

Elsevier Editorial System(tm) for Vision Research
Manuscript Draft

Manuscript Number: VR-10-252R2

Title: Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review

Article Type: Perception and action

Keywords: smooth pursuit eye movements, perception, motion, psychometric function, oculometric function, sensory noise, motor noise, perception-action dissociation

Corresponding Author: Dr. Miriam Spering, Ph.D.

Corresponding Author's Institution: New York University

First Author: Miriam Spering, Ph.D.

Order of Authors: Miriam Spering, Ph.D.; Anna Montagnini, Ph.D.

Manuscript Region of Origin: USA

Abstract: Many neurophysiological studies in monkeys have indicated that visual motion information for the guidance of perception and smooth pursuit eye movements is-at an early stage-processed in the same visual pathway in the brain, crucially involving the middle temporal area (MT). However, these studies left some questions unanswered: Are perception and pursuit driven by the same or independent neuronal signals within this pathway? Are the perceptual interpretation of visual motion information and the motor response to visual signals limited by the same source of neuronal noise? Here, we review psychophysical studies that were motivated by these questions and compared perception and pursuit behaviorally in healthy human observers. We further review studies that focused on the interaction between perception and pursuit. The majority of results point to similarities between perception and pursuit, but dissociations were also reported. We discuss recent developments in this research area and conclude with suggestions for common and separate principles for the guidance of perceptual and motor responses to visual motion information.

Oct 8, 2010

Dear Karl,

We are submitting a shortened and revised version of our manuscript "**Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review,**" by Miriam Spering and Anna Montagnini, for publication in the special issue of *Vision Research*.

We have followed all the suggestions made by you and the reviewer for shortening the ms; the main text is now 39 pages long.

We hope that the ms. can now be accepted for publication.

Best regards,

Miriam & Anna

All changes marked in blue ink. Note that we also marked paragraphs in blue ink when they were moved to other parts of the ms.

Reviewer #2: The authors addressed all points of criticism and changed their review accordingly.

1. However, the review is still quite long. In order to help to reader I suggest to shorten the review by presenting only one general summary of results and one general discussion instead of 4 summaries and comments after each mayor review section. A general condensed summary of the all results of the nicely reviewed papers of the different chapters may help the reader to get a better overview over the different investigations done so far to compare motion perception and smooth pursuit. Also a more general discussion about the difficulty to compare a dynamic motor response such as pursuit and with a perceptual judgment might be better. Since all parts for a general summary and discussion are already in the four different summaries and commentaries of the chapters, it is more a job of cutting, pasting and smoothing.

We cut the four summaries and only included individual sentences as commentaries in the respective sections where the studies in question were discussed. One of the summaries (formerly 2.1.3) was added to the final part 4 of the ms. as a general methodological discussion of a direct comparison between perception and pursuit [4.3; p.36 para.2 to p.37 para.1].

2. I suggest also to shorten the section of OFR and non-visual motion, i.e. the review of the papers of Boström & Warzecha (2010) and Hayashi et al. (2010) on pages 12-13 and the paragraph: 2.4.3 Pursuit and perception of non-visual motion. As described in the review it is unclear how to compare OFR and smooth pursuit and for auditory stimuli smooth pursuit is not possible and which excludes a comparison with perception.

OFR: we shortened the discussion of these two studies down to two sentences [p.10 para.3 to p.11 para.1].

Non-visual motion: we cut the two whole paragraphs on responses to auditory motion and motion expectation and now only include some references in the general-very brief-section on non-visual motion [2.4.3, p.28 para.1].

Minor comments:

3. Page 6, second sentence: suggestion to rephrase: "During the closed-loop phase, the velocity errors of the eyes seems to be minimized by a negative feedback loop, i. e. to stabilize the image of the target on the fovea the efference copy and the retinal target motion signal are compared."

We rephrased the sentence as suggested.

4. Page 15 line 5, as instead of than - to acceleration changes as the perceptual system.

Corrected.

5. Page 20: last paragraph: It should be mentioned that the pursuit target of the study of Spering and Gegenfurtner (2007b) was spatially separated from the visual context.

Added.

6. Page 35, first sentence, add briefly and can be instead of is: When a visual stimulus is briefly presented ., its perception can be blurred.

Done.

7. Page 36, the extra-retinal reference signal reflects the motor command of the eye movement

Added.

8. Page 40, Pursuit eye movements provide addition motion information derived from the efference copy signal of the corresponding eye movement that can be used and compared with the visual motion signal for better perceptual estimates than during fixation.

This sentence was in one of the summary sections which was deleted.

9. Page 40, second paragraph, line 9: whereas pursuit is an indirect interaction with our visual world by representing signals of moving objects in motor responses.

Rephrased as suggested, but we left out the word "indirect" (and "direct", as a matter of fact) as it really depends on the interpretation of the term "interaction" whether it is considered direct or indirect.

10. Page 40, second paragraph, last sentence: .; pursuit requires the selection of a single target or the construction of an object center

Great suggestion, rephrased.

11. Table 1, SEF ... microstimulation evokes pursuit during initiation but not during fixation DLPN Similar properties as MT

Table 1 was deleted.

Research highlights to Spering & Montagnini (Review)

- Perceptual and oculomotor responses to visual motion are guided by the same neuronal circuit
- We review psychophysical studies directly comparing perception and pursuit eye movements
- Behavioral evidence points to similarities and differences between both responses
- Dissociations might be due to differences in task requirements and temporal constraints

Do we track what we see?

**Common versus independent processing for motion perception and smooth pursuit eye
movements: A review**

Miriam Spering¹ & Anna Montagnini^{2*}

¹Department of Psychology & Center for Neural Science, New York University, New York

²Institut de Neurosciences Cognitives de la Méditerranée, CNRS and Aix-Marseille University

Marseille, France

*Corresponding author's address:

Dr. Anna Montagnini
Institut de Neurosciences Cognitives de la Méditerranée
UMR 6193
CNRS-Université de la Méditerranée
31, chemin Joseph Aiguier
13402 Marseille cedex
France
Email: Anna.Montagnini@incm.cnrs-mrs.fr

Abstract

Many neurophysiological studies in monkeys have indicated that visual motion information for the guidance of perception and smooth pursuit eye movements is—at an early stage—processed in the same visual pathway in the brain, crucially involving the middle temporal area (MT). However, these studies left some questions unanswered: Are perception and pursuit driven by the same or independent neuronal signals within this pathway? Are the perceptual interpretation of visual motion information and the motor response to visual signals limited by the same source of neuronal noise? Here, we review psychophysical studies that were motivated by these questions and compared perception and pursuit behaviorally in healthy human observers. We further review studies that focused on the interaction between perception and pursuit. The majority of results point to similarities between perception and pursuit, but dissociations were also reported. We discuss recent developments in this research area and conclude with suggestions for common and separate principles for the guidance of perceptual and motor responses to visual motion information.

Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review

Introduction

Imagine riding a bicycle on a busy four-lane street in Manhattan. Moving cars, delivery vans, and garbage trucks surround you. You have to avoid falling into unmarked construction sites and hitting pedestrians that randomly cross the street. In order to plan your movements and to survive in such a complex and dynamic visual environment, it is important to obtain a veridical percept of the visual scene. You have to estimate the direction and speed of vehicles around you and use this information fast to decide where to move next.

In primates, two types of voluntary eye movements critically support vision by centering and stabilizing the image of a visual object of interest on the fovea, the region on the retina where visual acuity is highest. *Saccadic eye movements* are discrete, ballistic movements that direct the eyes quickly toward a visual target; *smooth pursuit eye movements* are continuous, slow rotations of the eyes that compensate for motion of the visual target. These voluntary eye movements are not simply sensorimotor reflexes, but depend on the sophisticated sensory and cognitive processing capabilities that characterize our central nervous system (for reviews see Krauzlis, 2004; 2005).

Smooth pursuit eye movements are closely related to sensory inputs from the motion processing system. A large number of neurophysiological studies in awake behaving monkeys have linked neuronal activity in the primate's middle temporal area (MT) and the adjacent middle superior temporal area (MST) to both the perception of visual motion (e.g., Newsome, Britten, & Movshon, 1989; Newsome & Paré, 1988; Pasternak & Merigan, 1994; Rudolph & Pasternak, 1999; Salzman, Murasugi, Britten, & Newsome, 1992; but see Ilg & Churan, 2004) and the control of smooth pursuit eye movements (e.g., Dürsteler & Wurtz, 1988; Ilg & Thier, 2003; Komatsu & Wurtz, 1988; 1989). These findings are paralleled in human neuroimaging and patient studies (Huk & Heeger, 2000; Marcar, Zihl, & Cowey, 1997) and provide evidence for common processing of motion information for perception

and pursuit eye movements at an early stage. This common pathway links direction-selective retinal ganglion cells to areas MT and MST and to higher-order motion processing areas in the occipital, parietal and frontal cortex (e.g., Bremmer, Distler & Hoffmann, 1997; Culham, He, Dukelow, & Verstraten, 2001; Fukushima, 2003; Ilg & Churan, 2004; Orban, Sunaert, Todd, Van Hecke, & Marchal, 1999) through the lateral geniculate nucleus (LGN) and primary visual cortex (areas V1, V2).

However, these studies leave a number of questions open. Are perception and pursuit driven by the same or independent neuronal signals? Given their response variability, are perceptual and pursuit performance limited by the same source of neuronal noise? How do pursuit eye movements affect the perception of visual motion? In four parts, we review psychophysical studies in humans that have addressed these issues, with a focus on those published in the last ten years. We begin with a brief overview of the pursuit system (part 1) before addressing each of the questions stated above. Part 2 provides a summary of behavioral evidence for common and independent processing of visual motion information for perception and pursuit as well as a discussion of noise sources. Part 3 focuses on the interaction between perception and pursuit. In the final part 4, we review model ideas that have emerged recently in this active field of research and conclude with a summary of common and separate principles of motion processing for the guidance of perception and pursuit.

The research reviewed here is generally motivated by the question how sensory information is transformed into motor actions so that we can successfully interact with our dynamic visual environment. Pursuit eye movements are a relatively simple and well-understood motor behavior—we largely know how the sensory input and motor events related to pursuit are represented in the brain—and therefore provide an excellent model system to study this sensorimotor transformation. We continue a tradition of reviews on the visual signals that drive pursuit eye movements (Krauzlis & Stone, 1999; Lisberger, 2010; Lisberger, Morris, & Tychsen, 1987) and provide the first systematic review on the question whether motion information processing for perception and pursuit is common or independent. Due to limited space, we mention studies on other motion-guided eye movement systems (optokinetic

nystagmus, ocular following response) only briefly, and we do not review studies on saccades (for reviews on pursuit and saccades see Krauzlis & Stone, 1999; Orban de Xivry & Lefèvre, 2007). We further do not include neurophysiological studies, modeling studies, studies that focus on aspects of development, or those on pathologies in motion processing.

1. Characterizing Smooth Pursuit Eye Movements

1.1 Response latency, open-loop and closed-loop pursuit

Human smooth pursuit eye movements in response to a moving visual target usually have a latency of about 80-120 milliseconds (ms; Carl & Gellman, 1987; Krauzlis, 2004; see Merrison & Carpenter, 1991 for a report on express pursuit). In monkeys, pursuit latencies can be as low as 65 ms (Lisberger et al., 1987; Lisberger & Westbrook, 1985). The latency of the pursuit response generally depends on properties of the visual target such as luminance, size, velocity and position (e.g., Tychsen & Lisberger, 1986). Latency further depends on properties of the context such as the number of potential targets (Ferrera & Lisberger, 1995; Krauzlis, Zivotofsky & Miles, 1999; Spring & Gegenfurtner, 2008) and is influenced by cognitive factors such as the predictability of the target trajectory (e.g., Bahill & McDonald, 1983). Human observers are usually able to track a target moving up to a velocity of 100 degrees per second ($^{\circ}/s$; Meyer, Lasker, & Robinson, 1985). However, pursuit is often too slow with respect to the target, especially when target velocity exceeds $30^{\circ}/s$. To compensate for retinal image slip, smooth pursuit eye movements are substituted by *catch-up saccades* (De Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002).

The pursuit response is separated into an *open-loop* (initiation) and a *closed-loop* or *steady-state* (maintenance) phase (Lisberger et al., 1987; Tychsen & Lisberger, 1986). During the open-loop phase, the first ~100 ms of the eye movement, pursuit is primarily driven by visual motion (the retinal image velocity) of the target. The eye initially accelerates in the direction of the target, and later adjusts to target velocity. [During the closed-loop phase, the velocity error of the eyes seems to be minimized by a](#)

negative feedback loop, i.e., to stabilize the image of the target on the fovea the efference copy and the retinal target motion signal are compared. Moreover, memory of eye velocity has been reported to play a role in maintaining pursuit (Lisberger et al., 1987; Morris & Lisberger, 1987).

Other types of slow eye movements that are driven by visual motion are the ocular following response (OFR) and the optokinetic nystagmus (OKN), a subsystem of ocular following. Whereas pursuit is voluntary, these responses are low-level reflexes resembling the properties of early visual processing (Miles, Kawano, & Optican, 1986). The OFR is usually best elicited by brief, unexpected motion of a large part of the visual scene (e.g., a full-field random-dot pattern). It has a brief execution time and a considerably shorter latency than pursuit, 50-85 ms in humans and monkeys (Gellman, Carl, & Miles, 1990; Miles et al., 1986). Although pursuit and reflexive OKN and OFR differ in important aspects such as latency, both types of eye movements are driven by similar neural systems (see Dürsteler & Wurtz, 1988; Konen, Kleiser, Seitz, & Bremmer, 2005; Takemura, Murata, Kawano, & Miles, 2007) that have been reviewed extensively elsewhere (e.g., Ilg, 1997; 2002; Keller & Heinen, 1991; Krauzlis, 2004, 2005; Leigh & Zee, 2006; Thier & Ilg, 2005).

1.2 Pursuit Stimulus and Mechanisms for its Selection

Despite anecdotal reports to the contrary, primates are unable to smoothly track a purely imaginary object. Pursuit eye movements require *visual* motion signals (e.g., Lisberger, Morris, & Tychsen, 1987; Rashbass, 1961; Robinson, 1965). Although most laboratory studies have looked at pursuit in response to a single dot moving across a uniform background, pursuit can be elicited by a variety of motion stimuli, such as random-dot kinematograms (e.g., Heinen & Watamaniuk, 1998) or line figures (e.g., Masson & Stone, 2002). It can further be evoked in the absence of a physical motion stimulus, i.e., without retinal image motion, for instance by perceived or apparent image motion (e.g., Ilg & Thier, 2003; Madelain & Krauzlis, 2003; Steinbach, 1976; Wyatt, Pola, Fortune, & Posner, 1994) or by predicted motion (Barnes, 2008; Kowler & Steinman, 1979a; b; 1981).

In our natural visual environment, we rarely encounter motion of a single isolated object. Rather, an object of interest is usually surrounded by a dynamic visual context (see 2.2.1), requiring the observer to actively select a visual target. Target selection is one of the central requirements of the pursuit system. While we can perceptually keep track of multiple moving objects (for a review, see Cavanagh & Alvarez, 2005), we can only actively track one motion trajectory with our eyes. When confronted with multiple moving objects with equal salience at the same time, pursuit eye movements initially follow the direction of the average of all the available motion vectors (e.g., Ferrera & Lisberger, 1995; 1997; see 2.2.1). Vector averaging (VA) is usually a transient response reflecting conflicting motion inputs, and corrected in the direction of one selected object (*winner-take-all* response, WTA) during the later stage of the pursuit response. The time course for this shift from VA to WTA is reflected in the activity of neurons in areas MT and MST (Recanzone & Wurtz, 1999). The target selection process can be modulated by stimulus properties such as luminance contrast and color (Spring, Montagnini, & Gegenfurtner, 2008; see 2.3.2), as well as visual spatial or feature-based attention (Ferrera, 2000; Ferrera & Lisberger, 1995; Garbutt & Lisberger, 2006; Krauzlis, Zivotofsky, & Miles, 1999; Recanzone & Wurtz, 2000).

2. Common versus Independent Motion Signals for Perception and Pursuit

2.1 Precision of Motion Discrimination and Sources of Noise for Perception and Pursuit

Visual motion information is the main determinant of pursuit control. Pursuit eye movements represent a fast and direct linear readout of the direction and speed-tuned population activity of neurons in area MT (Groh, Born, & Newsome, 1997; Lisberger & Movshon, 1999; Newsome, Wurtz, & Komatsu, 1988). Similarly, perceptual judgments of motion are reflected by MT neuronal activity (Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Britten, & Movshon, 1989; Salzman et al., 1992). These findings have brought up two major questions. First, do perceptual and oculomotor accounts of motion information provide the same amount of information and are they affected by the

same neuronal noise? This question addresses the similarity between the two systems with regard to their accuracy and noise source (e.g., Gegenfurtner, Xing, Scott, & Hawken, 2003; Stone & Krauzlis, 2003). Second, how faithfully do oculomotor and perceptual outputs reflect the sensory input with regard to motion direction, speed and acceleration? This question focuses on the quantitative efficiency of either system independently, compared to sensory noise (e.g., Osborne, Lisberger, & Bialek, 2005; Rasche & Gegenfurtner, 2009).

2.1.1 Same or Different Accuracy–Same or Different Noise Source?

The studies reported here used detection and discrimination tasks for the visual motion features direction, speed, and acceleration. Binary perceptual and continuous pursuit responses were directly compared on the same trial by converting raw pursuit traces into probabilistic binary pursuit decisions about motion direction, speed or acceleration. Binary pursuit decisions could then be plotted as a function of the variable of interest, yielding *oculometric functions*. These could directly be compared to standard psychometric functions for the analysis of detection or discrimination thresholds and response precision, as indicated by the slope of the functions (**Fig. 1a,b**). When both responses are equally sensitive to changes in physical stimulus parameters, the psychometric and oculometric functions should largely overlap (**Fig. 1a**). If both responses differ with regard to their response precision, the response with higher precision should yield a steeper function (**Fig. 1b**). The question whether both responses share a common noise source that limits their performance was usually addressed by testing whether the response errors were correlated on a trial-by-trial basis.

Motion Direction and Speed. Two studies published at the same time (Gegenfurtner et al., 2003; Stone & Krauzlis, 2003) have tested perceptual and pursuit motion discrimination performance simultaneously—Gegenfurtner and colleagues (2003) compared the sensitivity of both systems to small changes in stimulus speed and Stone and Krauzlis (2003) used a direction discrimination task—while

keeping the retinal motion input to the perceptual and the pursuit system the same. Both studies report similarities in sensitivity for perception and pursuit, but come to different conclusions regarding the source of noise underlying perception and pursuit.

Gegenfurtner et al. (2003) presented a small visual target that either moved at a constant speed of $4^\circ/\text{s}$, or increased or decreased in speed (perturbation range: $\pm 0.75^\circ/\text{s}$) during steady-state pursuit. Observers were asked to report whether the target speed during perturbation was faster or slower than during the rest of the trial while smoothly tracking target motion with their eyes. In Stone and Krauzlis (2003), the target moved at a constant speed but along different directions, either straight horizontal or vertical (cardinal), or diagonally (up to $\pm 6^\circ$ off the cardinal axes). Observers had to indicate whether target motion direction was above or below (right or left) with respect to the horizontal (vertical) axis while smoothly tracking targets.

Figure 1 here

Both studies showed similar accuracy in perception and pursuit in discriminating target speed changes (for an example see **Fig. 1c,d**) and directions, and disagree with an older study (Watamaniuk & Heinen, 1999), where a primacy of perceptual accuracy had been reported, probably due to noisy oculomotor measurements. Both studies also propose a similar model (**Fig. 1e**) where an initial common stage of motion processing (with a common source of noise) is followed by two independent modules for perception and pursuit control, respectively, that are affected by two independent sources of additive noise. However, only Stone and Krauzlis (2003) found evidence for a significant trial-by-trial correlation between errors in perception and in pursuit, especially for low signal values where errors were most frequent, whereas Gegenfurtner and colleagues (2003) did not. These two studies provide strong behavioral evidence for common processing of motion information for perception and pursuit and therefore fit well with physiological reports, but leave the question open whether both systems are limited by the same source of noise.

A recent study came to a different conclusion and reported that the pursuit system was the more

faithful analyzer of visual motion: Tavassoli and Ringach (2010) used a task similar to the one in Gegenfurtner et al. (2003) and applied a single-cycle sinusoidal perturbation to target motion during steady-state pursuit. At the end of each trial, observers had to discriminate whether the peak (speed increase) or the trough (speed decrease) of the sinusoidal perturbation had occurred first. Pursuit discrimination performance was generally superior to perceptual performance and, in some cases, even sensitive to speed changes that remained unperceived. Interestingly, one out of four observers in Gegenfurtner et al. (2003) showed a similar pursuit performance benefit. Tavassoli and Ringach (2010) suggested that perceptual judgments might have been corrupted by larger amounts of noise and/or more heavily filtered, especially at low signal amplitude, where the motion input to the perceptual system is integrated across a larger temporal window (i.e., filtered with a low-pass temporal filter).

The studies by Gegenfurtner et al. (2003) and Tavassoli and Ringach (2010) have another result in common: perceptual and pursuit errors were uncorrelated on a trial-by-trial basis. One explanation for this discrepancy from the Stone and Krauzlis (2003) study could be the use of speed perturbations during steady-state pursuit in the Gegenfurtner et al. and in the Tavassoli and Ringach papers. Speed perturbations are a good method to probe the strength (gain) of the pursuit response by testing whether and how it is affected by changes in the visual input. Schwartz and Lisberger (1994) found that the response to a speed perturbation was modulated by both visual stimulus and motor features: a perturbation had a stronger effect during steady-state pursuit than during fixation. Gain-control mechanisms, as described in Lisberger (2010; his Fig. 8), are held responsible for this enhancement. We could then speculate that the neuronal signal acting as a modulatory gain of the pursuit signal could introduce a form of independent (multiplicative) noise in the oculomotor response to the perturbation in the studies by Gegenfurtner et al. and Tavassoli and Ringach, thereby disrupting the correlation between perceptual and pursuit responses without a large cost for pursuit discrimination performance.

Two recent studies directly compared the initial OFR and perception and reported differences between both. Boström and Warzecha (2010) found higher sensitivities in perception than in the OFR

and no correlation between responses; Hayashi, Sugita, Nishida, and Kawano (2010) found higher sensitivities in the OFR for high temporal frequencies. Because of the differences between pursuit and OFR (see *I.I*) it is unclear how these results compare to those obtained from comparisons between pursuit and perception and whether the close connection between perception and pursuit holds for perception and OFR.

Oblique effect. The *oblique effect*—a performance asymmetry (anisotropy) for the discrimination of motion direction and orientation in human observers with lower discrimination thresholds for cardinal than for diagonal directions (Ball & Sekuler, 1982; Furmanski & Engel, 2000)—is a well-known phenomenon in motion perception. Two psychophysical studies have compared perceptual and oculomotor accounts of the oblique effect—one reported an absence of the oblique effect in pursuit, the other found an oblique effect in perception *and* pursuit.

In one of the first reports of a dissociation between perception and pursuit observers had to discriminate between the directions of two objects that were presented in succession and either moved along horizontal or vertical (cardinal) axes or diagonal axes (Churchland, Gardner, Chou, Priebe, & Lisberger, 2003). In a 2-IFC task, observers reported whether the two target motions were the same or different. Perceptual discrimination performance was better if objects moved along the cardinal axes (oblique effect). Interestingly, this asymmetry was not reported for pursuit as assessed in a separate experiment. At the end of the open-loop interval—here at ~175 ms after eye movement onset—eye movement direction discriminated equally well between target motion directions, regardless of direction. An analysis of neuronal responses in anaesthetized monkeys to stimuli moving in different directions revealed no signature of directional anisotropies in area MT.

A follow-up study by Krukowski and Stone (2005), however, found a reliable oblique effect of comparable magnitude in perception and pursuit. These authors compared perception and pursuit responses on the same trial. In a 2-IFC paradigm, observers had to track stimulus motion and report the

interval that contained the more clockwise direction. The oblique effect in pursuit was found for the open-loop interval, as well as for the closed-loop interval (here defined as the time period 350-500 ms after eye movement onset). The absence of an oblique effect in open-loop pursuit in the Churchland et al. (2003) study could have been due to methodological choices (e.g., the use of only three reference directions) resulting in a lack in statistical power. The study by Krukowski and Stone (2005) addressed this problem and used a full set of cardinal and oblique reference directions. Given these similarities in directional asymmetries in perception and pursuit and the previous observation that MT neurons do not show an oblique effect (Churchland et al., 2003), Krukowski and Stone (2005) proposed a separation of information processing in or downstream from area MST.

In contrast to the claim by Churchland et al. (2003), other studies, using functional magnetic resonance imaging (fMRI) in humans (Furmanski and Engel, 2000), optical imaging in monkeys (Xu, Collins, Khaytin, Kaas, & Casagrande, 2006), or modeling (Rokem & Silver, 2009) indicate that neuronal responses in areas V1 and MT carry a signature of the oblique effect. However, none of the studies reported in this section provide direct evidence for a separation of motion processing information for perception and pursuit. Churchland et al. (2003) merely reported an effect in one domain and no effect in the other, and Krukowski and Stone (2005) reported oblique effects in both domains. Given that the neuronal basis for the oblique effect has only been studied in early visual areas including area MT, hypotheses about where a possible separation occurs—beyond the almost trivial assumption that this must happen downstream from area MT—are difficult to draw from these studies.

Acceleration. Many studies have found that humans are less sensitive to continuous changes in stimulus speed (acceleration) than to step changes in stimulus speed (Snowden & Braddick, 1991; Werkhoven, Snippe, & Toet, 1992). Given the similarities between perception and pursuit with regard to direction and speed discrimination, the pursuit system can be expected to show a similar lack of sensitivity to acceleration changes as the perceptual system. Watamaniuk and Heinen (2003) asked

human observers to discriminate the acceleration of stimuli that started at an initial speed between 4-8°/s and accelerated at a constant rate (range 0-30°/s). After each trial, observers had to judge whether the stimulus accelerated more or less than an implicit standard—the average acceleration of all the stimuli presented in the set. Perceptual and pursuit acceleration discrimination—based on the variability of eye acceleration during the interval 40-140 ms after eye movement onset—were compared to perceptual and pursuit discrimination of initial stimulus speed. Discrimination thresholds (*Weber fractions*, the proportional change in target speed or acceleration producing responses that differed from the mean stimulus 75% of the time) in perception and pursuit were generally larger for relative acceleration than for relative speed—replicating the original finding that humans are better in processing visual information about speed than acceleration—, and discrimination performance for perception and pursuit was similar. These findings again support the notion of common processing for perception and pursuit. On the neuronal level, the perceptual and behavioral insensitivity to acceleration changes is reflected in the finding that individual MT neurons are not tuned to acceleration; acceleration information is obtained from a population response of speed-sensitive neurons in area MT (Lisberger & Movshon, 1999; Price, Ono, Mustari, & Ibbotson, 2005).

2.1.2 Are Perception and Pursuit Faithful Read-Outs of Noisy Visual Motion?

Some of the studies discussed above (see 2.1.1) have analyzed the efficiency of pursuit in response to visual motion during the steady-state phase of the system, i.e. when eye velocity closely matches target velocity (Gegenfurtner et al., 2003; Stone & Krauzlis, 2003; Tavassoli & Ringach, 2010). However, these accounts are limited by a possible confound, because steady-state pursuit is affected by both the retinal motion signal and extraretinal oculomotor feedback—an efference copy signaling ongoing eye velocity (Robinson, 1965; Robinson, Gordon, & Gordon, 1986; for a review see Lisberger, Morris, & Tychsen, 1987). To characterize pursuit responses to visual motion signals alone, Osborne, Lisberger and Bialek (2005) analyzed the variability of monkeys' pursuit eye movements

during the initiation phase—here, the first 125 ms after pursuit onset. They concluded that pursuit variability was mostly due to sensory errors in estimating target motion parameters such as time of onset, direction and speed, accounting for ~92% of the pursuit variability. In a follow-up study, Osborne, Hohl, Bialek and Lisberger (2007) estimated the time course of the pursuit system's sensitivity to small changes in target direction, speed and time of onset. This analysis was based on pursuit variability during the first 300 ms after target motion onset. Thresholds decreased rapidly during open-loop pursuit and, in the case of motion direction, followed a similar time course to the one obtained from the analysis of neuronal activity in area MT (see Osborne, Bialek & Lisberger, 2004). These studies suggest that the pursuit response—even in the initiation phase—provides a faithful, and almost on-line account of motion information that is as efficient as perceptual judgments. However, this last assumption is weak, as it is based on a comparison of monkeys' pursuit direction discrimination with human perceptual direction discrimination data. Due to the differences in species and experimental paradigms, a direct, simultaneous evaluation of oculomotor and perceptual performance on a trial-by-trial basis is not possible.

To address this concern, Rasche and Gegenfurtner (2009) tested human observers on a speed discrimination task and directly compared perception and pursuit. These authors followed a similar mathematical analysis as described in Osborne et al. (2007) and, importantly, also took temporal correlations in the variability of pursuit velocity at different moments in time into account; the analysis was done for short (open-loop phase only, first 300 ms of pursuit) and long time intervals (open- and closed-loop pursuit, first 400-500 ms of pursuit). In contrast to findings by Osborne and colleagues, motor variability consistently affected pursuit in the initiation phase, thereby leading to higher speed discrimination thresholds in pursuit than in perception. Motor errors during this phase accounted for ~50% of the pursuit variability. Interestingly, when estimating oculometric thresholds on the basis of a longer time interval spanning both the initiation and steady-state phase, pursuit outperformed perceptual judgments, indicating that the temporal integration of motion information plays a major role

in this kind of analysis. Differences between species (humans versus monkeys) and the amount they were trained might explain the discrepancy between the studies by Osborne and colleagues and by Rasche and Gegenfurtner.

The neural substrate responsible for the differences in motion discriminability between perception and pursuit, as revealed by Rasche and Gegenfurtner (2009), is not clear. Following the logic of the studies by Osborne and colleagues, one would expect to see very little noise added to the system downstream from cortical motion processing areas V1 and MT, i.e., towards areas controlling motor output. If pursuit variability is mostly due to motor noise, however, substantial amounts of noise should be present in the oculomotor control system. A direct comparison of the variability in pursuit and neuronal responses in brain areas involved in transforming sensory signals into eye movement commands showed that little noise seems to be added in FEFsem and the floccular complex in the cerebellum (Medina & Lisberger, 2007; Schoppik, Nagel, & Lisberger, 2008; for a review see Lisberger, 2010, his Fig. 7). These results seem to provide direct evidence in support of the idea that motion processing for pursuit initiation does not imply any dramatic degradation of the visual signal. However, they are based on trial-by-trial comparisons between pursuit responses and neural activity in the respective areas, and do not involve a direct comparison with perception. The finding by Rasche and Gegenfurtner (2009) that pursuit discriminability outperformed perception is clearly inconsistent with the idea that motor noise is added at later stages. Further studies are needed to help explain the discrepancies between different behavioral studies and differences found for pursuit initiation and maintenance. In particular, a true direct comparison between neural activity, pursuit and perception, with well-matched time intervals for analysis, is still missing.

2.2 Motion Segmentation and Object Motion Integration

Traditionally, it has been assumed that pursuit eye movements depend solely on the retinal motion input and on later feedback from the oculomotor system (Robinson, 1965; Robinson, Gordon &

Gordon, 1986). However, there is evidence that higher-level visual and perceptual mechanisms (for reviews, see Hafed & Krauzlis, 2010; Krauzlis & Stone, 1999; Masson, Montagnini & Ilg, 2010) as well as cognitive factors (for a review see Barnes, 2008) play a major role in pursuit control. In order to reflect this, some studies have compared perception and pursuit in more complex visual scenes where different motion signals are present at different positions of the visual field. In such situations, an accurate interpretation of the scene requires a reconstruction of the correspondence between different motion signals and different locations (*motion segmentation*), and the integration of spatially different motion signals into a coherent visual object (*object motion integration*).

2.2.1 Contextual Effects on Perception and Pursuit

In our natural environment, visual objects are usually embedded in and sometimes partially occluded by a richly structured, dynamic visual context. In order to track such a visual object with the eyes, its motion signals have to be integrated into a coherent pattern and spatially segregated from other motion signals in the visual context. When the pursuit system has to select a target in the presence of a second moving distractor, the initial pursuit response usually follows the *vector average* of both motion signals (Lisberger & Ferrera, 1997), i.e., it goes in the direction of the average motion signal, unless the response is cued towards one of the two targets (Ferrera & Lisberger, 1995; Garbutt & Lisberger, 2006), or the observer receives information about one target's motion trajectory (Recanzone & Wurtz, 1999; Spering, Gegenfurtner, & Kerzel, 2006). Similarly, pursuit follows the vector average when a visual target is surrounded by a dynamic visual context. A context moving along with the pursuit target increases pursuit velocity; a stationary context or a context moving opposite to the pursuit target decreases pursuit velocity (e.g., Masson, Proteau, & Mestre, 1995; Spering & Gegenfurtner, 2007a).

However, these studies have not examined perceptual responses. The phenomenon of *induced motion* reveals that the perceptual system can be unable to segregate motion signals from spatially different sources: a moving object in the periphery can induce motion so that a stationary, fixated target

object appears to move in the opposite direction to the physically moving object (Duncker, 1929; Zivotofsky, 2005; see also Anstis & Casco, 2006; Nawrot & Sekuler, 1990). How do perception and pursuit respond to speed perturbations in a central target that is surrounded by a dynamic visual context? Spring and Gegenfurtner (2007b) were the first to report profoundly differential effects in perception and pursuit. They compared both responses in a speed discrimination task in which changes in target speed had to be segregated from speed changes in the visual context. A small target surrounded by a **spatially separated** moving visual context either moved at a constant speed of 11°/s or briefly increased or decreased in speed (perturbation range $\pm 6^\circ$). The context moved at a constant speed or changed speed simultaneously with the target, but in an independent direction (e.g., in a given trial, the target could increase in speed while the context decreased in speed). Observers had to track the target and indicate whether it had increased or decreased in speed. Pursuit eye movements clearly followed the vector average of target and context motion (**Fig. 2a**; see also Kodaka, Miura, Suehiro, Takemura, & Kawano, 2004; Lindner, Schwarz, & Ilg, 2001; Miura, Kobayashi, & Kawano, 2009; Schwarz & Ilg, 1999; Spring & Gegenfurtner, 2007a; Suehiro et al., 1999). Perceptual responses, however, went in the direction of the induced motion: Observers systematically underestimated target velocity when context velocity increased, and overestimated target velocity when context velocity decreased (**Fig. 2b**). In trials with constant target velocity, a brief increase in context speed alone therefore produced a transient increase in eye velocity and a decrease in perceived target velocity (for similar findings in perception, see Schweigart, Mergner, & Barnes, 2003).

These opposite effects of context perturbations on perception and pursuit (**Fig. 2c**) resemble the structure of receptive fields in area MT. Parafoveal and peripheral MT neurons have large receptive fields (> 10 deg, Pack & Born, 2001; see also Komatsu & Wurtz, 1988) and integrate motion signals over space, sometimes taking into account information from outside the receptive field (Allman, Miezin, & McGuinness, 1985; Born, Groh, Zhao, & Lukasewyc, 2000; Frost & Nakayama, 1983). One type of MT neurons responds best to wide-field motion stimuli, which extend the area of the classical

receptive field. The other type of MT neurons does not respond to these stimuli; it inhibits information from the surround. The perceptual responses reported in Spering and Gegenfurtner (2007b) might have been controlled by motion-sensitive neurons with inhibitory surrounds whereas pursuit responses might have been based on activity in neurons with excitatory receptive-field structures that spatially sum over larger regions of the visual field. [The dissociation reported in Spering and Gegenfurtner \(2007b\) can therefore be reconciled with the idea of common pathways—it merely indicates that motion information for perception and pursuit can, under some circumstances, be processed differently or by different populations of neurons in areas MT/MST.](#)

Figure 2 here

There is also evidence that perturbations in the visual context can affect perception and pursuit similarly. Debono, Schütz, Spering, & Gegenfurtner (2010, this issue) asked observers to indicate the motion direction of a RDK that moved horizontally or in a diagonal direction slightly off the horizontal axis, while concurrently recording eye movements. In some trials, a portion of the dots in an extrafoveal location, at different positions relative to the observer's center of gaze, were perturbed in direction. Both perception and pursuit were most influenced if the perturbation angle was similar to the motion direction angle of the RDK, and if the perturbation was close to the fovea. Both systems can therefore integrate motion signals over the same spatial range.

2.2.2 Object Motion Integration for Perception and Pursuit

Aperture Problem. Most studies presented so far have used single dots or dot patterns as the pursuit target. For more complex moving objects, an important question is whether perception and pursuit follow global object motion, or a combination of retinal motion signals of each local object component. Under particular stimulus conditions, such as those described by the *aperture problem* (Wallach, 1935), motion segmentation and motion integration can be difficult, leading to an ambiguous interpretation of the visual scene and to multistable percepts. The aperture problem occurs for instance

when a moving object is occluded and only one edge is visible through a small aperture. The moving edge then appears to move orthogonally to its orientation (**Fig. 3a**, red arrow), irrespective of the global object motion (**Fig. 3a**, green arrow).

Aperture-problem like situations have been used to study the ability of the motion processing system to integrate local motion signals into a coherent global percept. Some studies directly compared perception and pursuit (Beutter & Stone, 2000), others studied both systems independently but in parallel, using similar stimuli and comparing a wide range of visual features (e.g., Castet, Lorenceau, Shiffrar, & Bonnet, 1993; Lorenceau, Shiffrar, Wells, & Castet, 1993; Masson & Stone, 2002; Wallace, Stone, & Masson, 2005).

Figure 3 here

Beutter and Stone (2000) analyzed motion direction perception and the direction of steady-state pursuit eye movements in response to line-figure parallelograms moving behind stationary rectangular apertures, such that only the motion of a segment of each side of the object was visible (**Fig. 3b**, left). The motion trajectory of the stimulus was either tilted to the right (-10°) or left ($+10^\circ$). When the apertures were visible (**Fig. 3b**, middle), perception and pursuit followed the true (physical, global) right- or leftward tilted motion of the parallelogram (see red and blue eye traces, respectively, in **Fig. 3b**, middle), indicating that motion signals of individual components were integrated into a coherent object. Directional judgments in perception and pursuit were correlated on a trial-by-trial basis, indicating common processing. In contrast, when the apertures were not distinguishable from the background (**Fig. 3b**, right), responses followed the incoherent motion direction of local line segments along the orientation of the aperture (see eye traces in **Fig. 3b**, right; for an earlier report of similar perceptual results, see Lorenceau & Shiffrar, 1992). Overall performance (when compared to the true motion direction) was lower in perception and pursuit than with visible apertures. Directional judgments in perception and pursuit were compared with three model predictions for motion integration (for a review, see Bradley & Goyal, 2008; Weiss, Simoncelli, & Adelson, 2002): The

intersection of constraints (IOC) rule predicts that responses follow the direction of true object motion. The *vector average* (VA) rule predicts responses in the direction of the average motion signal (see 2.2.1), in this case the orientation of the line segments. Finally, the *terminator motion* rule predicts responses in the direction of corner or endpoint motion, in this case the orientation of the aperture. With visible apertures, perception and pursuit followed the IOC; with invisible apertures, responses were in between the IOC and terminator motion model. Surprisingly, the direction of the vector average had only a small effect on perceived and pursued motion direction, although VA is a robust and common rule for the integration of motion signals from multiple targets for open-loop pursuit (see 2.2.1), but possibly not for steady-state pursuit (see also Spering, Gegenfurtner & Kerzel, 2006).

When a tilted line is moving horizontally, local motion (line-orientation related) signals (dashed red lines in stimulus orientation in **Fig. 3c**, top) are not in agreement with the line's global (horizontal) motion (solid red lines in **Fig. 3c**, top). Castet et al. (1993) presented these stimuli briefly and asked observers to indicate their motion direction. The perceived direction was biased towards the strongest local motion signal, the direction orthogonal to line-orientation (see also Lorenceau et al., 1993). Similarly, pursuit in response to a horizontally moving tilted line or tilted parallelogram stimulus was initially biased toward the edge-orthogonal direction—the vector average of the object's line segments in the case of the parallelogram—and only later corrected towards the object's global motion (Montagnini, Mamassian, Perrinet, Castet, & Masson, 2007; Masson & Stone, 2002). **Figure 3c** shows pursuit eye velocity in response to a rightward moving vertical or tilted line for three different stimulus speeds for one representative observer. For the tilted line, the initial bias in the line-orthogonal direction is indicated by an early transient positive component in vertical eye velocity (see raw vertical eye velocity traces in **Fig. 3c**, right). The size of the vertical bias depended on target speed (see unbiased eye velocity traces in **Fig. 3c**, right), in line with the general finding that visual stimulus properties (line length, luminance contrast, speed) affect oculomotor (Wallace, Stone & Masson, 2005, Montagnini et al., 2007) and perceptual accounts of the aperture problem (Castet et al., 1993;

Lorencean et al., 1993) similarly.

These studies show that perception and pursuit integrate local motion information similarly. The neurophysiological basis of the local motion direction bias induced by the aperture problem, as well as the dynamic evolution of the bias, has been clearly demonstrated in area MT (Pack & Born, 2001; Born, Pack, Ponce, & Yi, 2006), suggesting that the perceptual and pursuit tracking error observed in humans and monkeys is a result of the common input to both responses from area MT. One fundamental advantage of studying pursuit judgments of motion integration as compared to perception is that the pursuit response is updated continuously. Different pursuit phases can therefore reflect the temporal dynamics of motion integration—from local to global motion tracking—, whereas perceptual judgments may be based either on motion signals at a specific moment in time or on the averaged signals across the whole presentation time. This might be the reason why no study to date has systematically compared oculomotor and perceptual accounts of the aperture problem within the same paradigm, and on a trial-by-trial basis. Montagnini et al. (2007) proposed a recurrent Bayesian model that mimics perceptual motion integration and allows qualitative predictions of pursuit responses to ambiguous motion stimuli. This model has recently been extended to include two modules for motion perception and eye movements and now allows quantitative predictions for perceived motion and pursuit eye movements (Boghadi, Montagnini, Mamassian, Perrinet, & Masson, 2010; this issue).

Biological Motion. Another example of complex motion is that of biological motion—the representation of human or animal movement patterns (Johansson, 1973). In the laboratory, biological motion is reproduced by point-light stimuli (often termed *point-like walkers*) with each point corresponding to a main joint. Biological motion is of interest here, because it requires motion integration of local signals, which (by themselves) provide little information about the object’s global motion. It has been suggested that the ability to perceive coherent biological motion—and therefore the ability to integrate local biological motion signals into a global percept—relies on both local and global

mechanisms, using the local motion of individual dots corresponding to body parts, as well as the global motion of the whole body (Troje, 2008).

A recent study compared perceptual and pursuit responses to biological motion stimuli. Orban de Xivry, Coppe, Lefèvre and Missal (2010) asked observers to discriminate the heading direction of point-light walkers, and, in a separate experiment, to track them with their eyes. The net motion of the stimuli was null, as though the walker was moving on a treadmill. Control stimuli were built by spatially scrambling the position of the walker-points so that global motion differed while local motion remained unchanged. Although the analysis of the psychophysical task was less rigorous than in other studies comparing perception and pursuit, the general result was that both perceptual direction discrimination accuracy and pursuit *velocity gain* (a standard steady-state pursuit measure calculated as eye velocity divided by target velocity) were significantly higher for the biological motion stimulus than for scrambled motion. This finding is particularly interesting considering that area MT, the key area for the processing of translational motion, seems less crucially involved in the processing of this complex motion: MT lesions in human patients did not necessarily disrupt biological motion processing (Billino, Braun, Böhm, Bremmer, & Gegenfurtner, 2009). The neural substrate of biological motion processing includes areas other than MT, lying outside the “classic” motion pathway, such as a region on the superior temporal sulcus as well as occipital and fusiform face areas (Grossman & Blake, 2002; Michels, Lappe, & Vaina, 2005). The link between perception and pursuit might therefore extend to other cortical areas that are usually devoted to the processing of form rather than motion.

2.3 Visual Features Modulating Motion Perception and Pursuit

Perception and pursuit of moving objects can be influenced by visual features unrelated to the object’s motion properties, such as luminance contrast and color. The studies reviewed in this section report similarities in how perception and pursuit process visual motion when the moving target’s luminance contrast is low, or when it is modulated by color.

2.3.1 Luminance Contrast

Motion perception is strongly influenced by the moving target's luminance contrast. A low-contrast stimulus moving at a given speed is perceived to move slower than a high-contrast stimulus moving at the same speed (Thompson, 1982; Stone & Thompson, 1992; for a model see Weiss, Simoncelli, & Adelson, 2002). A corresponding phenomenon to perceptual slowing was demonstrated in the pursuit response in humans (e.g., Sperling, Kerzel, Braun, Hawken, & Gegenfurtner, 2005) and monkeys (Priebe & Lisberger, 2004). As a function of contrast, pursuit latency decreased and velocity gain increased. Although perception and pursuit have not been compared on a trial-by-trial basis, these studies imply that stimulus contrast influences perception and pursuit similarly. Note that the finding of perceptual slowing holds for relatively slow speeds only. For higher speeds, a paradoxical increase of perceived speed has been observed at low contrast (Thompson, Brooks, & Hammett, 2006). To our knowledge, this effect has not yet been studied in pursuit eye movements.

2.3.2 Color

When a moving stimulus is *isoluminant* to the background—when it has the same luminance than the background and differs from the background only in color—the stimulus is usually perceived to move up to 50% slower than a luminance-defined stimulus moving at the same physical speed (Cavanagh, Tyler, & Favreau, 1984; Gegenfurtner & Hawken, 1995; Gegenfurtner et al., 1994) or even perceived to stand still (Lu, Lesmes, & Sperling 1999). This effect of perceptual slowing has been found with relatively slow-moving stimuli ($< 4^\circ/\text{s}$). Impairments have recently also been reported for pursuit eye movements. Braun et al. (2008) measured the effects of isoluminant stimuli on pursuit characteristics and compared speed judgments to luminance- and color-defined targets during fixation and pursuit (see also 3.1.2). The strongest impairments in response to color stimuli were found during the initiation phase: Pursuit latency was delayed by 50 ms, and initial eye acceleration was reduced.

Interestingly, pursuit slowing and latency increases were also found for stimuli moving at higher speeds (up to 10.3°/s). Only a small but significant difference was observed for steady-state pursuit velocity. Motion signals from color stimuli are therefore weaker in driving both perception and pursuit.

Spering, Montagnini and Gegenfurtner (2008) come to a similar conclusion in a study comparing target preferences for color and luminance in pursuit, saccades, and perception. Observers initially tracked a horizontally moving target that split into a color- and a luminance-defined component. After the split, the two stimuli either moved in two diagonal directions (pursuit task) or reappeared in two peripheral locations (saccade task). Observers had to choose the more salient stimulus with their eyes. In separate experiments, we measured perceptual salience judgments during pursuit/saccades. Perceptual judgments and early pursuit responses were strongly biased towards the luminance stimulus (whereas saccades, in comparison, showed a clear preference for color). In about one third of all trials, pursuit was reversed towards the color stimulus by a saccade occurring at ~65 ms after pursuit onset. Apart from the interesting dissociation in target preference between pursuit and saccades—indicating different processing mechanisms for target selection in the two types of eye movement—this study reveals a close relationship between perception and the earliest pursuit response with regard to the processing of color and luminance information.

While these studies show that color information is less readily available to the motion perception and pursuit system, there is also evidence that chromatic motion information can be used as a cue for the interpretation of visual motion direction, specifically, for motion integration and segmentation (for reviews, see Dobkins & Albright, 2003; Gegenfurtner & Hawken, 1996). Dobkins and Sampath (2008) reported that the influence of color information as a motion-segmentation cue might be stronger for perception than for eye movements. However, these authors studied a mixture of pursuit and OKN and did not differentiate their results based on the type of eye movement observed. Conclusions regarding color information as a motion-segmentation cue for either pursuit or OKN and the finding that perception and eye movements might use motion information differently therefore have

to be treated cautiously.

2.4 Perception and Pursuit of Physical versus Perceived Motion

A particularly interesting type of motion stimulus is illusory motion, where perceived and physical stimulus motion do not match. A reliable pursuit response can be elicited and maintained in the absence of visual motion on the retina, provided the observer perceives visual motion. This was first demonstrated by Steinbach (1976), who attached two light-emitting diodes (LEDs) on the opposite sides of a wheel riding along a horizontal track in front of an observer sitting in the dark. Observers not only perceived a rolling wheel, but were also able to track its imagined center smoothly with their eyes. Recent studies compared perception and pursuit in response to apparent motion stimuli such as illusory contours and the motion aftereffect. We briefly review studies on non-visual motion to address the claim that pursuit can be elicited in the complete absence of a visual stimulus.

2.4.1 Apparent Motion and Moving Illusory Contours

Madelain and Krauzlis (2003) used a directionally ambiguous multi-stable stimulus—a physical image that evokes two possible perceptual representations (here, left- and rightward motion)—and compared perceptual and pursuit reversals in motion direction with regard to their timing. The stimulus was an array of Kanitza-style illusory squares defined by illusory contours, which were produced by circular inducers placed at the corners of the square (see **Fig. 4a**). The orientation of the inducers was changed rapidly on every presentation frame, evoking a bi-directional motion percept (i.e., left- and rightwards) of the illusory squares. An auditory tone was presented at a random time during each trial and observers had to indicate in a 2-AFC task whether the tone occurred before or after the perceptual reversal. Eye movements were tracked concurrently. This study provides three interesting results: First, accurate pursuit (with a steady-state velocity gain close to 1) of illusory motion is possible (see also Van der Steen, Tamminga, & Collewyn, 1983; Lamontagne, Gosselin, & Pivik, 2002). Second,

perceived reversals were correlated with reversals in pursuit direction. Third, pursuit reversals consistently followed perceptual reversals by ~50 ms, suggesting that pursuit can provide a real-time readout of perceived motion. [This study and others reported here observed that pursuit follows the visual percept, rather than retinal motion information.](#) Note that this finding does not imply causality with regard to the perception-pursuit relationship, as causal effects have not been systematically analyzed in this context.

Figure 4 here

Ilg and Thier (1999; 2003) compared pursuit and neuronal responses in monkeys to illusory motion using a stimulus, in which the only visual information was carried by peripheral contour-inducers and the target center was only imaginary (see **Fig. 4b**). Again, monkeys were perfectly capable of tracking the imaginary target with a steady-state gain close to 1, whereas pursuit of a single, extra-foveal stimulus at the same eccentricity as the inducers was much less efficient. The activity of MT neurons was significantly reduced, but the activity in a subpopulation of neurons in areas MST and FEF was similar to that observed for pursuit in response to real contours under foveal stimulation. These findings indicate that [MT carries signals related to visual image motion, whereas MST and FEF activity might reflect the extra-retinal eye movement signal \(efference copy\), implying that common neuronal processing of motion information for perception and pursuit is not strictly limited to MT.](#) Interestingly, in a more recent study, Biber and Ilg (2008) found that pursuit latency increased considerably for illusory contours versus real contours. In contrast to what has been reported for real contours (see 2.2.2), when the illusory contour was tilted with respect to its motion direction, initial pursuit responses still followed the true contour motion, and showed only a small bias in the direction orthogonal to the contour orientation. These two results suggest that retinal motion information might be a more important driving signal for pursuit initiation than for steady-state pursuit, when the motion percept seems to dominate.

2.4.2 Motion Aftereffect

Studies on the motion aftereffect (MAE)—a visual illusion that arises from prolonged adaptation to a moving pattern, causing observers to subsequently perceive stationary objects as moving in the opposite direction to the adapting pattern—provide more evidence for similarities in perception and pursuit. Under some circumstances, the MAE can drive a reliable pursuit response in humans (Braun, Pracejus, & Gegenfurtner, 2006; Watamaniuk & Heinen, 2007) and monkeys (Gardner, Tokiyama, & Lisberger, 2004). In their study, Braun et al. (2006) directly compared the effect of a MAE on perception and pursuit. Observers were first adapted to a vertical sine-wave grating presented at high (100%) or medium (40%) contrast that moved continuously to the left or right at $\sim 8^\circ/\text{s}$ for 30 s during fixation. Observers were asked to indicate the motion direction of a subsequently presented test grating (left, right, or stationary) while their eye movements were recorded. Gratings at medium, but not at high contrast, reliably elicited a MAE in pursuit—a response to a physically stationary test grating that was perceived to move in the opposite direction to the adapting stimulus. Conversely, the eyes remained stationary in response to a stimulus that moved in the adapted direction but was perceived to be stationary. The velocities at which the stimulus was subjectively perceived as stationary were almost identical for perception and pursuit, indicating MAEs of similar magnitude in perception and pursuit. These findings again support the assumption of a close link between motion processing for perception and pursuit and suggest a common neural substrate for adaptation in perception and pursuit in area MT (see Gardner, Tokiyama & Lisberger; 2004; Kohn & Movshon, 2004; Watamaniuk & Heinen, 2007).

2.4.3 Pursuit and Perception of Non-Visual Motion

In his influential study on pursuit in response to perceived motion, Steinbach (1976) noted: “[...] the fundamental requirement for pursuit is the appreciation of an object in motion with respect to the observer irrespective of retinal stimulation, and [...] irrespective of the sense modality through which motion is assessed.” (p. 1371). Interestingly, tracking of non-visual objects such as auditory,

tactile or proprioceptive targets with pursuit eye movements has been reported as very poor, with particularly low velocity gains in response to moving auditory stimuli (Berryhill, Chiu, & Hughes, 2006; Boucher, Lee, Cohen, & Hughes, 2004; Gauthier & Hofferer, 1976). These findings exclude a comparison between perception and pursuit, even though motion perception of non-visual targets can be intact. Pursuit can further be affected by non-visual signals such as cognitive expectations about target motion direction and there is some evidence that perception is affected similarly (Krauzlis & Adler, 2001). Motion expectation is also a powerful drive for anticipatory smooth pursuit, i.e. pursuit performed before the actual availability of *visual* target motion information (for a review, see Barnes 2008), but this phenomenon does not have a perceptual correlate and so again excludes a direct comparison between perception and pursuit.

3. Interaction of Perception and Pursuit

3.1 Effects of Pursuit on Perception

When a visual stimulus is briefly presented before or during a saccadic eye movement, its perception can be blurred or even suppressed. This loss of sensitivity for visual information during saccades is known as *saccadic suppression* (e.g., Bridgeman, Hendry, & Stark, 1975; Burr, Holt, Johnstone, & Ross, 1982) and both retinal and extra-retinal mechanisms have been proposed to explain this phenomenon (for reviews see Krekelberg, 2010; Wurtz, 2008). During a saccade, the eyes can move at speeds up to 1000°/s (e.g., Carpenter, 1988) and saccadic suppression might help preventing spatial instability due to saccade-induced, rapid large-field shifts of the retinal image (Ross, Morrone, Goldberg, & Burr, 2001). As a side note, it is interesting that motion perception can be intact during saccades (Castet & Masson, 2000). During pursuit eye movements, where the eyes move at much slower speeds than during saccades, no systematic suppression has been reported during the initiation phase (Schütz, Braun, & Gegenfurtner, 2007). However, it is well documented that the execution of pursuit eye movements can cause misperceptions of stationary and moving objects (e.g., Morvan &

Wexler, 2009; Souman, Hooge, & Wertheim, 2005; for a review, see Freeman, Champion, & Warren, 2010). On the other hand, recent studies have found perceptual benefits during pursuit eye movements (e.g., Hafed & Krauzlis, 2006; Spering, Schütz, Braun, & Gegenfurtner, 2010). Finally, other studies have reported that pursuit has no effect on perception (e.g., Krukowski et al., 2003). The evidence for whether and under which circumstances pursuit helps or impairs motion perception, and what aspects of vision suffer or benefit, and how, is therefore mixed.

3.1.1 Pursuit Impairs Motion Perception

Tracking a moving object with pursuit eye movements always produces a motion signal on the retina, induced by the motion of the stationary background. Because we generally perceive stationary objects as stationary and moving objects as moving, even during pursuit, this movement-induced retinal motion signal has to be cancelled to maintain perceptual stability. This cancellation might be achieved through a comparison of an external (retinal) motion signal with an internal (extra-retinal) reference signal that reflects the [motor command of the](#) eye movement (von Helmholtz, 1910/1962; von Holst & Mittelstaedt, 1950). But although the notion of a system that compensates movement-induced motion signals is well established and the underlying neural network well studied (e.g., Thier, Haarmeier, Chakraborty, Lindner, & Tikhonov, 2001), compensation during pursuit eye movements is usually imperfect. Misperceptions include stationary objects, objects moving along with the pursuit target, and objects moving perpendicular to the pursuit target.

In the Filehne illusion, a briefly presented stationary object appears to move in the direction opposite to the pursuit eye movement (Filehne, 1922; Freeman & Banks, 1998; Haarmeier & Thier, 1996, 1998; Mack & Herman, 1973). The Aubert-Fleischl phenomenon describes a case in which a visual object appears to move slower when it is smoothly tracked than when the observer views it during fixation (Aubert, 1887; Turano & Heidenreich, 1999; von Fleischl, 1882; Wertheim & van Gelder, 1990). Finally, objects that move perpendicularly (Souman, Hooge, & Wertheim, 2005) or

diagonally (Festinger, Sedgwick, & Holtzman, 1976; Morvan & Wexler, 2009) relative to the pursuit trajectory are perceived to move at an angle rotated further away from the pursuit target. These misperceptions might be due to an imperfect compensation for eye movement-induced retinal image motion (e.g., Haarmeier, Thier, Repnow, & Petersen, 1997). Freeman et al. (2010) recently developed an alternative explanation and showed that a simple Bayesian model can explain various misperceptions during pursuit. This model is based on the general idea that prior expectations increasingly influence perceptual decisions as sensory signals become uncertain (e.g., Stocker & Simoncelli, 2006). The finding that stimulus speed is more difficult to discriminate during pursuit than during fixation could therefore be explained by the assumption that we are expecting the world to be stationary, or, in other words, that the prior for motion is centered at zero (Weiss et al., 2002) both for stimulus motion and eye movements (Freeman et al., 2010).

3.1.2 Pursuit Enhances Motion Perception

Pursuit might impair perception under some circumstances, but it can also enhance it, in line with the idea that eye movements generally improve vision (Land, 2006). Hagedorn and Krauzlis (2006) asked observers to judge the coherence of a partially occluded line object (a “chevron”) that moved in a circle behind two occluders (**Fig. 4c**). Observers either maintained fixation in the center between the two occluders (**Fig. 4c**, left), or tracked the fixation spot that moved circularly along with the occluders (**Fig. 4c**, right), while the line object was fixed in space. Both eye movement conditions yield similar retinal image motion. Perceptual coherence (the perceived alignment of the segments behind the two occluders) was better during pursuit than during fixation, regardless of image features such as shape, added noise or presence of a reference frame. These results show that ongoing motor commands derived from pursuit eye movements can be used to perceptually disambiguate spatial relationships between sensory features of visual objects.

Moreover, these motor commands can also inform perceptual judgments about motion

direction. In Spering et al. (2010), observers had to judge whether a linearly moving target (ball) would hit or miss a stationary vertical line (goal). Ball and goal were presented briefly for 100-500 milliseconds, and disappeared from the screen together before the perceptual judgment was prompted. Observers were asked to either pursue the ball or fixate. In one version of the experiment, observers fixated on a stationary ball while the goal was moving towards fixation. In this condition, retinal stimulation was similar to the pursuit condition. In another version of the experiment, observers fixated on the goal while the ball was moving towards fixation. Results show that perceptual performance was significantly better during pursuit than during fixation, regardless of fixation position. The performance difference between pursuit and fixation has to be due to extra-retinal motion direction information gained from the pursuit response—through an efference copy signal as well as the pursuit direction error (the angular velocity difference between eye and ball). Pursuit, even if it is not perfectly accurate, can therefore aid the prediction of visual motion in space. However, pursuit does not seem to benefit the temporal predictions of visual motion (i.e., about the time when a target will reach a certain position), as demonstrated with a task in which observers had to judge time-to-contact of an accelerating object (Benguigui & Bennett, 2010).

A similar advantage of pursuit over fixation was found for the perception of *motion smear*, which is generally elicited by a single moving image when viewed during fixation on a secondary stimulus. Interestingly, perceived motion smear was lower when evoked by a stationary stimulus and viewed during pursuit than when evoked by a moving stimulus and viewed during fixation (Bedell & Lott, 1996). Given the similarity of retinal motion input in both conditions, the advantage has to be—again—attributed to an extra-retinal motion signal, which benefits perception.

Braun and colleagues (2008) showed that pursuit improves perceptual judgments of speed when the moving stimulus is modulated by color. Speed judgments of moving isoluminant stimuli were veridical during pursuit but impaired during fixation. Here, judgments reflected a substantial slowing up to 30%. This finding is surprising, given that pursuit initiation and acceleration to isoluminant

targets is slowed down. Therefore, motion information about isoluminant stimuli seems to be available during steady-state pursuit, but not during fixation. Pursuit also influences the perception of color itself—pursuit can, interestingly and almost paradoxically improve the sensitivity to color (Schütz, Braun & Gegenfurtner, 2009; Schütz, Braun, Kerzel, & Gegenfurtner, 2008). A detailed description of these studies goes beyond the scope of the current review.

3.1.3 Pursuit Does Not Affect Perception

Other studies found that pursuit does not always inform perception (Freeman, Champion, Sumnall, & Snowden, 2009; Krukowski et al., 2003; Tavassoli & Ringach 2010). Krukowski et al. (2003) found no advantage of pursuit over fixation in a perceptual direction discrimination task. Direction thresholds were similar during fixation and pursuit, and perceptual performance was not related to pursuit gain. These authors used a memory task with two intervals in which a visual motion signal had to be compared to an internal reference. Freeman et al. (2009) also used a 2-IFC task in which observers had to indicate which interval contained the faster background motion, while pursuing a target that moved across the background. Observers based their judgments mostly on relative motion between target and background and did not take retinal motion information into account, even if they received feedback on their own eye velocity after each trial. An important difference to many studies reported in the previous sections is that here, observers were asked to judge the speed of the motion surrounding the pursuit target and not that of the pursuit target itself. The finding that pursuit is more sensitive to small speed changes than perception (Tavassoli & Ringach; 2010; see 2.1.1) shows that visual signals can drive eye movements in the absence of a corresponding conscious visual percept. Generally, the availability of internal motion signals (speed or direction) to the perceptual system seems to depend on task requirements.

4. Principles for Motion Processing for Perception and Pursuit

Although the perception of visual motion and pursuit eye movements have been shown to be closely linked, pursuit can also be independent of a concurrent visual percept. This difference is in line with the more general idea that visual information undergoes partly independent processing for visual perception and the guidance of motor action (Goodale & Milner, 1992) and might therefore not surprise some readers. Furthermore, perceptual and pursuit responses are given through different effectors, implying a necessary separation of the information streams toward the motor-output end. Performance differences between both responses also fit well with the notion that motion perception and pursuit eye movements have inherently different task demands. Perception serves the visual representation and interpretation of moving objects, whereas pursuit eye movements imply an interaction with our visual world through [the representation of visual motion signals in motor responses](#). Both responses further underlie different temporal constraints—they differ in response time—and spatio-temporal constraints: it is possible to covertly track multiple moving objects, but not to simultaneously track them all with the gaze; pursuit requires the selection of a single target [or the construction of an object center within a larger moving pattern](#).

Yet, the evidence in favor of a largely common neural substrate for motion perception and pursuit control—at least throughout the visual part of the processing stage—is overwhelming, suggesting that a functional separation into a perception and an action pathway is unlikely for an earlier stage of visual motion processing. Dissociations between perception and pursuit should also be surprising to those who believe that a discrepancy between what we perceive and what we track with our eyes might be strategically inefficient and potentially dangerous—a notion that matches our daily life experience.

We hypothesize that behavioral differences between perception and pursuit are optimal responses to functional differences between the perceptual and the oculomotor system with regard to task demands and temporal constraints and are therefore compatible with an overall agreement of the two modalities. These functional differences might require partly independent computational solutions for the processing of visual motion information.

4.1 Different Responses to Different Task Demands

When the observer sees a moving object of interest and decides (or is instructed) to track it, the pursuit control system has to provide a continuous quantitative estimate of the required force that has to be applied to the eye muscle in order to move the eye while minimizing retinal slip (e.g., Robinson, 1965; Robinson, Gordon & Gordon, 1986). The initiation of a pursuit eye movement requires the efficient use of time-varying information transmitted by direction- and speed-tuned neurons in the visual cortex (e.g., Lisberger & Movshon, 1999). Interestingly, the earliest phase of pursuit—the first ~40 ms—is relatively unselective for visual stimulus features other than motion direction (Lisberger, Morris, & Tychsen, 1987; Rashbass, 1961), probably a cost of the relatively short latency of 80-120 ms (compare to 200-250 ms in saccades). During the pursuit maintenance phase, the eye velocity feedback signal helps to maintain steady-state pursuit. However, in healthy untrained observers, steady-state pursuit velocity gain is usually smaller than 1, indicating that the eye lags behind the target (providing a driving signal for catch-up saccades; De Brouwer et al., 2002). These observations indicate that the pursuit eye movement system can be surprisingly imprecise with regard to velocity matching. Initially, it seems to be the pursuit system's "job" to program an eye movement fast and into the correct direction with relatively little time spent on the extraction of precise visual signals.

The perceptual system, on the other hand, has to detect or discriminate particular visual features and must therefore provide a precise, deep analysis of visual signals. As an aside, it is not clear whether these different task demands are inherent to the systems or whether they are a result of the way pursuit and perception are usually tested. In all psychophysical studies reported here, observers had a specific task with regard to perception (e.g., "report whether the target became faster or slower"), but not with regard to pursuit, where the instruction was to simply track the stimulus with the eyes. It might be interesting to test whether variations to the pursuit instruction (e.g., "track the target's speed change"), thereby matching the level of scrutiny required from both systems, could influence results.

4.2 Continuous versus Discrete Responses: Differences in Temporal Resolution and Time Course

Pursuit eye movements usually start at around 80-120 ms after stimulus motion onset and vary dynamically over time, providing a continuous, analog readout of motion signals. In contrast, motion perception is typically tested at discrete moments in time and usually takes the form of a discrete, binary response. However, observers will most likely base their perceptual judgments on the entire time period in which a motion signal was presented. The size of the temporal integration window could therefore be larger for perception than for pursuit. The uncertainty about the temporal resolution of the perceptual response is (or should be) a major concern in studies that directly compare perception and pursuit, because the use of a larger time window for motion integration essentially low-pass-filters the perceptual response. One way to address this problem is to present stimuli for short time periods only and, where applicable, to use visual masking techniques to enforce a more rigorous control of presentation time. These measures allow better control over the amount of time available to accumulate sensory evidence for a perceptual decision. However, an analysis of pursuit for different time intervals has to take into account that pursuit at different times might be dominated by different visual signals.

Wilmer and Nakayama (2007) investigated accuracy differences in speed estimation between early and late pursuit stages (before and after the first catch-up saccade). Given the known differences between early and late pursuit, this study aimed at identifying the (potentially separate) mechanisms driving these two pursuit stages. The correlation between the moment-to-moment pursuit accuracy across time and the perceptual performance was measured in two 2-IFC speed discrimination tasks. These involved two kinds of stimuli, presumably driving the early vs. late pursuit phase, respectively. Given the relative independence of early pursuit responses to motion information other than direction, this phase has been associated with “low-level” motion signals (here: a drifting luminance-modulated sinusoidal grating), whereas “high-level” motion information seems to be the more important driving signal for the pursuit maintenance phase (here: contrast-modulated circularly drifting rings with no net-luminance motion). Results showed that early

pursuit was predicted by the precision of low-level speed estimation, whereas late pursuit was predicted by the precision of high-level speed estimation. According to Wilmer and Nakayama (2007), catch-up saccades mark the transition from low-level to high-level motion computation. This study has methodological and theoretical implications for the direct comparison between perception and pursuit. First, it underlines that stimuli and behavioral tasks have to be matched well to the requirements of the tested pursuit phase. Second, it raises the question whether there is a corresponding phenomenon in perception that operates the transition between different motion processing mechanisms. In their commentary on the study by Wilmer and Nakayama (2007), Krauzlis and Hafed (2007) suggested that the occurrence of the catch-up saccade could simply be temporally correlated with the transition, rather than causally related to it.

4.3 Methodological Considerations in the Comparison Between Perception and Pursuit

Differences in task demands (4.1) and different response times (4.2) are two crucial methodological issues to consider when comparing binary perceptual judgments and a dynamic motor response such as pursuit directly, on a trial-by-trial basis. First, perception and pursuit are not independent and pursuit can both impair and enhance perceptual performance, with the direction of the effect depending on the particular task (see 3.1). Second, perception and pursuit differ with regard to the time that both systems have available to make a decision. Most studies controlled for the effect of temporal integration by manipulating target presentation duration as well as the pursuit analysis interval. However, none of these studies analyzed speed-accuracy trade-offs to test a possible effect of perceptual reaction time on perceptual performance and the perception-pursuit comparison. In other words, temporal integration of motion information for perceptual judgments could occur beyond the limits of the stimulus presentation interval (especially in the absence of visual masking) and responses with longer reaction times could therefore lead to better perceptual performance. Third, most studies required observers to commit to a dual task—tracking a visual stimulus and making a perceptual decision simultaneously—imposing a different load on attention and working memory than the separate

testing of both responses. Although this does not necessarily require a shift of attention away from the pursuit target, there might have been an overall cost related to higher cognitive load.

4.4 Vector Averaging as a Distinctive Characteristic of Pursuit Initiation

These differences between perception and pursuit with regard to task demands and timing might explain why both responses are sometimes dominated by different computational mechanism. As described above (see 2.2.1), when challenged by a time-critical task such as target selection, the pursuit system is programmed to follow the “quick and dirty” solution of the VA, with the possibility to correct the initial choice later, when target selection has been accomplished. A VA solution is not only optimal in minimizing retinal slip, but it is also the “best guess” (leading to a statistically minimal tracking error) in the case in which there is no a-priori reason to favor one moving object over the other. The VA is a robust phenomenon often observed during pursuit initiation.

For perception, reports of VA are less common (but see Yo & Wilson, 1992). In our daily life, we do not usually rely on the average of perceived motion vectors to make a perceptual decision. Imagine a Lisberger and Ferrera (1997)-like situation, where two targets move towards the fovea, in our natural environment. If two cars move towards a common location from different positions, we would probably get nervous about a possible crash rather than having the impression of a global motion along the VA direction—although our eyes might well choose the average motion path. Many studies have reported that perception integrates motion information from two sources by following the motion contrast—the difference between two motion signals (for a review see Spering & Gegenfurtner, 2008)—again possibly reflecting differences in task requirements and timing.

4.5 Accumulate-to-threshold model

On a mechanistic level, processing differences between perception and pursuit might be reflected in a model where the same visual signals, but different internal decision signals, guide both responses (for a

similar idea, developed for the comparison between pursuit and saccades, see Liston & Krauzlis, 2005). Following a simple “accumulate-to-threshold” model, differences in behavior could result from a combination of same or different internal decision signals driving perception and pursuit to same or different response thresholds (**Fig. 5**).

Figure 5 here

For example, latency and sensitivity differences between perception and pursuit might be the result of different underlying response thresholds for perception and pursuit. A lower response threshold (as shown in **Fig. 5** for pursuit) usually leads to faster responses but also to a higher number of errors, and therefore to an overall lower sensitivity. Note that this accumulate-to-threshold model is a simplified model, designed to visualize some of the behavioral differences between perceptual and motor decisions (such as differences in sensitivity or response latency). However, this model does not allow any predictions for responses in more complex stimulus environments, e.g. when more than one stimulus is present and a target has to be selected; the model does not elucidate the processes underlying perceptual and visuomotor decision-making. In showing that perception and pursuit mostly share the same visual input, the studies discussed in this review provide a first step towards such a model of perception and pursuit. However, testing this model would require a speed-accuracy type of analysis, which has not been performed yet in studies that directly compared perception and pursuit (see also 2.1.3).

4.6 Different Neuronal Substrates beyond MT/MST?

Many studies reviewed here concluded that the similarity between perception and pursuit is grounded on the largely common underlying neuronal processing, especially in areas MT and MST. However, as mentioned throughout this review, a separation must occur—most likely downstream from MT/MST. Several cortical areas other than MT/MST partake in the processing of motion information for pursuit control (e.g., the frontal and supplementary eye fields and the cerebellum; see Krauzlis, 2004; Lisberger, 2010), but are probably less involved in motion processing for perception. Where in the brain the

perceptual decisions about visual motion are taken is much less clear, although an important role has been assigned to area LIP (Williams, Elfar, Eskandar, Toth, & Assad, 2003). This study reported that neuronal activity in LIP correlated with the perceived motion direction of an apparent motion stimulus, while activity in area MT did not reflect subjective perception. This finding underlines the importance of higher parietal areas for the formation of perceptual decisions. In sum, areas MT/MST are crucial for the processing of visual motion information for both perception and pursuit, but they are not the final processing stage.

Conclusion

This review summarized studies from an active field of research which has developed in the last ~20 years by fusing two traditionally independent research lines—classic psychophysics of visual motion on the one hand, and the oculomotor control-theory approach on the other hand—into a unique conceptual framework and a common set of experimental techniques. Some of the challenges for future research in this area will be to understand the involvement of higher-level brain areas beyond MT/MST in motion processing for perception and action, to generalize the principles identified here to other action systems, and to test existing model ideas by analyzing speed-accuracy trade-offs between perception and pursuit.

Acknowledgements

Supported by German Research Foundation fellowship SP1172/1-1 to MS and by EC IP Project FP6-015879 ‘FACETS’ to AM. The authors would like to thank Guillaume Masson and Alexander Schütz for helpful comments on an earlier version of the manuscript.

References

- Allman, J.M., Miezin, F., & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception, 14*, 105-126.
- Anstis, S. & Casco, C. (2006). Induced movement: The flying bluebottle illusion. *Journal of Vision, 6*, 1087-1092.

- Aubert, H. (1887). Die Bewegungsempfindung (The sense of motion). *Pflügers Archiv*, 40, 459-480.
- Bahill, A.T. & McDonald, J.D. (1983). Smooth pursuit eye movements in response to predictable target motions. *Vision Research*, 23, 1573-1583.
- Ball, K. & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science* 218, 697-698.
- Barnes, G.R. (2008). Cognitive processes involved in smooth pursuit eye movements. *Brain & Cognition*, 68, 309-326.
- Bedell, H.E. & Lott, L.A. (1996). Suppression of motion-produced smear during smooth pursuit eye movements. *Current Biology*, 6, 1032-1034.
- Benguigui, N. & Bennett, S.J. (2010). Ocular pursuit and the estimation of time-to-contact with accelerating objects in prediction motion are controlled independently based on first-order estimates. *Experimental Brain Research*, 202, 327-339.
- Beutter, B.R. & Stone, L.S. (2000). Motion coherence affects human perception and pursuit similarly. *Visual Neuroscience*, 17, 139-153.
- Berryhill, M.E., Chiu, T., & Hughes, H.C. (2006). Smooth pursuit of nonvisual motion. *Journal of Neurophysiology*, 96, 461-465.
- Biber, U. & Ilg, U.J. (2008). Initiation of smooth pursuit eye movements by real and illusory contours, *Vision Research*, 48, 1002-1013.
- Billino, J., Braun, D.I., Böhm, K.-D., Bremmer, F., & Gegenfurtner, K.R. (2009). Cortical networks for motion processing: Effects of focal brain lesions on perception of different motion types. *Neuropsychologia*, 47, 2133-2144.
- Bogadhi A.R., Montagnini A., Mamassian P., Perrinet L.U. & Masson G.S. (2010). Pursuing motion illusions: a realistic oculomotor framework for Bayesian inference. *Vision Research*, xx, xx-xx.
- Born, R.T., Groh, J.T., Zhao, R., & Lukasewyc, S.J. (2000). Segregation of object and background motion in visual area MT: effects of microstimulation on eye movements. *Neuron*, 2, 725-734.
- Born, R., Pack, C., Ponce, C., & Yi, S. (2006). Temporal evolution of 2-dimensional direction signals used to guide eye movements. *Journal of Neurophysiology* 95, 284-300.
- Boström, K.J. & Warzecha, A.K. (2010). Open-loop speed discrimination performance of ocular following response and perception. *Vision Research*, 50, 870-882.
- Boucher, L., Lee, A., Cohen, Y.E., & Hughes, H.C. (2004). Ocular tracking as a measure of auditory motion perception. *Journal of Physiology (Paris)*, 98, 235-248.
- Bradley, D.C. & Goyal, M.S. (2008). Velocity computation in the primate visual system. *Nature Reviews Neuroscience*, 9, 686-695.
- Braun, D.I., Mennie, N., Rasche, C., Schütz, A.C., Hawken, M.J., & Gegenfurtner, K.R. (2008). Smooth pursuit eye movements to isoluminant targets. *Journal of Neurophysiology*, 100, 1287-1300.
- Braun, D.I., Pracejus, L., & Gegenfurtner, K.R. (2006). Motion aftereffect elicits smooth pursuit eye movements. *Journal of Vision*, 6, 671-684.
- Bremmer, F., Distler, C., & Hoffmann, K.P. (1997). Eye position effects in monkey cortex. II. Pursuit- and fixation-related activity in posterior parietal areas LIP and 7A. *Journal of Neurophysiology*, 77, 962-977.
- Bremmer, F., Schlack, A., Shah, N.J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., & Fink, G.R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29, 287-296.
- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of visual world during saccadic eye movements. *Vision Research*, 15, 719-722.
- Britten, K.H., Shadlen, M.N., Newsome, W.T., & Movshon, J.A. (1992). The analysis of visual motion: a comparison of neuronal and psychophysical performance. *Journal of Neuroscience*, 12, 4745-4765.

- Burr, D.C., Holt, J., Johnstone, J.R. & Ross, J. (1982). Selective depression of motion selectivity during saccades. *Journal of Physiology (London)*, 333, 1-15.
- Carl, J.R. & Gellman, R.S. (1987). Human smooth pursuit: stimulus-dependent responses. *Journal of Neurophysiology*, 57, 1446-1463.
- Carpenter, R.H.S. (1988). *Movements of the eyes* Pion: London.
- Castet, E., Lorenceau, J., Shiffrar, M., & Bonnet, C. (1993). Perceived speed of moving lines depends on orientation, length, speed and luminance. *Vision Research*, 33, 1921-1936.
- Castet, E. & Masson, G.S. (2000). Motion perception during saccadic eye movements. *Nature Neuroscience*, 3, 177-183.
- Cavanagh, P. & Alvarez, G.A. (2005). Tracking multiple targets with multifocal attention. *Trends in Cognitive Science*, 9, 349-354.
- Cavanagh, P., Tyler, C.W., & Favreau, O.E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America A*, 1, 893-899.
- Churchland, A.K., Gardner, J.L., Chou, I., Priebe, N., & Lisberger, S.G. (2003). Directional anisotropies reveal a functional segregation of visual motion processing for perception and action. *Neuron*, 37, 1001-1011.
- Culham, J., He, S., Dukelow, S., & Verstraten, F.A. (2001). Visual motion and the human brain: what has neuroimaging told us? *Acta Psychologica*, 107, 69-94.
- Debono, K., Schütz, A.C., Spering, M., & Gegenfurtner, K.R. (2010). Receptive fields for smooth pursuit eye movements and motion perception. *Vision Research*, xx, xx-xx.
- De Brouwer, S., Yuksel, D., Blohm, G., Missal, M., & Lefèvre, P. (2002). What triggers catch-up saccades during visual tracking? *Journal of Neurophysiology*, 87, 1646-1650.
- Dobkins, K.R. & Albright, T.D. (2003). Merging processing streams: color cues for motion detection and interpretation. In L. Chalupa & J.S. Werner (Eds.), *The visual neurosciences* (pp. 1217-1228). Cambridge, MA: MIT Press.
- Dobkins, K.R. & Sampath, V. (2008). The use of chromatic information for motion segmentation: Differences between psychophysical and eye-movement measures. *Perception*, 37, 993-1009.
- Dürsteler, M.R. & Wurtz, R.H. (1988). Pursuit and optokinetic deficits following chemical lesions of cortical areas MT and MST. *Journal of Neurophysiology*, 60, 940-965.
- Duncker, K. (1929). Über induzierte Bewegung: Ein Beitrag zur Theorie optisch wahrgenommener Bewegung [On induced motion: A contribution to the theory of optically perceived motion]. *Psychologische Forschung*, 12, 180-259.
- Ferrera, V.P. (2000). Task-dependent modulation of the sensorimotor transformation for smooth pursuit eye movements. *Journal of Neurophysiology*, 84, 2725-2738.
- Ferrera, V.P. & Lisberger, S.J. (1995). Attention and target selection for smooth pursuit eye movements. *Journal of Neuroscience*, 15, 7472-7484.
- Ferrera, V.P. & Lisberger, S.G. (1997). Neuronal responses in visual areas MT and MST during smooth pursuit target selection. *Journal of Neurophysiology*, 78, 1433-1446.
- Festinger, L., Sedgwick, H.A., & Holtzman, J.D. (1976). Visual perception during smooth pursuit eye movements. *Vision Research*, 16, 1377-1386.
- Filehne, W.U. (1922). Über das optische Wahrnehmen von Bewegungen [On the visual perception of movement]. *Zeitschrift für Sinnesphysiologie*, 53, 134-145.
- Freeman, T.C.A. & Banks, M.S. (1998). Perceived head-centric speed is affected by both extra-retinal and retinal errors. *Vision Research*, 38, 941-945.
- Freeman, T.C.A., Champion, R.A., Sumnall, J.H., & Snowden, R.J. (2009). Do we have direct access to retinal image motion during smooth pursuit eye movements? *Journal of Vision*, 9, 1-11.
- Freeman, T.C.A., Champion, R.A., & Warren, P.A. (2010). A Bayesian model of perceived head-centered velocity during smooth pursuit eye movement. *Current Biology*, 20, 757-762.
- Frost, B.J. & Nakayama, K. (1983). Single visual neurons code opposite motion independent of

- direction. *Science*, 220, 744-745.
- Fukushima, K. (2003). Frontal cortical control of smooth-pursuit. *Current Opinion in Neurobiology*, 13, 647-654.
- Furmanski, C.S. & Engel, S.A. (2000). An oblique effect in human primary visual cortex. *Nature Neuroscience*, 3, 535-536.
- Garbutt S. & Lisberger S.G. (2006). Directional cuing of target choice in human smooth pursuit eye movements. *Journal of Neuroscience*, 26, 12479-12486.
- Gardner, J.L. & Lisberger, S.G. (2002). Serial linkage of target selection for orienting and tracking eye movements. *Nature Neuroscience*, 5, 892-899.
- Gardner, J.L., Tokiyama, S.N., & Lisberger, S.G. (2004). A population decoding framework for motion aftereffects on smooth pursuit eye movements. *Journal of Neuroscience*, 24, 9035-9048.
- Gauthier, G.M. & Hofferer, J.M. (1976). Eye movements in response to real and apparent motions of acoustic targets. *Perceptual & Motor Skills*, 42, 963-971.
- Gegenfurtner, K.R. & Hawken, M.J. (1995). Temporal and chromatic properties of motions mechanisms. *Vision Research*, 35, 1547-1563.
- Gegenfurtner, K.R. & Hawken, M.J. (1996). Interaction of motion and color in the visual pathways. *Trends in Neurosciences*, 19, 394-401.
- Gegenfurtner, K.R., Kiper, D.C., Beusmans, J.M., Carandini, M., Zaidi, Q., & Movshon, J.A. (1994). Chromatic properties of neurons in macaque MT. *Visual Neurosciences*, 11, 455-466.
- Gegenfurtner, K.R., Xing, D., Scott, B.H., Hawken, M.J. (2003). A comparison of pursuit eye movement and perceptual performance in speed discrimination. *Journal of Vision*, 3, 865-876.
- Gellman, R.S., Carl, J.R., & Miles, F.A. (1990). Short-latency ocular following responses in man. *Visual Neuroscience*, 5, 107-122.
- Goodale, M.A. & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15, 97-112.
- Groh, J.M., Born, R.T., & Newsome, W.T. (1997). How is a sensory map read out? Effects of microstimulation in visual area MT on saccades and smooth pursuit eye movements. *Journal of Neuroscience*, 17, 4312-4330.
- Grossman, E.D. & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, 35, 1167-1175.
- Hafed, Z.M. & Krauzlis, R.J. (2006). Ongoing eye movements constrain visual perception. *Nature Neuroscience*, 9, 1449-1457.
- Hafed, Z.M. & Krauzlis, R.J. (2010). Interactions between perception and smooth pursuit eye movements. In U.J. Ilg & G.S. Masson (Eds.), *Dynamics of visual motion processing: neuronal, behavioral, and computational approaches* (pp.189-211). New York: Springer.
- Haarmeier, P. & Thier, P. (1996). Modification of the Filehne illusion by conditioning visual stimuli. *Vision Research*, 36, 741-750.
- Haarmeier, P. & Thier, P. (1998). An electrophysiological correlate of visual motion awareness in man. *Journal of Cognitive Neuroscience*, 10, 464-471.
- Haarmeier, P., Thier, P., Repnow, M., & Petersen, D. (1997). False perception of motion in a patient who cannot compensate for eye movements. *Nature*, 389, 849-852.
- Hayashi, R., Sugita, Y., Nishida, S., & Kawano, K. (2010). How motion signals are integrated across frequencies: study on motion perception and ocular following responses using multiple-slit stimuli. *Journal of Neurophysiology*, 103, 230-243.
- Heinen, S.J. & Watamaniuk, S.J.N. (1998). Spatial integration in human smooth pursuit. *Vision Research*, 38, 3785-3794.
- Huk, A.C. & Heeger, D.J. (2000). Task-related modulation of visual cortex. *Journal of Neurophysiology*, 83, 3525-3536.

- Ilg, U.J. (1997). Slow eye movements. *Progress in Neurobiology*, 53, 293-329.
- Ilg, U.J. (2002). Smooth pursuit eye movements: from low-level to high-level vision. *Progress in Brain Research*, 140, 279-298.
- Ilg, U.J. & Churan, J. (2004). Motion perception without explicit activity in areas MT and MST. *Journal of Neurophysiology*, 92, 1512-1523.
- Ilg, U.J. & Thier, P. (1999). Eye movements of rhesus monkeys directed towards imaginary targets. *Vision Research*, 39, 2143-2150.
- Ilg, U.J. & Thier, P. (2003). Visual tracking neurons in primate area MST are activated by smooth-pursuit eye movements of an “imaginary” target. *Journal of Neurophysiology*, 90, 1489-1502.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perceptions & Psychophysics*, 14, 201-211.
- Keller, E.L. & Heinen, S.J. (1991). Generation of smooth-pursuit eye movements: neuronal mechanisms and pathways. *Neuroscience Research*, 11, 79-107.
- Kodaka, Y., Miura, K., Suehiro, K., Takemura, A., Kawano, K. (2004). Ocular tracking of moving targets: effects of perturbing the background. *Journal of Neurophysiology*, 91, 2474-2483.
- Kohn, A. & Movshon, J.A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience*, 7, 764-772.
- Komatsu, H. & Wurtz, R.H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *Journal of Neurophysiology*, 60, 580-603.
- Komatsu, H. & Wurtz, R.H. (1989). Modulation of pursuit eye movements by stimulation of cortical areas MT and MST. *Journal of Neurophysiology*, 62, 31-47.
- Konen, C.S., Kleiser, R., Seitz, R.J., & Bremmer, F. (2005). An fMRI study of optokinetic nystagmus and smooth pursuit eye movements in humans. *Experimental Brain Research*, 135, 203-216.
- Kowler, E. & McKee, S.P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research*, 27, 993-1015.
- Kowler, E. & Steinman, R.M. (1979a). The effect of expectations on slow oculomotor control. I. Periodic target steps. *Vision Research*, 19, 619-632.
- Kowler, E. & Steinman, R.M. (1979b). The effect of expectations on slow oculomotor control. II. Single target displacements. *Vision Research*, 19, 633-646.
- Kowler, E. & Steinman, R.M. (1981). The effect of expectations on slow oculomotor control – III. Guessing unpredictable target displacements. *Vision Research*, 21, 191-203.
- Krauzlis, R.J. (2004). Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology*, 91, 591-603.
- Krauzlis, R.J. (2005). The control of voluntary eye movements: new perspectives. *Neuroscientist*, 91, 124-137.
- Krauzlis, R.J. & Adler, S.A. (2001). Effects of directional expectations on motion perception and pursuit eye movements. *Visual Neuroscience*, 18, 365-376.
- Krauzlis, R.J. & Dill, N. (2002). Neural correlates of target choice for pursuit and saccades in the primate superior colliculus. *Neuron*, 35, 355-363.
- Krauzlis, R.J. & Hafed, Z.M. (2007). Finding our way around the sensory-motor corner. *Neuron*, 54, 852-854.
- Krauzlis, R.J. & Stone, L.S. (1999). Tracking with the mind’s eye. *Trends in Neurosciences*, 22, 544-550.
- Krauzlis, R.J., Zivotofsky, A.Z., & Miles, F.A. (1999). Target selection for pursuit and saccadic eye movements in humans. *Journal of Cognitive Neuroscience*, 11, 641-649.
- Krekelberg, B. (2010). Saccadic suppression. *Current Biology*, 20, 228-229.
- Krukowski, A.E., Pirog, K.A., Beutter, B.B., Brooks, K.R., & Stone, L.S. (2003). Human discrimination of visual direction of motion with and without smooth pursuit eye movements. *Journal of Vision*, 3, 831-840.

- Krukowski, A.E. & Stone, L.S. (2005). Expansion and direction space around the cardinal axes revealed by smooth pursuit eye movements. *Neuron*, 45, 315-323.
- Lamontagne, C., Gosselin, F., & Pivik, T. (2002). Sigma smooth pursuit eye tracking: constant k values revisited. *Experimental Brain Research*, 143, 130-132.
- Land, M.F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research*, 25, 296-324.
- Leigh, R.J. & Zee, D.S. (2006). *The neurology of eye movements*. 4th ed. Oxford: Oxford University Press.
- Lindner, A., Schwarz, U., Ilg, U.J. (2001). Cancellation of self-induced retinal image motion during smooth pursuit eye movements. *Vision Research*, 41, 1685-1694.
- Lisberger, S.G. (1994). Neural basis for motor learning in the vestibuloocular reflex of primates. III. Computational and behavioral analysis of the sites of learning. *Journal of Neurophysiology*, 72, 974-998.
- Lisberger, S.G. (2010). Visual guidance of smooth-pursuit eye movements: sensation, action, and what happens in between. *Neuron*, 66, 477-491.
- Lisberger, S.G., Ferrera, V.P. (1997). Vector averaging for smooth pursuit eye movements initiated by two moving targets in monkeys. *Journal of Neuroscience*, 17, 7490-7502.
- Lisberger, S.G., Morris, E.J., & Tychsen, L. (1987). Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annual Review of Neuroscience*, 10, 97-129.
- Lisberger, S.G. & Movshon, J.A. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *Journal of Neuroscience*, 19, 2222-2246.
- Lisberger, S.G. & Westbrook, L.E. (1985). Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *Journal of Neuroscience*, 5, 1662-1673.
- Liston, D. & Krauzlis, R.J. (2005). Shared decision signal explains performance and timing of pursuit and saccadic eye movements. *Journal of Vision*, 5, 678-689.
- Lorenceau, J. & Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research*, 32, 263-273.
- Lorenceau, J., Shiffrar, M., Wells, N., & Castet, E. (1993). Different motion sensitive units are involved in recovering the direction of moving lines. *Vision Research*, 33, 1207-1217.
- Lu, Z.L., Lesmes, L.A., & Sperling, G. (1999). Perceptual motion standstill in rapidly moving chromatic displays. *Proceedings of the Academy of Sciences USA*, 96, 15374-15379.
- Mack, A., & Herman, E. (1973). Position constancy during pursuit eye movements: an investigation of the Filehne illusion. *Quarterly Journal of Experimental Psychology*, 25, 71-84.
- Madelain, L. & Krauzlis, R.J. (2003). Pursuit of the ineffable: perceptual and motor reversals during the tracking of apparent motion. *Journal of Vision*, 3, 642-653.
- Marcar, V.L., Zihl, J., Cowey, A. (1997). Comparing the visual deficits of a motion blind patient with the visual deficits of monkeys with area MT removed. *Neuropsychologia*, 35, 1459-1465.
- Masson, G.S., Montagnini, A., & Ilg, U.J. (2010). When the brain meets the eye: tracking object motion. In U.J. Ilg & G.S. Masson (Eds.), *Dynamics of visual motion processing: neuronal, behavioral, and computational approaches* (pp.189-211). New York: Springer.
- Masson, G.S., Proteau, L. & Mestre, D.R. (1995). Effects of stationary and moving textured backgrounds on the visuo-oculo-manual tracking in humans. *Vision Research*, 35, 837-852.
- Masson, G.S. & Stone, L.S. (2002). From following edges to pursuing objects. *Journal of Neurophysiology*, 88, 2869-2873.
- Medina, J.F. & Lisberger, S.G. (2007). Variation, signal, and noise in cerebellar sensory-motor processing for smooth-pursuit eye movements. *Journal of Neuroscience*, 27, 6832-6842.
- Merrison, A.F.A. & Carpenter, R.H.S. (1991). "Express" smooth pursuit. *Vision Research*, 35, 1459-1462.
- Meyer, C.H., Lasker, A.G., & Robinson, D.A. (1985). The upper limit of human smooth pursuit

- velocity. *Vision Research*, 25, 561-563.
- Michels, L., Lappe, M. & Vaina, L.M. (2005). Visual areas involved in the perception of human movement from dynamic form analysis. *Neuroreport*, 16, 1073-1041.
- Miles, F.A., Kawano, K., & Optican, L.M. (1986). Short-latency ocular following responses of monkey. I. Dependence on temporospatial properties of visual input. *Journal of Neurophysiology*, 56, 1321-1354.
- Miura, K., Kobayashi, Y., & Kawano, K. (2009). Ocular responses to brief motion of textured backgrounds during smooth pursuit in humans. *Journal of Neurophysiology*, 102, 1736-1747.
- Montagnini, A., Mamassian, P., Perrinet, L., & Masson, G.S. (2007). Visual tracking of ambiguous moving objects: A recursive Bayesian model. *Journal of Vision*, 7(9), 406.
- Montagnini, A., Mamassian, P., Perrinet, L., Castet, E., & Masson, G.S. (2007). Bayesian modeling of dynamic motion integration. *Journal of Physiology (Paris)*, 101, 64-77.
- Morris, E.J. & Lisberger, S.G. (1987). Different responses to small visual errors during initiation and maintenance of smooth-pursuit eye movements in monkeys. *Journal of Neurophysiology*, 58, 1351-1369.
- Morvan, C. & Wexler, M. (2009). The nonlinear structure of motion perception during smooth eye movements. *Journal of Vision*, 9, 1-13.
- Nawrot, M. & Sekuler, R. (1990). Assimilation and contrast in motion perception: explorations in cooperativity. *Vision Research*, 30, 1439-1451.
- Newsome, W.T., Britten, K.H., & Movshon, J.A. (1989). Neuronal correlates of a perceptual decision. *Nature*, 341, 52-54.
- Newsome, W.T. & Paré, E.B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, 8, 2201-2211.
- Orban, G.A., Sunaert, S., Todd, J.T., Van Hecke, P., & Marchal, G. (1999). Human cortical regions involved in extracting depth from motion. *Neuron*, 24, 929-940.
- Orban de Xivry, J.J. & Lefèvre, P. (2007). Saccades and pursuit: two outcomes of a single sensorimotor process. *Journal of Physiology*, 584, 11-23.
- Orban de Xivry, J.J., Coppe, S., Lefèvre, P., & Missal, M. (2010). Biological motion drives perception and action. *Journal of Vision*, 10, 1-11.
- Osborne, L.C., Bialek, W., & Lisberger, S.G. (2004). Time course of information about motion direction in visual area MT of macaque monkeys. *Journal of Neuroscience*, 24, 3210-3222.
- Osborne, L.C., Hohl, S.S., Bialek, W., & Lisberger, S.G. (2007). Time course of precision in smooth-pursuit eye movements in monkeys. *Journal of Neuroscience*, 27, 2987-2998.
- Osborne, L.C., Lisberger, S.G., & Bialek, W. (2005). A sensory source for motor variation. *Nature*, 437, 412-416.
- Pack, C. & Born, R. (2001). Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature*, 409, 1040-1042.
- Pasternak, T. & Merigan, W.H. (1994). Motion perception following lesions of the superior temporal sulcus in the monkey. *Cerebral Cortex*, 4, 247-259.
- Price, N.S., Ono, S., Mustari, M.J., & Ibbotson, M.R. (2005). Comparing acceleration and speed tuning in macaque MT: physiology and modeling. *Journal of Neurophysiology*, 94, 3451-3464.
- Priebe, N.J. & Lisberger, S.G. (2004). Estimating target speed from the population response in visual area MT. *Journal of Neuroscience*, 24, 1907-1916.
- Rasche, C. & Gegenfurtner, K.R. (2009). Precision of speed discrimination and smooth pursuit eye movements. *Vision Research*, 49, 514-523.
- Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology*, 159, 326-338.
- Recanzone, G.H. & Wurtz, R.H. (1999). Shift in smooth pursuit initiation and MT and MST neuronal activity under different stimulus conditions. *Journal of Neurophysiology*, 82, 1710-1727.

- Recanzone, G.H. & Wurtz, R.H. (2000). Effects of attention on MT and MST neuronal activity during pursuit initiation. *Journal of Neurophysiology*, *83*, 777-790.
- Robinson, D.A. (1965). The mechanics of human smooth pursuit eye movement. *Journal of Physiology*, *180*, 569-591.
- Robinson, D.A., Gordon, J.L. & Gordon, S.E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics*, *55*, 43-57.
- Rokem, A. & Silver, M.A. (2009). A model of encoding and decoding in V1 and MT accounts for motion perception anisotropies in the human visual system. *Brain Research*, *1299*, 3-16.
- Ross, J., Morrone, M.C., Goldberg, M.E., & Burr, D.C. (2001). Changes in visual perception at the time of saccades. *Trends in Neuroscience*, *24*, 113-121.
- Rudolph, K. & Pasternak, T. (1999). Transient and permanent deficits in motion perception after lesions of cortical areas MT and MST in the macaque monkey. *Cerebral Cortex*, *6*, 814-822.
- Salzman, C.D., Murasugi, C.M., Britten, K.H., & Newsome, W.T. (1992). Microstimulation in visual area MT: effects on direction discrimination performance. *Journal of Neuroscience*, *12*, 2331-2355.
- Schlack, A., Hoffmann, K.P., & Bremmer, F. (2003). Selectivity of macaque ventral intraparietal area (area VIP) for smooth pursuit eye movements. *Journal of Physiology*, *551*, 551-561.
- Schoppik, D., Nagel, K.I., & Lisberger, S.G. (2008). Cortical mechanisms of smooth pursuit eye movements revealed by dynamic covariations of neural and behavioral responses. *Neuron*, *58*, 248-260.
- Schütz, A.C., Braun, D.I., & Gegenfurtner, K.R. (2007). Contrast sensitivity during the initiation of smooth pursuit eye movements. *Vision Research*, *47*, 2767-2777.
- Schütz, A.C., Braun, D.I., & Gegenfurtner, K.R. (2009). Chromatic contrast sensitivity during optokinetic nystagmus, visually enhanced vestibulo-ocular reflex, and smooth pursuit eye movements. *Journal of Neurophysiology*, *101*, 2317-2327.
- Schütz, A.C., Braun, D.I., Kerzel, D. & Gegenfurtner, K.R. (2008). Improved visual sensitivity during smooth pursuit eye movements. *Nature Neuroscience*, *11*, 1211-1216.
- Schwarz, U. & Ilg, U.J. (1999). Asymmetry in visual motion processing. *Neuroreport*, *10*, 2477-2480.
- Schwartz, J.D. & Lisberger, S.D. (1994). Initial tracking conditions modulate the gain of visuo-motor transmission for smooth pursuit eye movements in monkeys. *Visual Neuroscience*, *11*, 411-424.
- Schweigart, G., Mergner, T., & Barnes, G.R. (2003). Object motion perception is shaped by the motor control mechanism of ocular pursuit. *Experimental Brain Research*, *148*, 350-365.
- Snowden, R.J. & Braddick, O.J. (1991). The temporal integration and resolution of velocity signals. *Vision Research*, *31*, 907-914.
- Souman, J.L., Hooge, I.T., & Wertheim, A.H. (2005). Perceived motion direction during smooth pursuit eye movements. *Experimental Brain Research*, *164*, 376-386.
- Spering, M. & Gegenfurtner, K.R. (2007a). Contextual effects on smooth pursuit eye movements. *Journal of Neurophysiology*, *97*, 1353-1367.
- Spering, M. & Gegenfurtner, K.R. (2007b). Contrast and assimilation in motion perception and smooth pursuit eye movements. *Journal of Neurophysiology*, *98*, 1355-1363.
- Spering, M. & Gegenfurtner, K.R. (2008). Contextual effects on motion perception and smooth pursuit eye movements. *Brain Research*, *1225*, 76-85.
- Spering, M., Gegenfurtner, K.R., & Kerzel, D. (2006). Distractor interference during smooth pursuit eye movements. *Journal of Experimental Psychology: Human Perception & Performance*, *32*, 1136-1154.
- Spering, M., Kerzel, D., Braun, D.I., Hawken, M.J., & Gegenfurtner, K.R. (2005). Effects of contrast on smooth pursuit eye movements. *Journal of Vision*, *5*, 455-465.
- Spering, M., Montagnini, A., & Gegenfurtner, K.R. (2008). Competition between color and luminance for target selection in smooth pursuit and saccadic eye movements. *Journal of Vision*, *8*, 1-19.

- Spring, M., Schütz, A.C., Braun, D.I., & Gegenfurtner, K.R. (2010). Keep your eyes on the ball: smooth pursuit eye movements enhance prediction of visual motion. *Journal of Neurophysiology*, under review.
- Steinbach, M.J. (1976). Pursuing the perceptual rather than the retinal stimulus. *Vision Research*, 16, 1371-1376.
- Stocker, A.A. & Simoncelli, E.P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience*, 9, 578-585.
- Stone, L.S. & Krauzlis, R.J. (2003). Shared motion signals for human perceptual decisions and oculomotor actions. *Journal of Vision*, 3, 725-736.
- Stone, L.S. & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research*, 32, 1535-1549.
- Suehiro, K., Miura, K., Kodaka, Y., Inoue, Y., Takemura, A., & Kawano, K. (1999). Effects of smooth pursuit eye movement on ocular responses to sudden background motion in humans. *Neuroscience Research*, 35, 329-338.
- Takemura, A., Murato, Y., Kawano, K., & Miles, F.A. (2007). Deficits in short-latency tracking eye movements after chemical lesions in monkey cortical areas MT and MST. *Journal of Neuroscience*, 27, 529-541.
- Tavassoli, A. & Ringach, D.L. (2010). When your eyes see more than you do. *Current Biology*, 20, 93-94.
- Thier, P., Haarmeier, T., Chakraborty, S., Lindner, A., & Tikhonov, A. (2001). Cortical substrates of perceptual stability during eye movements. *Neuroimage*, 14, 33-39.
- Thier, P. & Ilg, U.J. (2005). The neural basis of smooth-pursuit eye movements. *Current Opinion in Neurobiology*, 15, 645-652.
- Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research*, 22, 377-380.
- Thompson, P., Brooks, K., & Hammett, S.T. (2006). Speed can go up as well as down at low contrast: implications for models of motion perception. *Vision Research*, 46, 782-786.
- Troje, N.F. (2008). Biological motion perception. In A. Basbaum, et al. (Eds.), *The senses: A comprehensive reference. Vol. 2: Vision II* (pp. 231-238). Oxford: Elsevier.
- Turano, K.A. & Heidenreich, S.M. (1999). Eye movements affect the perceived speed of visual motion. *Vision Research*, 39, 1177-1187.
- Tychsen, L. & Lisberger, S.G. (1986). Visual motion processing for the initiation of smooth-pursuit eye movements in humans. *Journal of Neurophysiology*, 56, 953-968.
- van der Steen, J., Tamminga, E.P. & Collewijn H. (1983). A comparison of oculomotor pursuit of a target in circular real, beta or sigma motion. *Vision Research*, 23, 1655-1661.
- von Fleischl, E. (1882). Physiologisch-optische Notizen [Notes on physiological optics]. *Sitzungsberichte der Akademie der Wissenschaften Wien*, 3, 7-25.
- von Helmholtz, H.(1910/1962). *Handbuch der physiologischen Optik [Treatise on physiological optics]*. (Vol. 3). New York: Dover.
- von Holst, E. & Mittelstaedt, H. (1950). Das Reafferenzprinzip [The reafference principle]. *Naturwissenschaften*, 37, 464-476.
- Wallace, J.M., Stone, L.S., & Masson, G.S. (2005). Object motion computation for the initiation of smooth pursuit eye movements in humans. *Journal of Neurophysiology*, 93, 2279-2293.
- Wallach, H. (1935). Über visuell wahrgenommene Bewegungsrichtung. *Psychological Research*, 20, 325-380.
- Watamaniuk, S.N. & Heinen, S.J. (1999). Human smooth pursuit direction discrimination. *Vision Research*, 39, 59-70.
- Watamaniuk, S.N. & Heinen, S.J. (2003). Perceptual and oculomotor evidence of limitations on processing accelerating motion. *Journal of Vision*, 3, 698-709.
- Watamaniuk, S.N. & Heinen, S.J. (2007). Storage of an oculomotor motion aftereffect. *Vision*

- Research*, 47, 466-473.
- Weiss, Y., Simoncelli, E.P., & Adelson, E.H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, 5, 598-604.
- Werkhoven, P., Snippe, H.P., & Toet, A. (1992). Visual processing of optic acceleration. *Vision Research*, 32, 2313-2329.
- Wertheim, A.H. & van Gelder, P. (1990). An acceleration illusion caused by underestimation of stimulus velocity during pursuit eye movements: Aubert-Fleischl revisited. *Perception*, 19, 471-482.
- Williams, Z.M., Elfar, J.C., Eskandar, E.N., Toth, L.J., & Assad, J.A. (2003). Parietal activity and the perceived direction of ambiguous motion. *Nature Neuroscience*, 6, 616-623.
- Wilmer, J.B. & Nakayama, K. (2007). Two distinct visual motion mechanisms for smooth pursuit: evidence from individual differences. *Neuron* 54, 987-1000.
- Wurtz, R.H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, 48, 2070-2089.
- Wyatt, H.J., Pola, J., Fortune, B., & Posner, M. (1994). Smooth pursuit eye movements with imaginary targets defined by extrafoveal cues. *Vision Research*, 34, 803-820.
- Xu, X., Collins, C.E., Khaytin, I., Kaas, J.H., & Casagrande, V.A. (2006). Unequal representation of cardinal vs. oblique orientations in the middle temporal visual area. *Proceedings of the National Academy of Sciences USA*, 103, 17490-17495.
- Yo, C. & Wilson, H.R. (1992). Perceived direction of moving two-dimensional patterns depends on duration, contrast and eccentricity. *Vision Research*, 32, 135-147.
- Zivotofsky, A.Z. (2005). A dissociation between perception and action in open-loop smooth-pursuit ocular tracking of the Duncker illusion. *Neuroscience Letters*, 376, 81-86.

Figure captions

Figure 1. a,b: Schematic results for a comparison between psychometric (blue) and oculometric (red) functions plotted as the probability of a response in a particular direction over stimulus strength in arbitrary coordinates. In a, both functions overlap, indicating similarities in response precision. In b, the slope of the oculometric function is steeper, indicating higher sensitivity of pursuit. **c,d:** Example data from Gegenfurtner et al. (2003, p. 869; to be printed with permission) for two observers. Psychometric and oculometric functions have similar slopes. **e:** Noise model from Stone and Krauzlis (2003, p. 731; to be printed with permission). In response to a given stimulus direction θ , a motion signal is generated and transformed into output signals driving perception and pursuit, respectively. At each stage, noise (η) is added to the signal. Because of their shared noise (η_v), the two output signals are partially correlated. Because of the independent noise for perception (η_p) and pursuit (η_m) the correlation is not perfect.

Figure 2. Pursuit and perceptual responses to speed perturbations in target and context obtained in Spering and Gegenfurtner (2007b). All data are for five observers. **a.** Mean eye velocity responses to context perturbations at fixed target speed $11.3^\circ/\text{s}$. Error bars are SEM. **b.** Mean perceptual judgments of target speed change. **c.** Correlations between two model predictions (VA and motion contrast) and perception (blue) and pursuit (red). Class boundaries divide the plot into zones in which responses are classified as VA-type or contrast-type responses. Data points falling in between the boundaries are considered as unclassified, which means that responses are well predicted by both models as correlation coefficients did not significantly differ from each other (adapted from Spering and Gegenfurtner, 2007b, p. 1358).

Figure 3. a. Schematic illustration of the aperture problem. A moving edge seen through an aperture

appears to move orthogonally to its orientation, in this case diagonally right and up (solid red arrow). The object's global or true motion path, in this case to the right (green arrow), can be decomposed into two local vector components, one parallel to the visible edge (dashed red arrow) and one orthogonal (solid red arrow). Only the orthogonal component is visible and drives motion perception. **b.** Line figure parallelogram as used in Beutter and Stone (2000). Left: Schematic of the parallelogram. Only the solid white lines were visible. Middle: Stimulus with visible apertures and example eye movement traces from one observer. Right: Invisible apertures and example eye movement traces. Eye traces are from Beutter and Stone (2000, p. 143; to be printed with permission). **c.** Top: Schematic of the visual stimulus used in Montagnini et al. (2007). Red arrows correspond to the global (or 2D, solid line) and local (or 1D, dashed line) motion signal direction. Bottom: Mean eye velocity (left: horizontal, right: vertical) for one representative observer in response to a tilted (solid lines) or a vertical (dashed lines) moving line; colors denote responses to three different stimulus speeds. The right-bottom panel shows the “unbiased” pursuit response, obtained by subtracting vertical eye velocity in response to the vertical line from vertical eye velocity to the tilted line (adapted from Montagnini, Mamassian, Perrinet & Masson, 2007).

Figure 4. Apparent and illusory motion stimuli. **a.** Kanitza-style stimulus used in Madelain and Krauzlis (2003; p. 644, to be printed with permission). **b.** Hourglass-shaped stimulus with blanked target center as used in Ilg and Thier (2003). In the main experiment, monkeys were instructed to track the invisible, “imaginary” target center. **c.** Occluded line object (termed a “chevron”) from Hafed and Krauzlis (2006, p. 1450; to be printed with permission). Only the white line segments were visible. Left: fixation condition, right: pursuit condition.

Figure 5. Hypothetical and simplified mechanisms for the control of perceptual and pursuit responses to motion input. Differences in latency and sensitivity between both systems could be explained by (1)

the same decision signal (either D1 or D2) guiding perception and pursuit to different thresholds, (2) by different decision signals D1 and D2 guiding to the same threshold, or (3) by different decision signals guiding to different thresholds.

Figure 1

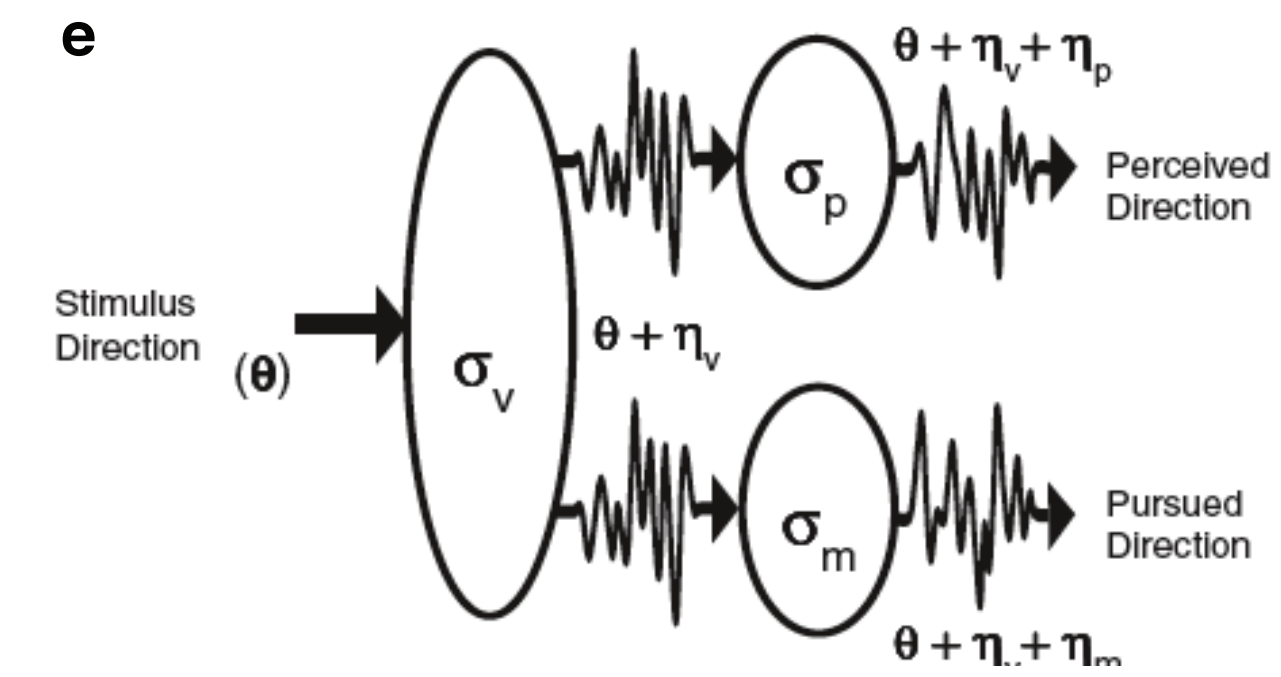
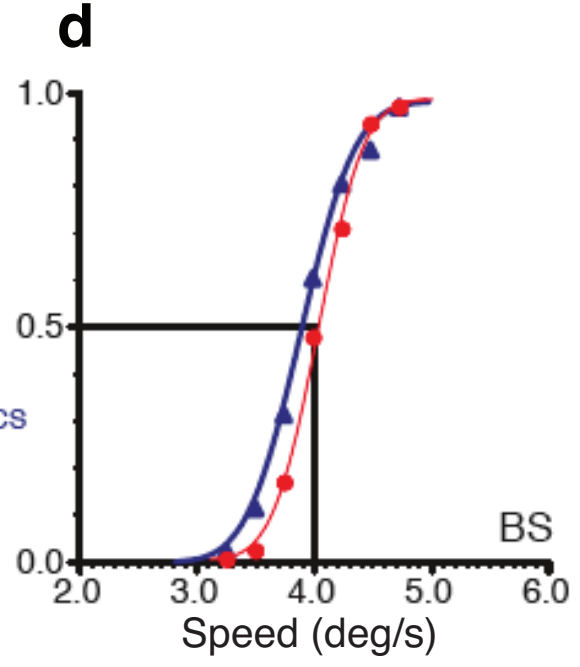
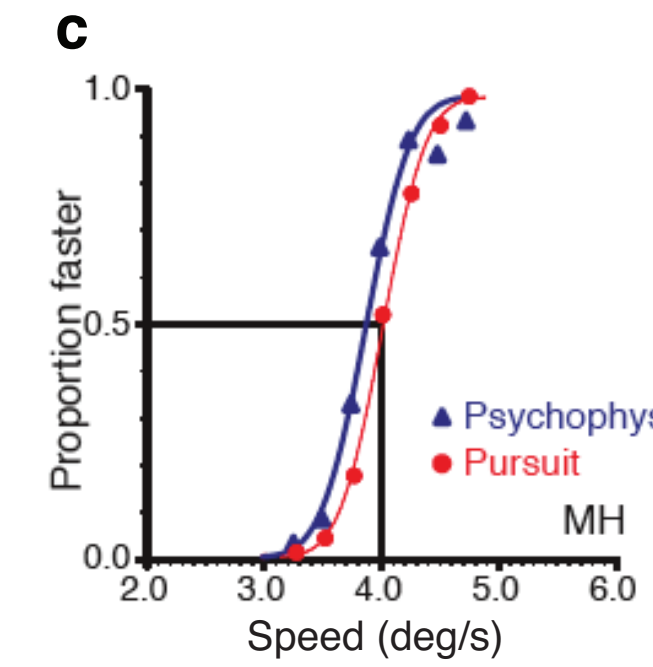
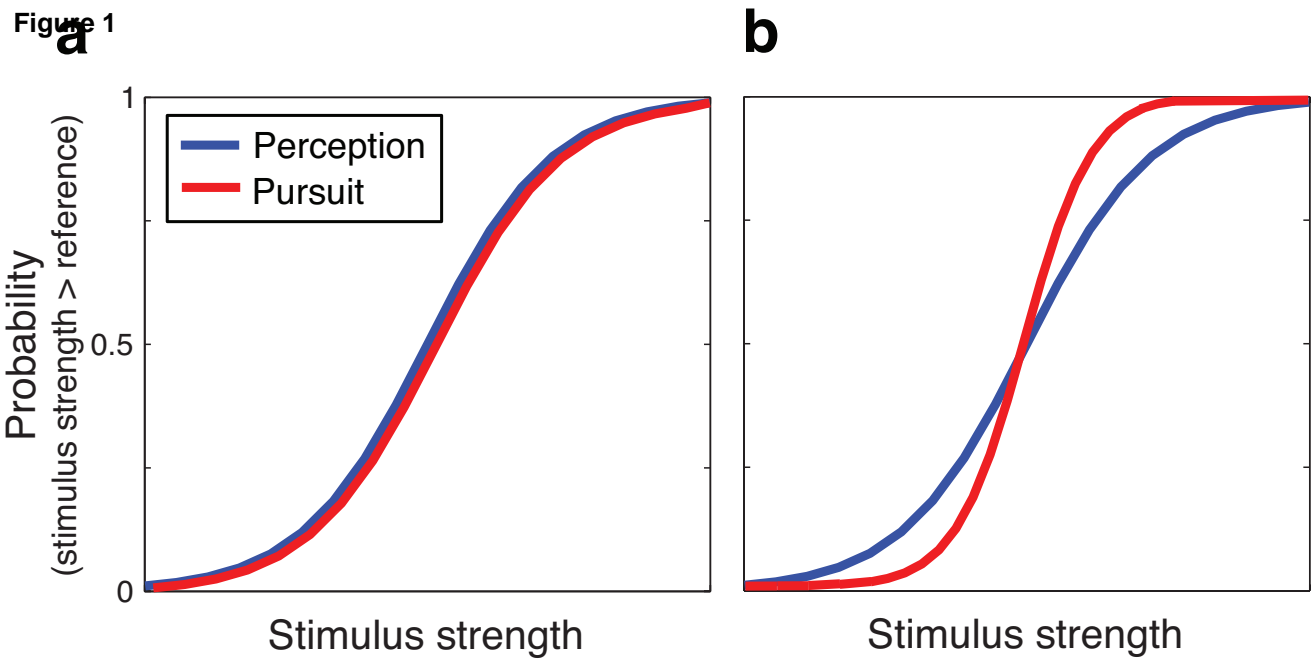


Figure 2

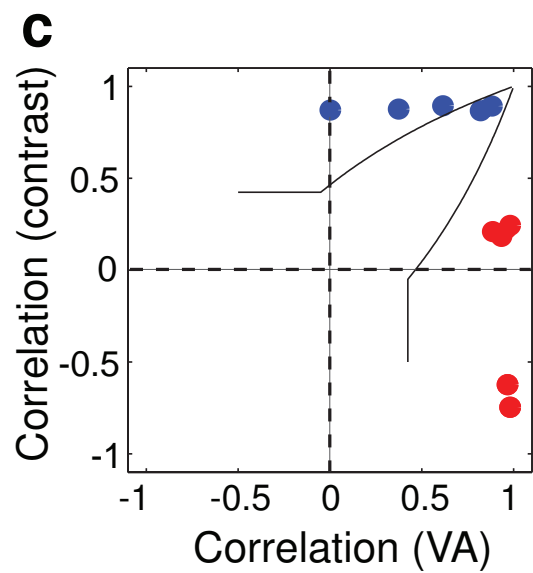
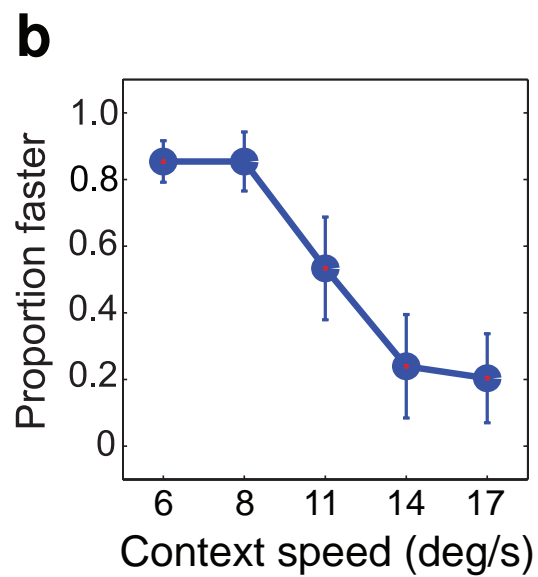
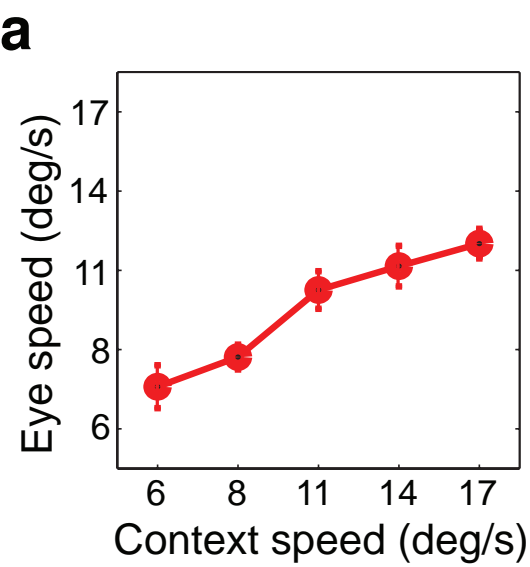
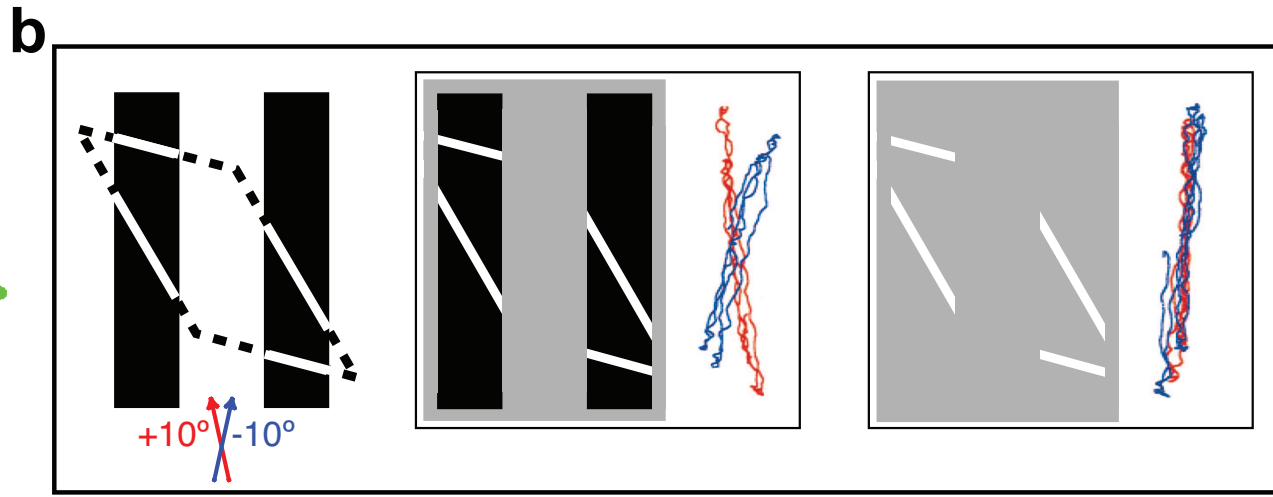
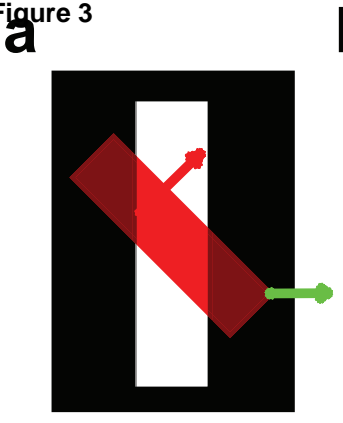
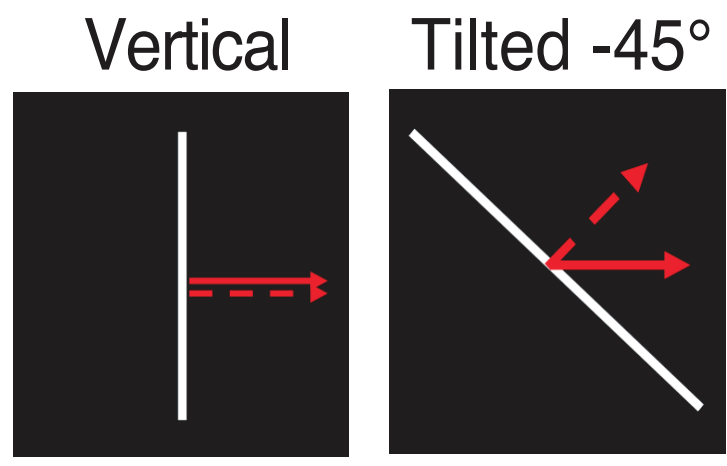


Figure 3

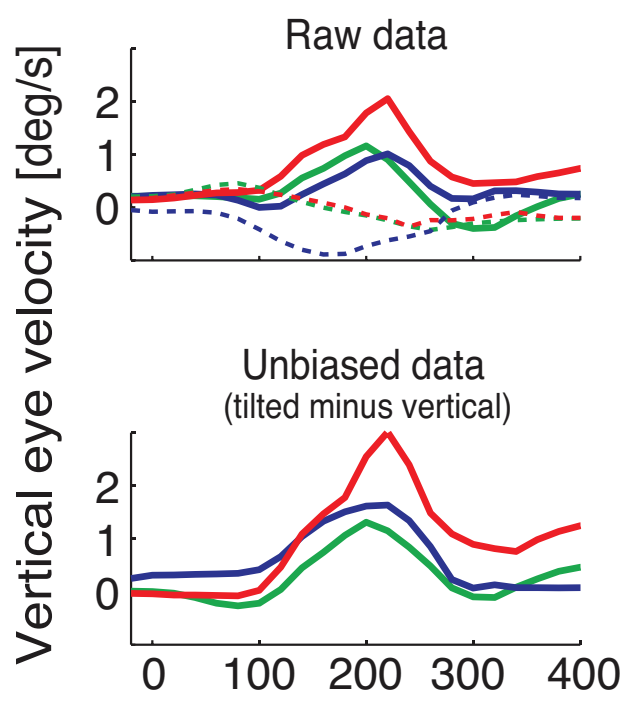
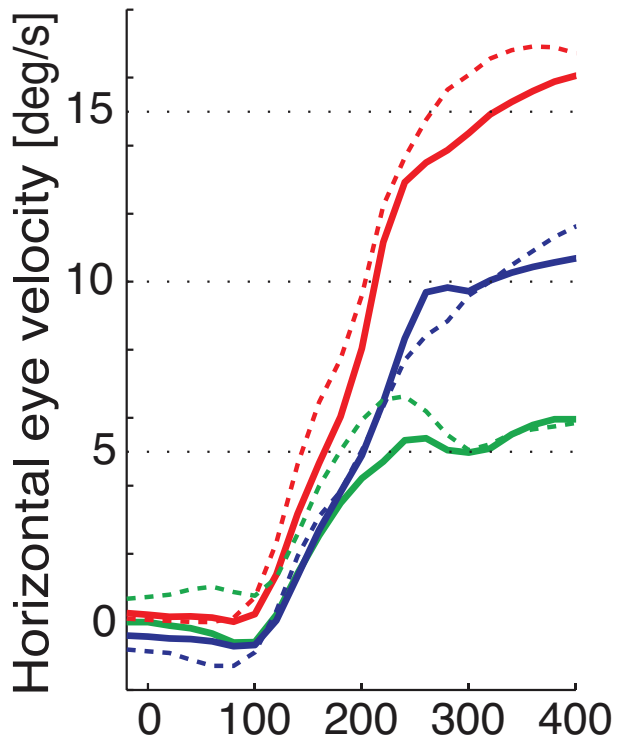


c



Global (2D) motion
 Local (1D) motion

Tilted 5 deg/s
 Tilted 10 deg/s
 Tilted 15 deg/s
 Vertical 5 deg/s
 Vertical 10 deg/s
 Vertical 15 deg/s



Time from target motion onset [ms]

Figure 4

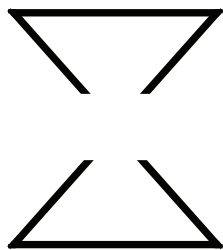
a

Frame A

Frame B



b



c

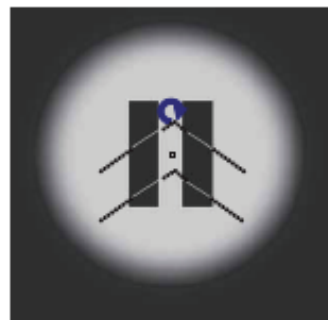


Figure 5

