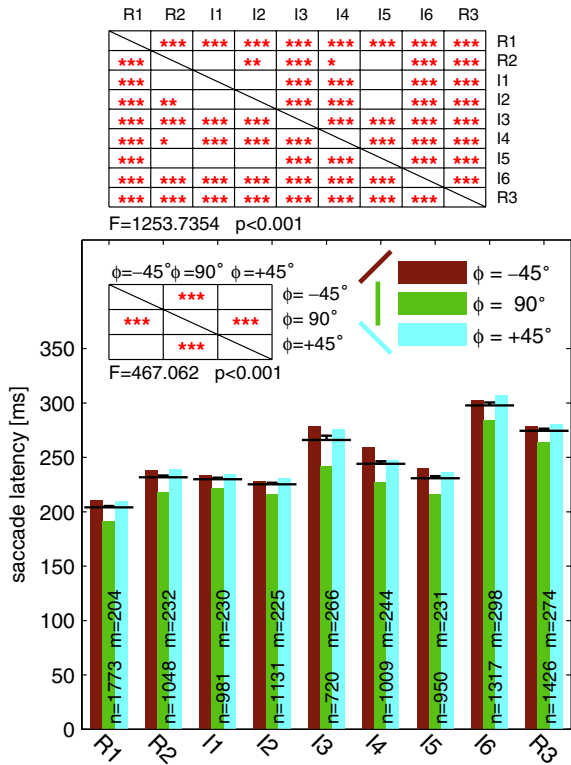


Fig. 5. Initial saccade latency: Labelling and statistical analysis as explained in Fig. 3.

significant. The only significant interaction was between the factors subject and stimulus ($p < 0.001$). Although the quality of pursuit varied considerably across the whole range of stimuli, mean steady-state gain only spanned from 0.84 to 0.99, suggesting that the stimuli afforded an equal effort to pursue, since they contained a central red dot which was presented 200 ms after target motion onset.

The main finding concerning the classic pursuit parameters is thus that *tilted* contours evoked longer initial pursuit and saccade latencies compared to *not-tilted* contours independent of stimulus type. In addition, there is a tendency for ICs to elicit longer saccade and pursuit latencies compared to RCs.

3.5. Pursuit initiation towards real contours

We try to provide the necessary information to determine the directional error during pursuit initiation. Therefore, we present the mean horizontal (Fig. 7a) and vertical (Fig. 7b) de-saccaded eye velocity profiles of a typical subject (H.B.) during pursuit of a RC (R1) moving to the left. The same colour or grey scale code for orientations as in Figs. 3–6 is used. Most of the response characteristics shown in Figs. 3–6 are also evident in the eye velocity profiles of this subject.

Pursuit onset latency for the *not-tilted* contour was clearly shorter as for the *tilted* bar stimuli (compare Fig. 3). Similarly, initial saccade latency in the *not-tilted* condition was clearly shorter as for the *tilted* contour as

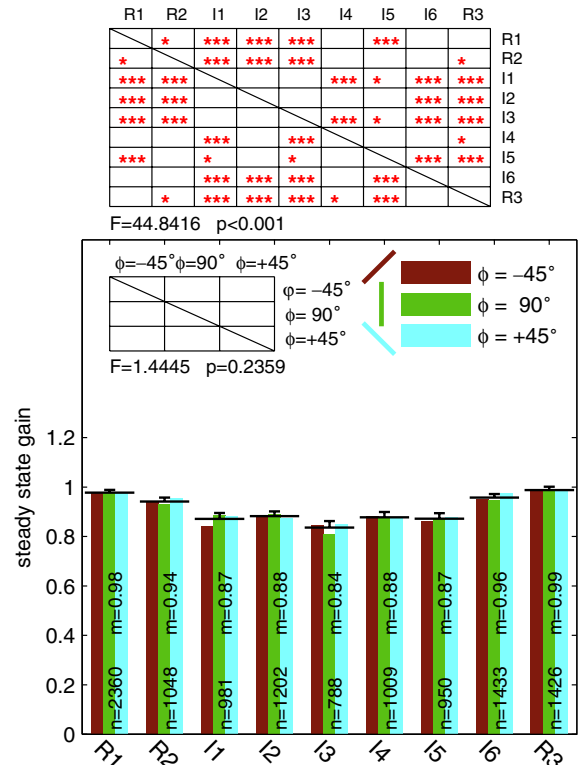


Fig. 6. Steady-state gain: Labelling and statistical analysis as explained in Fig. 3.

shown by the histograms of saccade frequency (compare Fig. 5). Approx. 400 ms after target motion onset, the likelihood of secondary catch-up saccades was increased. During steady-state pursuit expressed after initial saccade offset, the target was being tracked precisely, though noticeable oscillation around target velocity occurred (*dark grey or red and light grey or blue traces* in Fig. 7a). Although the stimulus moved exclusively horizontally, a build-up of vertical velocity could be detected for the *tilted* contours during the initiation of pursuit, well before onset of the initial saccade. A clockwise tilted contour (-45°) elicited an upward eye movement resulting in a peak directional error of 20.8° . A counter-clockwise tilted contour (45°) elicited a downward eye movement resulting in an error of 35.3° . Note that the initial directional error was corrected approx. 350 ms after target motion onset, as indicated by the inversion of the vertical eye velocity.

3.6. Pursuit initiation towards illusory contours

To allow a direct comparison of pursuit initiation elicited by real and illusory contours, we present eye velocity profiles elicited by ICs (I2) in Fig. 8 exactly as shown for RCs in Fig. 7 for the same typical subject H.B. for leftward target movements. While Fig. 7 shows a pronounced difference in the horizontal velocity profiles elicited by the three different stimulus orientations, the horizontal velocity profiles elicited by the three different orientations of the IC are

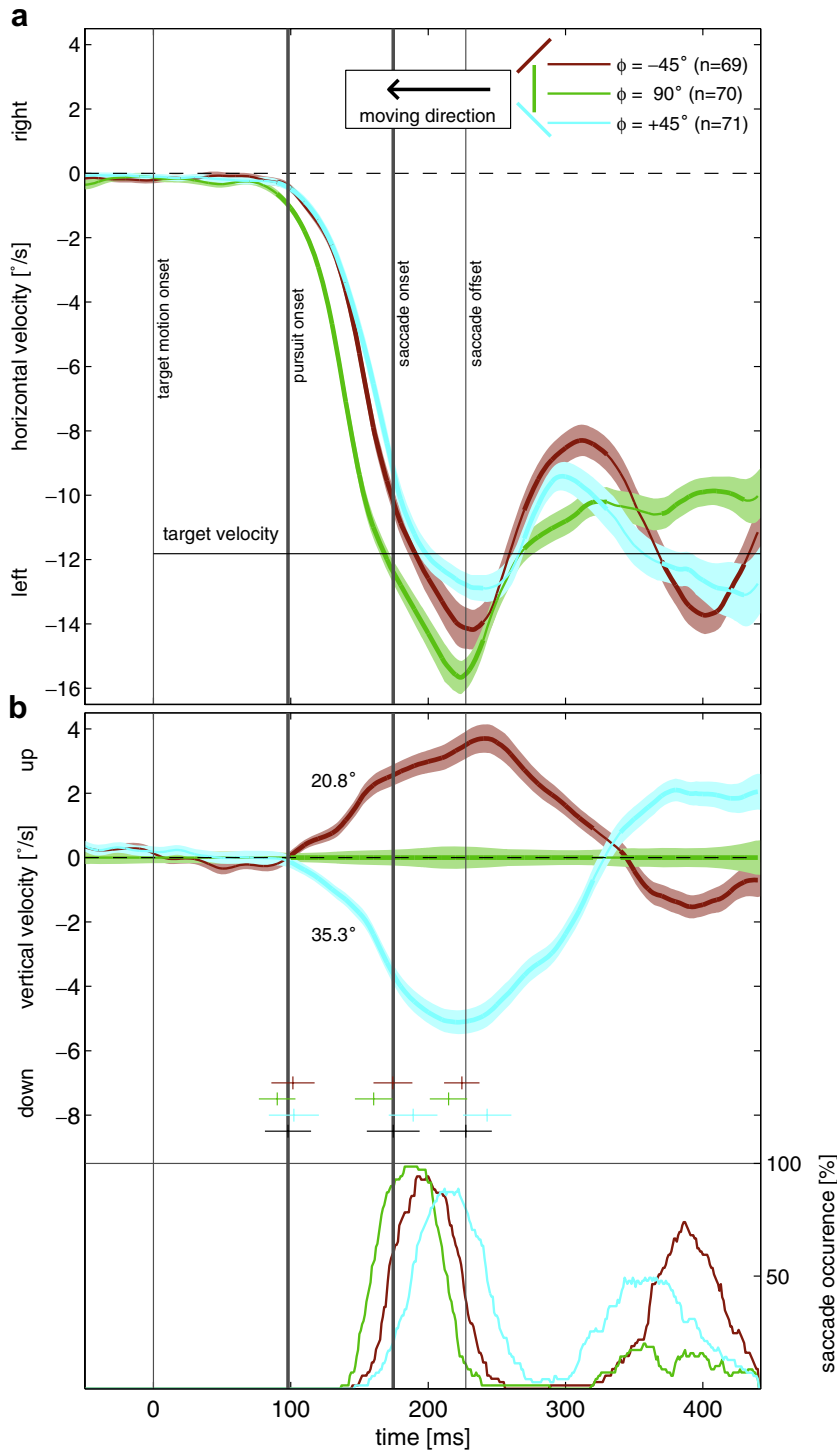


Fig. 7. De-saccaded velocity profiles during pursuit of real contours: (a) Comparison of mean horizontal velocity profiles of a typical subject (H.B.) during pursuit of differently oriented real contours (R1). Each profile is enveloped by the standard error of its mean. Bold line width indicates that at least two profiles at this moment in time are significantly different (ANOVA, $\alpha = 0.05$). The number of single trials for each profile (n) is given in the legend. Colour code for the orientations: red or dark grey: $\phi = -45^\circ$, green or grey: $\phi = 90^\circ$, blue or light grey: $\phi = +45^\circ$. Target moving direction was to the left (black arrow). Bold vertical lines indicate pursuit onset and saccade onset. Thin vertical lines show target motion onset and saccade offset. The thin horizontal line depicts target velocity (12°/s). (b) Comparison of the mean vertical velocity profiles. The peak directional errors elicited by the *tilted* contours profiles are given by the numbers next to each profile. The error bars next to the vertical lines represent the standard deviation of combined (black) and individual orientations (coloured) of the corresponding property. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

quite similar. In addition, the secondary catch-up saccades executed towards the RC seem to be absent during pursuit

of ICs. Finally, the vertical eye velocity remains close to zero for the entire displayed time period. Consequently,

the peak directional errors (-4.0° and 10°) are greatly diminished or disappeared.

3.7. Comparison of directional errors elicited by all stimuli

In order to compare the directional error resulting from all stimuli used in our study, we present these errors in

Fig. 9. Since there is no pronounced difference in the directional errors of both *tilted* orientations ($\varphi = -45^\circ$ and $\varphi = +45^\circ$), we pooled our data for both orientations. Therefore, the means given in Fig. 9 represent grand averages combining all subjects, orientations and moving directions, and the standard error bars reflect the variance caused by subjects, orientations and moving directions.

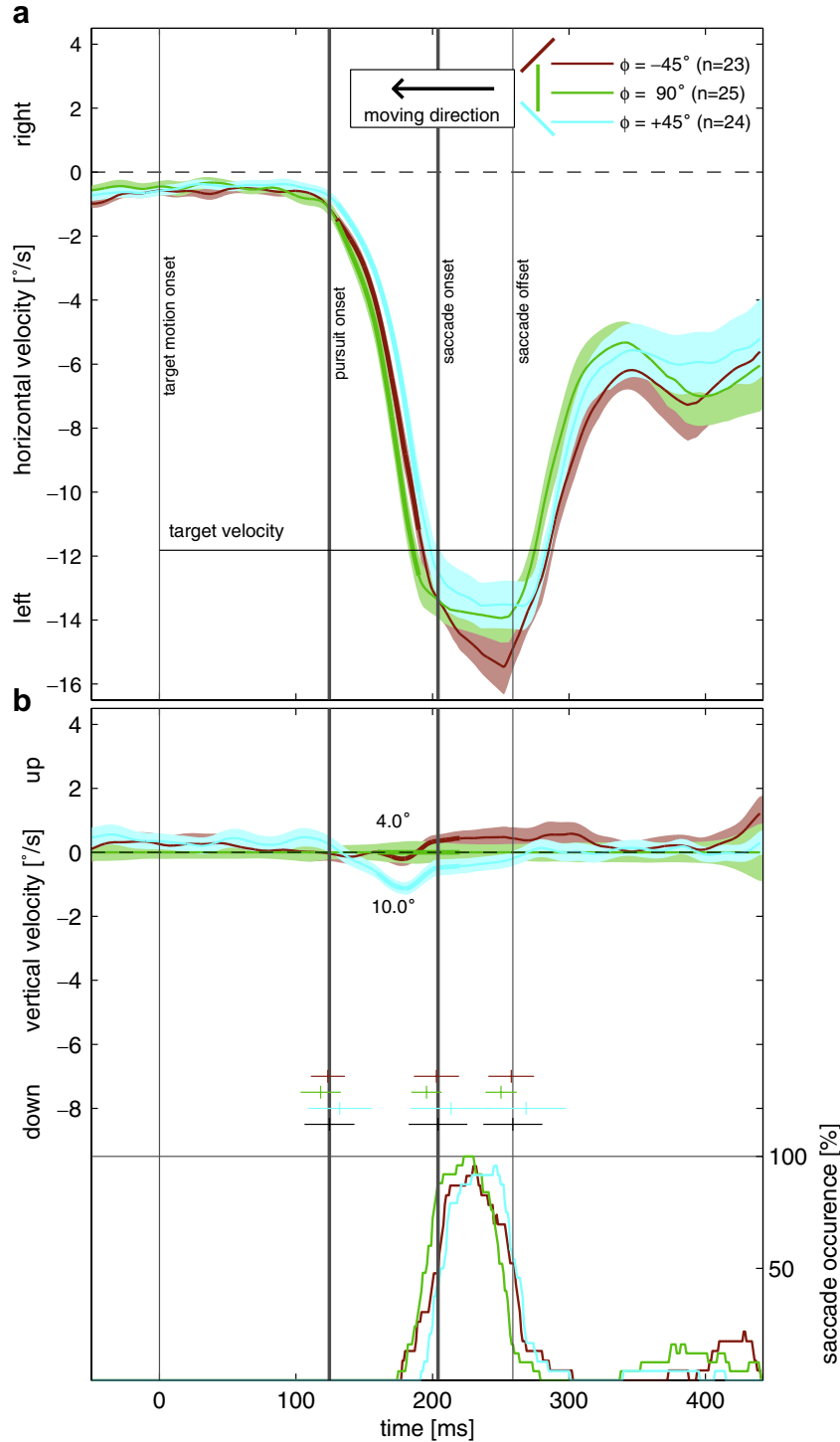


Fig. 8. De-saccaded velocity profiles during pursuit of an illusory contour: (a) Comparison of mean horizontal velocity profiles of one subject during pursuit of differently oriented ICs (I_2). Labelling as in Fig. 7. (b) vertical velocity profiles. All trials were taken from the same subject (H.B.) as in Fig. 7.

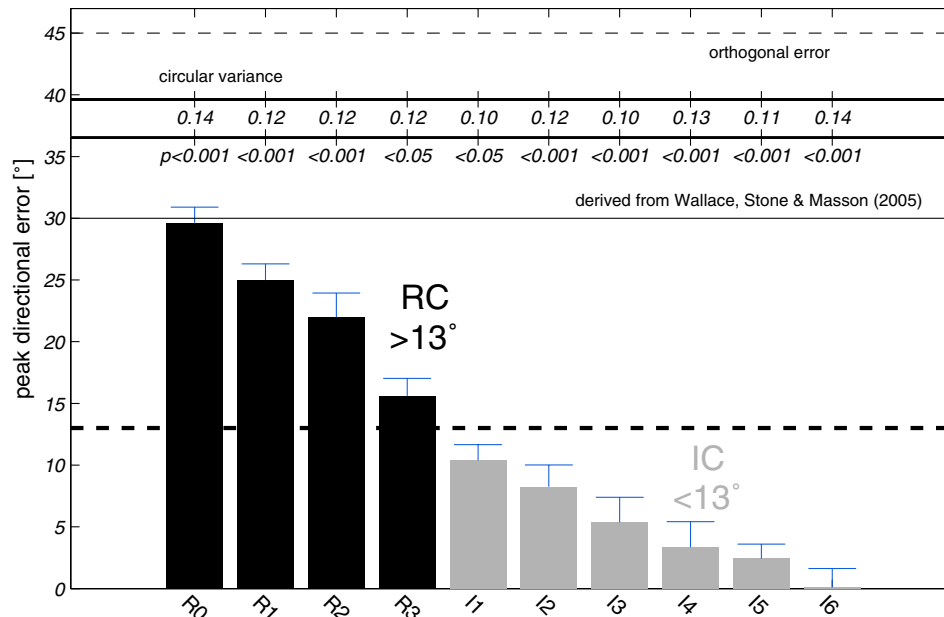


Fig. 9. Summary of peak directional errors measured during pursuit initiation for both real and illusory contours. Moving directions and both *tilted* orientations ($\varphi = -45^\circ$ and $\varphi = +45^\circ$) are pooled. The error bars denote the standard error of the mean across subjects, moving directions and orientations (RC, real contours; IC, illusory contours). For real contours, a peak directional error of around 30° was expected. The directional errors were tested against predefined values chosen as described in the text: 0° and 13° . All RCs elicited a directional error larger than 13° and all ICs an error smaller than 13° (p -values on lower additional axis in the upper part of the figure). The mean circular variance over all stimuli, orientations, subjects and recording sessions was 0.1172. Circular variances for each single stimulus are given on the upper additional axis in the upper part of the figure.

With respect to the directional error elicited by RCs, we asked whether the directional error depends on contrast, target speed, and subjects' prediction. The direction error is a function of contrast, as the rather small directional error (15.6°) obtained in the low contrast condition ($R3$) shows. In addition, the error shows a dependency on target speed as documented by the values obtained with $R0$ and $R1$. Note that with $R0$ target speed was $16^\circ/\text{s}$, resulting in an error of 29.6° , while target speed with $R1$ was $12^\circ/\text{s}$, resulting in an error of 25° .

One might speculate whether the initial direction error could be abolished by subjects' prediction of the target trajectory. With $R2$, which employed only horizontal moving directions, the subjects should have learned that the stimulus moved exclusively horizontally. However, the initial direction error was *not* abolished, merely slightly reduced to 22° compared to 25° with $R1$. Therefore, we decided to present the ICs moving only in horizontal directions in order to increase trial repetitions without increasing the entire length of an experimental session.

When we tested the peak directional error against 0° (Fischer, 1995), i.e. no directional error at all, only the directional error elicited by $I6$ was not significant, but all other stimuli were: $I5$ ($p < 0.05$), $I4$ ($p < 0.01$), remaining stimuli ($p < 0.001$). In addition, we tested all directional errors against a specified value of 13° representing the border between errors elicited by RCs and ICs. The resulting p -values are also given in Fig. 9. In brief, the directional errors obtained by RCs are significantly larger than 13° , while the errors elicited by IC were significantly smaller

than 13° ($p < 0.001$). With respect to the three different *edge-type* stimuli $I1$, $I2$ & $I3$ the amount of directional error was proportional to the individual support ratio of the stimulus. In the two *line-type* stimuli $I4$ & $I5$ only small directional errors could be detected. Finally, two additional comments related to the directional error of all stimuli can be made. First, the fact that the circular variance is constant for all stimuli shows that the lower values of directional error are not a consequence of increased directional scatter. Second, the directional error obtained in the *not-tilted* contour condition is not significantly different ($p > 0.065$) from zero in all experiments with all stimuli.

4. Discussion

We investigated the initiation of smooth pursuit elicited by real and various illusory contours. During pursuit of RCs, an initial tracking direction error occurs during pre-saccadic pursuit initiation approximately perpendicular to the contour's orientation, which was already shown in previous studies for both humans (Masson & Stone, 2002; Wallace et al., 2005) and monkeys (Pack & Born, 2001). We were able to confirm the previously described (Wallace et al., 2005) dependency of the directional error on target speed (compare $R0$ & $R1$ in Fig. 9). Since we were also interested in the role of prediction in this process, we initially tested six possible directions in one stimulus ($R0 + R1$) and compared it to an experiment with two possible directions, purely horizontal ($R2$). Our subjects could not predict upcoming target direction, but knew that the

target moved either leftward or rightward, because they were informed about possible target trajectories before the experimental session. In this condition, the initial directional error was only slightly diminished. The knowledge of horizontal target trajectory did not abolish the initial error. Similarly, a recent human study by Montagnini, Spering, and Masson (2006) reported a preserved directional error despite predictive target trajectories. A similar effect was reported for monkeys by Born et al. (2006), who showed that cuing of the upcoming moving direction did not abolish the initial tracking error. If the same moving direction was presented repeatedly within a block of trials, only a small reduction of the tracking error was found (see Fig. 9 Born et al., 2006). Finally, the directional error was considerably reduced during pursuit initiation towards ICs.

4.1. Classic pursuit parameters in this study

The main finding regarding classic pursuit parameters is that both saccade and pursuit onset latencies were higher for *tilted* vs. *not-tilted* contours. These longer latencies were observed for all stimuli used in our study. Scott-Brown and Heeley (2001) found that *tilted* contours appeared to be moving faster than *not-tilted* contours in a speed discrimination task. So the higher saccade and pursuit latencies for *tilted* contours may represent a behavioural manifestation of this psychophysical observation. It is important to note that the reduction in perceived speed is physical, not illusory. The horizontal velocity of a vertical bar moving horizontally across a circular aperture can easily be estimated. This horizontal velocity drops as the angle between bar orientation and horizontal decreases until it reaches zero for a (infinite) horizontal bar. This explanation also holds for the prolonged eye movement latencies in our study. The question emerges why these differences were not reported in earlier studies addressing the initiation of pursuit elicited by *tilted* contours (Masson & Stone, 2002; Wallace et al., 2005). One might speculate whether the longer latencies for *tilted* bars are a consequence of the misdirection of eye movements. There are two arguments against this explanation: first, we determined pursuit onset on the absolute eye velocity, not the horizontal velocity. Second, in the condition of illusory contours, we did not observe directional errors but still observed increased pursuit and saccade latencies for the *tilted* contour condition.

Human pursuit onset latencies are inversely proportional to the pursued object's size. The initial eye acceleration increases accordingly (Heinen & Watamaniuk, 1998) and is proportional to target velocity (Carl & Gellman, 1987; Tychsen & Lisberger, 1986). Moreover manual reaction times decrease with target velocity (Hohnsbein & Mateeff, 1992). Eye movement latencies can be as short as approx. 80 ms, but occur only in relation to the OFR, i.e. when large field stimuli are applied. However, typical latencies for SPEM are around 100 ms (Carl & Gellman, 1987). This expectation was met over the whole range of stimuli used.

Longer latency values with *R3* can be explained by the low contrast of this stimulus (O'Mullane and Knox, 1999). Lower acceleration values in the *I6* stimulus are due to more peripheral and sparse visual stimulation. Similar eye acceleration values are reported for pursuit initiation of rhesus monkeys towards an imaginary target (Ilg & Thier, 1999). Generally, ICs evoked higher saccade latencies, which could be explained by additional neuronal computations in order to reconstruct the illusory contours. Not surprisingly, using low contrast (*R3*) and thereby decreasing the detectability of the stimulus also increased saccade latency.

4.2. Initial direction error in this study

According to previously published data (Wallace et al., 2005), a directional error of 45°, i.e. an eye movement orthogonal to the contour orientation, could occur when tracking a bar stimulus 35° in length at a speed of 15°/s. Comparing the properties and parameters of the stimulus used here (*R0 + R1*) and those employed by Wallace et al. (2005), we expected a peak direction error of approx. 30°. This expectation was met as evident from the mean values combining all subjects, see Fig. 9. Most importantly, we found that the introduction of ICs significantly reduced the initial tracking direction error. An IC as short as 1° (*I2*) sufficed to induce this effect. In a recent human study (Wallace et al., 2005) two parallelograms termed “square diamond” and “elongated diamond” by the authors, equivalent to *not-tilted* and *tilted* contours in our study, were modified by applying a Gaussian filter to dim either the edges or the corners of these simple line-drawing objects. The resulting figures were similar to the illusory contours of the *edge-type* in our study. When observers were asked to track the original not-filtered parallelograms, only the “elongated diamonds”, corresponding to the *tilted* bars in our study, produced an initial tracking direction error. This tracking error was reduced when the filtered objects were shown. Similarly the tracking direction error was reduced with illusory contours in our study. Therefore, with respect to the absent direction error in the case of an illusory contour, the results from Wallace et al. (2005) are in perfect agreement with ours. However, Wallace and his colleagues showed an increased directional tracking error for lower contrast. We found that in *R3*, the stimulus with low contrast, the directional error was reduced compared to *R2*, the stimulus with high contrast. This is opposite to what was found by Wallace and colleagues. In order to explain this discrepancy, it must be noted that the low contrast used in our study (1.7%) is outside the contrast range used by Wallace (10–90%). It is not very likely that the direction error approximates infinity for contrast values approaching zero. Instead, it is close at hand to assume that the error decreases for very low contrast values. The directional error observed in our low contrast condition (*R3*) connects the directional error observed by Wallace at 10% and zero.

Apart from the lack of initial direction error we could also detect a lack of secondary catch-up saccades when tracking ICs. We suggest two reasons for this. First, since there is a lower steady-state gain compared to RCs, the threshold to trigger corrective saccades may be elevated, too. Second, since pursuit onset latency and initial saccade latency were delayed during tracking of the IC, the occurrence of the secondary catch-up saccades might also be delayed and therefore were not recorded because our data acquisition emphasised pursuit initiation.

4.3. Raw motion signal dominates pursuit initiation

The fact that the initial direction of pursuit directed towards a *tilted* real contour is approximately perpendicular to its orientation and that the direction of pursuit initiation directed towards a theta motion stimulus is dominated by the movement of the single dots indicates that pursuit initiation is dominated by a raw motion signal. Obviously, a *tilted* IC or the theta motion stimulus does not provide such a raw motion signal, resulting in an absence of pursuit initiation modulation.

4.4. Anatomical and functional connectivity considerations

The early processing of a moving contour comprises two time dependent operations: first, the veridical direction of a real contour movement is most likely computed by an iterative process using feed-forward and feed-back connections between V1 and MT. These reciprocal connections provided the basis for a computational model to solve the *aperture problem* over time (Bayerl & Neumann, 2004). Second, based on the knowledge obtained from single-unit recordings in monkeys, it seems reasonable to assume that the neuronal representation of the illusory contours is achieved in V2 (Peterhans & von der Heydt, 1989). More recently, it was shown that the responses to static Kanizsa type illusory figures were more pronounced and occurred earlier in V2 compared to V1 (Lee & Nguyen, 2001).

Similar evidence comes from functional brain imaging studies in humans (for a review see Seghier & Vuilleumier, 2006). In a recent fMRI study using an adaptation protocol, it could be shown that the representation of illusory contours was only weak in early visual areas such as V1 or V2, but more pronounced in higher areas such as V7 and LOC (Montaser-Kouhsari, Landy, Heeger, & Larsson, 2007). It is important to note that only the first operation is able to affect the initiation of pursuit eye movements as our data clearly shows. This is surprising since connections between areas V2 and MT exist in the rhesus monkey (Maunsell & van Essen, 1983; Ungerleider & Desimone, 1986). An interesting question for future experiments is whether the temporal development of directional tuning in MT neurons is also present for illusory contours.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2008.01.021.

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