Open-loop speed discrimination performance of ocular following response and perception

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ABSTRACT

So far, it remains largely unresolved to what extent neuronal noise affects behavioral responses. Here, we investigate, where in the human visual motion pathway noise originates that limits the performance of the entire system. In particular, we ask whether perception and eye movements are limited by a common noise source, or whether processing stages after the separation into different streams limit their performance. We use the ocular following response of human subjects and a simultaneously performed psycho-physical paradigm to directly compare perceptual and oculomotor system with respect to their speed discrimination ability. Our results show that on the open-loop condition the perceptual system is superior to the oculomotor system and that the responses of both systems are not correlated. Two alternative conclusions can be drawn from these findings. Either the perceptual and oculomotor pathway are effectively separate, or the amount of post-sensory (motor) noise is not negligible in comparison to the amount of sensory noise. In view of well-established experimental findings and due to plausibility considerations, we favor the latter conclusion.

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1. Introduction

The human visual system is designed to guide us through a complex and often dangerous world. However, just like any real-world system, the visual system is not perfect. The imperfections show up in the form of systematic errors and statistical fluctuations of the motor response, the latter phenomenon is known as *variability*. Since the variability eventually limits the overall performance, it is of great interest, where in the visual pathway and to what amount noise arises.

We compare the discrimination performance of both oculomotor system and perception to find noise sources within the visual motion pathway that affect behavioral variability. Oculomotor responses vary from trial to trial (see e.g. Kowler & McKee, 1987; Rasche & Gegenfurtner, 2009; Stone & Krauzlis, 2003). Similarly, perceptual decisions about, say, the speed or the direction of stimulus motion vary between trials even on the presentation of identical stimuli (see e.g. Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; De Bruyn & Orban, 1988; Shadlen, Britten, Newsome, & Movshon, 1996; Watamaniuk & Heinen, 1999). If both perception and oculomotor behavior are mainly limited by noise in the common processing pathway, their level of performance should be similar and their responses should be correlated. How-

ever, if there is dominating noise after the division into separate pathways, one system is likely to perform better than the other and responses do not need to correlate.

When a moving stimulus is shown that covers a large part of the visual field, the eyes of the observer automatically start to follow the motion and regularly perform saccades into the reverse direction. This reflexive, sawtooth-like ocular tracking of a moving scene is known as the *optokinetic nystagmus* (OKN). For example, we can activate OKN by looking out the window of a running train. The smooth, saccade-free initial part of the OKN is also known as the *ocular following response* (OFR) (Buttner & Kremmyda, 2007; Gellman, Carl, & Miles, 1990; Miles, 1997; Miles, Kawano, & Optican, 1986). In another visual task, when attention is paid to a small target that starts to move against a structured or non-structured background, the eyes smoothly track the target after an initial catch-up saccade. This behavior is known as *smooth pursuit* (SP) (Heinen & Keller, 2004; Ilg, 1997; Robinson, 1965; Tychsen & Lisberger, 1986). There is good evidence that the systems responsible for ocular following and for smooth pursuit share common brain areas (Dürsteler & Wurtz, 1988; Newsome, Wurtz, Dursteler, & Mikami, 1985; Petit & Haxby, 1999; Takemura, Murata, Kawano, & Miles, 2007), although it is not clear whether or not the neuronal populations involved in the two tasks are identical in detail (Ilg, 1997).

Perceptual and oculomotor performance have previously been compared with respect to smooth pursuit (Beutter & Stone, 1998, 2000; Churchland, Gardner, Chou, Priebe, & Lisberger, 2003;

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Dobkins, Stoner, & Albright, 1998; Gegenfurtner, Xing, Scott, & Hawken, 2003; Haarmeier & Thier, 2006; Kowler & McKee, 1987; Krauzlis & Adler, 2001; Osborne, Hohl, Bialek, & Lisberger, 2007; Rasche & Gegenfurtner, 2009; Stone & Krauzlis, 2003; Watamaniuk & Heinen, 1999, 2003). Here we concentrate on OFR because its reflexiveness ensures a minimal cognitive contribution (Gellman et al., 1990; Ilg, 1997; Miles, 1997, 1998). Also, the absence of saccades in the OFR facilitates our analysis of the eye traces.

The oculomotor system can roughly be broken down into two main subsystems: The sensory system and the post-sensory system which takes on post-processing of sensory output and coordination of motor action. As for the sensory subsystem, there is strong evidence that perception and oculomotor system share a common neuronal pathway, starting from light receptors and low-level processing in the retina and the lateral geniculate nucleus (LGN), proceeding to elementary motion detectors in the visual cortex (V1) up to the medial temporal (MT) and medial superior temporal cortex (MST) (Britten et al., 1996; Liu & Newsome, 2005; Newsome, Britten, & Movshon, 1989; Takemura et al., 2007). There is a parallel subcortical pathway involving the *nucleus of the optic tract* (NOT) which contributes to OKN and SP, but not to motion perception. However, the subcortical pathway affects the indirect (late) component to the OKN rather than the direct (early) component which constitutes the OFR (Buttner & Kremmyda, 2007; Ilg, 1997; Ilg, Bremmer, & Hoffmann, 1993; Ilg & Hoffmann, 1996; Schiff, Cohen, Buttner-Ennever, & Matsuo, 1990; Yakushin et al., 2000).

At first sight, it appears plausible that both the sensory and post-sensory subsystem contribute to the response variability to a similar extent. Both systems involve many neurons, each of which can be expected to add variability due to the stochastic nature of ion channels and synaptic transmission underlying any neural activity (see e.g. Faisal, Selen, & Wolpert, 2008). In addition, the motor system's final translation of electrochemical processes into mechanical movement has been found to be afflicted with additional impreciseness (van Beers, Haggard, & Wolpert, 2004). Recent studies (Huang & Lisberger, 2009; Osborne, Lisberger, & Bialek, 2005; Osborne et al., 2007), however, provide evidence that the imperfection of the oculomotor system is mainly caused by noise in the sensory system, hence by stochastic errors in the estimation of stimulus properties. Other experimental studies (Gegenfurtner et al., 2003; Kowler & McKee, 1987; Rasche & Gegenfurtner, 2009), however, speak against this conclusion, which is also known as the *sensory noise hypothesis*.

In the present study we compare perception and OFR with respect to their capability to discriminate between two motion stimuli that differ in speed. The speed discrimination performance of the perceptual system is determined by a two alternative forced choice (2AFC) paradigm: The subject observes pairs of moving stimuli and decides which one appears to be faster. The stimuli in our experiments are random dot patterns that cover a large part of the visual field and evoke reflexive eye movements in the direction of stimulus motion. We use random dot patterns because they contain a wide range of spatial frequencies and thus can be assumed to stimulate a large population of motion detectors (Adelson & Bergen, 1985; Priebe, Lisberger, & Movshon, 2006; Simoncelli & Heeger, 1998). The speed discrimination performance of the oculomotor system is determined by analyzing the ocular responses recorded by an eye tracker while the subject performs the perceptual task. The simultaneity of both measurements enables us to investigate correlations between the perceptual and oculomotor responses. In order to compare psychophysical and oculomotor data, the latter are transformed into a binary "oculomotor decision" analog to the psychophysical decision. If there is a common noise source shared by both oculomotor and perceptual system, and if the additional noise after the separation of the corresponding pathways is relatively weak, then the responses of both systems should be mutually correlated.

The oculomotor system can be conceived as a control loop circuit, where the signals from the retina containing motion information feed into a sensorimotor pathway that controls the eye movements. The eye movements cause a shift of the retinal image that adds onto stimulus motion, and this takes effect on subsequent eye movements. The open-loop period is the time interval, where the eye movements are solely based on the visual information of the initial phase, where the feedback loop is still open. Hence, in the case of a stationary observer who does not move his eyes prior to response onset, retinal stimulus displacements in the open-loop phase are solely caused by motion in the surroundings and not by eye movements. In our experiments we ask subjects to initially fixate a spot and then deliver short-term stimuli so that the initiated reflexive eye movements are exclusively based on open-loop neural processing.

Our main findings are that (1) the speed discrimination performance of the oculomotor system is systematically lower than that of the perceptual system and that (2) there is no significant correlation between the eye movements and the perceptual decision. From these two findings two alternative conclusions can be derived: Either (1) there is *sufficient additional post-sensory (motor) noise* to bring the discrimination performance of the oculomotor system below that of the perceptual system and to destroy the correlation between the responses of these systems, or (2) the pathways leading from the visual input to the perceptual and oculomotor output are *effectively separate*. There are several anatomical and lesion studies that speak in favor of the same brain areas being involved in early stages of perception and oculomotor response (see Section 4). Although it cannot be excluded with certainty that oculomotor and perceptual system involve different neuronal sub-populations within these areas, we find such a scenario highly implausible. Hence we altogether favor the first of the two conclusions, namely that there is a considerable amount of post-sensory noise entering the oculomotor pathway.

2. Materials and methods

2.1. Visual stimulation

The stimulus consists of a moving random pattern of black dots (0.01 cd/cm^2) on white ground (107.6 cd/cm^2), with an average density of two dots per deg^2, each dot having a diameter of 0.15 deg (deg = degree viewing angle). We decided against the usual random dot pattern with white dots on black ground because on our monitor they can be perceived to show a tail when moving, which could serve as a speed cue to the subject. The dots are distributed across the entire screen. When a moving dot leaves the screen on one side, it re-enters the screen on the opposite side at the same vertical position. The pattern of dots is randomly generated at the beginning of each stimulus sequence. The screen is a 40×30 cm^2 CRT monitor (Iiyama Vision Master 506) driven at 160 Hz with a resolution of 800×600 pixels. The stimulus is generated by an Apple PowerMac G5 at 2×2 GHz and is programmed in Objective-C/Cocoa/OpenGL. All displayed items are anti-aliased so that movement appears smooth and dots appear as circles. The viewing distance is 57 cm, so that 1 cm on the screen corresponds to approximately 1 deg viewing angle.

It is known that the ocular following response becomes more pronounced when it is executed shortly after a saccade, an effect called *post-saccadic enhancement* (PSE) (Gellman et al., 1990; Miles et al., 1986). To see whether this effect alters the ocular and psychophysical discrimination performance, we conducted two different experiments per subject. One with an initial centering saccade

(PSE condition) and one without it (non-PSE condition). On the PSE condition, the temporal sequence of the stimulus is as follows. A static random dot pattern appears together with a fixation cross, the latter positioned 10 deg left from the center of the screen. 50 ms after the subject has put the focus on the fixation cross, it disappears and reappears in the center. As soon as the subject puts the focus on the central fixation cross, it disappears and after a post-saccadic delay of 50 ms the dot pattern moves randomly to the left or right for a duration of 75 ms. The sequence is delivered twice per trial, each with different stimulus parameters (see below), and with an intermediate interval of 500 ms showing the blank white screen. The focus of the eye gaze was recognized within a window of 2 deg horizontal width. On the non-PSE condition, the fixation spot is shown only in the center.

One of the two stimuli shown per trial is the *reference stimulus* moving randomly to the left or right at 10 deg/s. The other one is the *test stimulus* moving randomly to the left or right (independent from the reference stimulus) at a speed chosen from $\{4, 7, 10, 13, 16\}$ deg/s in a pseudo-random fashion. At the end of each trial the subject has to indicate which of the two stimuli appeared to be faster by pressing a corresponding key. A visual feedback was given, informing the subject whether or not his/her choice was correct. The reaction time was not limited and not measured. When acquiring data for the naive subjects (see below), four experimental sessions were held for each condition (PSE and non-PSE). Each session consisted of the presentation of 40 trials for each combination of the reference with one of five test stimuli and lasted between 15 and 20 min. The authors performed only one session for each condition with 100 trials per stimulus combination and session.

It is necessary to keep subjects from using other cues except the perceived motion for their judgment. We generated a new random dot pattern independently for test and reference stimulus to keep the subject from comparing the position of identical sub-patterns. Also, the direction of motion is randomly chosen to be left or right for each stimulus separately, in order to prevent the subject from using the end position of their eyes as a speed cue, and to attenuate potential anticipatory effects in the ocular response. (For anticipatory effects in the smooth pursuit response see Kowler, Martins, & Pavel, 1984; Kowler & McKee, 1987.) Lastly, the ordering of test and reference stimulus was randomized in each trial in order to cancel out selection biases.

Gellman et al. (1990) have shown that the OFR is more pronounced at stimulus speeds higher than those we have tested, in terms of shorter latencies and higher amplitudes, up to a speed of about 40 deg/s. However, the gain, i.e. the ratio of elicited eye speed (170 ms after motion onset) and stimulus speed, decreases for stimulus speeds above 10 deg/s, so the responses to different stimulus speeds become less separated from each other. From Fig. 3 in Gellman et al. (1990) we derive that for a stimulus speed of 5, 10, 20, 40, 80 deg/s the gain yields 0.57, 0.64, 0.51, 0.31, 0.17. Hence, a speed range centered about 10 deg/s is expected to be well-suited for obtaining an optimal discrimination performance of the OFR. Control experiments for a speed range centered about 20 deg/s (data not shown here) showed a considerably poorer ocular discrimination performance and thus confirmed this expectation.

2.2. Subjects and preparation

The subjects were instructed to focus the fixation spot as long as it was present and otherwise pay attention to the overall stimulus speed. They were instructed to pay attention to the overall motion of the cloud but not to individual dots. This was done in order to minimize potential contributions of the smooth pursuit system. All subjects had normal (ChR, MaE, PhG, AnO) or corrected-to-normal (KJB, AKW) binocular vision and were seated in a darkened

room with their head stabilized by a chin support and a bite board, in order to minimize tracker noise.

The naive subjects (ChR, MaE, PhG, AnO) underwent a training phase before evaluating their speed discrimination performance, because, as discussed above, many naive subjects had serious difficulties discriminating between the different speeds. In a first training session the stimulus duration was set to 125 ms. Otherwise the first training session was identical to the final experimental procedure. In addition, naive subjects performed a training session with this relatively long stimulus duration with 20 trials for each combination of test- and reference speed immediately before each experimental session. For each subject only one session was held per day. There were six final participants in the study, two of which are the authors.

2.3. Data acquisition

The gaze position of the left eye was recorded by an infrared eye tracker (EyeLink 1000, SR Research, Canada) running at 500 Hz sample rate and using pupil and corneal reflex detection. The eye tracker was connected to a Host PC running the controller software, which was itself remotely controlled by the Stimulus PC via Ethernet. No online filtering was applied to the data, all filtering and post-processing took place offline and was carried out with MATLAB™. After each presentation of a trial, i.e. a sequence containing one test and one reference stimulus, subjects indicated the stimulus they perceived as being faster by pressing a key. These perceptual decisions were recorded together with the eye movements.

2.4. Data evaluation

2.4.1. Different integration methods

While the perceptual decision is a discrete event, the ocular following response is a continuous process. In order to directly compare the precision of perceptual and oculomotor system, we had to somehow transform the continuous process into a binary value. As a general procedure, one may choose a time interval over which to integrate the eye velocity data. Our default method was to perform no integration and take the eye velocity at a discrete point in time t, a strategy that was also chosen by Osborne et al. (2007) and Rasche and Gegenfurtner (2009). Since the eye data were beforehand filtered by a 20 ms running average to reduce measurement noise, the discrete time point t actually corresponds to a time window of that size. We have also applied a second method that additionally involves an integration over 100 ms, centered on the respective time point t. The interval length of 100 ms has been chosen because of its common use in the literature (Gegenfurtner et al., 2003; Kowler & McKee, 1987; Watamaniuk & Heinen, 1999). An integration over 100 ms flattens fluctuations of down to 10 Hz, which lies in the range of physically possible, natural movements of the eye. Microsaccades, tremor movements and eyeball jitter will be considerably reduced, so the filtered data are somewhat artificially clean. Lastly, we have also applied a third method which involves a cumulative integration from stimulus motion onset at $t = 0$ up to time t. This filtering removes not only natural eyeball jitter but also reduces the main response itself. It yields the change in eye position since stimulus motion onset.

In the following we will focus on the first integration method, since, as it turned out, the second method did not improve the so-determined oculomotor performance, and the third method even diminished it considerably.

2.4.2. Psychometric and oculometric functions

In order to determine the noise contributions of the sensory and the post-sensory (motor) part of the OFR system, we directly compare the discrimination performance of perception and oculomotor

system. This can be done using an oculometric function derived from the eye responses, analog to the psychometric function derived from the psychophysical task.

In our 2AFC paradigm the subject has to decide which of two presented stimuli appears to be faster. We use the standard techniques of signal detection theory (Green & Swets, 1966) to generate a psychometric function from the proportion of answers "test stimulus appears faster". In short, the psychometric function is interpreted as the probability that the activation strength Y_x of the neuronal correlate of the test stimulus of (variable) speed x is larger than activation strength Y_r of the neuronal correlate of the reference stimulus of (fixed) speed r,

$$\Psi_r(x) = \mathscr{P}\{Y_r \leqslant Y_x\}, \tag{1}$$

where $\mathscr{P}$ denotes probability. On the assumption that the activation strengths are Gaussian distributed, the psychometric function $\Psi_r(x)$ is a cumulative Gaussian centered at r,

$$\Psi_r(x) = \Phi\left(\frac{x - r}{\tilde{\sigma}}\right), \tag{2}$$

where $\Phi(z)$ is the standard cumulative Gaussian distribution and where $\tilde{\sigma}$ is the width of the distribution which we will call the *effective noise*. It is not a direct measure of the internal variability, that is, of the *true* amount of internal noise. Rather, the effective noise $\tilde{\sigma}$ is also influenced by the resolution of the internal stimulus representation, i.e. by the separation of individual activation strengths.

We now apply the same methods to the oculomotor response. Instead of considering the internal neuronal activation strength Y_x, we consider the eye speed $\dot{e}_x(t)$ elicited by a stimulus of speed x, t seconds after motion onset. For each trial and for each test speed $x_1, \ldots x_n$, we calculate an "oculomotor decision" by comparing the eye speed in response to both reference and test stimulus at time t. By averaging over all trials we obtain an estimation of the probabilities $p_1, \ldots, p_n$ of "test stimulus evokes stronger response" for test speeds of $x_1, \ldots, x_n$. Fitting a cumulative Gaussian gives the "oculometric function"

$$\Omega_r(t, x) = \mathscr{P}\{\dot{E}_r(t) \leqslant \dot{E}_x(t)\}, \tag{3}$$

where $\dot{E}_r(t)$ and $\dot{E}_x(t)$ are the random numbers of the eye speed elicited at time t by the reference and test stimulus, respectively. From the oculometric function we estimate the amount of effective oculomotor noise, i.e. the standard deviation of the fitted cumulative Gaussian.

In the literature, the methods for obtaining an oculometric curve are slightly different from ours, because there the stimuli are not presented in pairs so that direct comparison is not possible. Instead, a separate set of responses to the reference ("non-signal") stimulus is statistically compared against a set of responses to the test ("signal") stimulus with varying signal strength (here, speed). We found these methods being used by Beutter and Stone (1998), Gegenfurtner et al. (2003), Kowler and McKee (1987), Rasche and Gegenfurtner (2009), Stone and Krauzlis (2003), Watamaniuk and Heinen (1999). It should be noted that our method is not inferior to the standard method, but it is rather more accurate as it involves a trial-by-trial discrimination of reference and test stimulus.

2.4.3. Tracker noise

It is of vital importance for our conclusions that we separate the measurement noise introduced by the eye tracker from the intrinsic biological variability of the ocular responses. In the following we present a technique that is, to our knowledge, novel and may be applied also in other experimental situations, where measurement noise must be separated from intrinsic variability.

The eye tracker generates a certain amount of gaze position and velocity noise that compromises the discriminability performance of the measured ocular responses. The measured eye gaze position at time t is represented by a random variable $E_{\text{ocm}}(t)$ which is itself a sum of the true eye position $E(t)$ and a time-independent noise term N_{track} due to tracker noise. The true eye position itself can be decomposed into an ideal, noise-free term $e(t) = \langle E(t) \rangle$ and a noise term $N_{\text{oc}}(t)$ due to oculomotor variability, so that we arrive at

$$E_{\text{ocm}}(t) = e(t) + N_{\text{oc}}(t) + N_{\text{track}}. \tag{4}$$

The mean and variance of the measured eye position E_{ocm} are then given by

$$\mu_{\text{ocm}}(t) = e(t), \tag{5}$$
$$\sigma_{\text{ocm}}^2(t) = \sigma_{\text{oc}}^2(t) + \sigma_{\text{track}}^2, \tag{6}$$

respectively. By using the methods described in the previous section, the measured eye speed reveals a certain discrimination performance at time t, from which we derive the effective noise $\tilde{\sigma}_{\text{ocm}}(t)$. This value depends on both the ideal response $e(t)$ and the sum of physiological and measurement-induced variability.

To separate the latter two noise sources, we let the eye tracker measure a stationary artificial eye (Fourward Technologies Inc., Buena Vista, USA). The standard deviation of the noise on the gaze position of the artificial eye falls below 0.01 deg and the corresponding velocity noise undercuts 10 deg/s. The filtering (running average 20 ms) reduces the position noise to below 0.005 deg and the speed noise to below 0.2 deg/s. We let the eye tracker measure 2×150 trials (150 for the reference stimulus, 150 for the test stimulus), according to the maximum number of trials per condition used in our experiments, and obtain tracker noise velocity data by digital derivation. This gives us an estimate for the eye tracker noise variable N_{track} in the form of 2×150 realizations of that variable, suited for our experimental situation. We add the unfiltered tracker noise data to the mean response of a given subject to a given stimulus, and thus obtain *surrogate data* which obey the relation

$$E_{\text{surr}}(t) = e(t) + N_{\text{track}}. \tag{7}$$

For each reference and test stimulus r and x, respectively, we obtain surrogate data which we now treat in the same way as normal data (involving filtering and analyzing), so that we can infer the effective noise $\tilde{\sigma}_{\text{track}}(t)$ induced by the eye tracker at time t for that particular subject in that particular experimental session. We took the mean response only of rightward eye movement as the basis for the surrogate data, and not, more easily but potentially problematically, the mean responses of eye movements in both directions. However, there were no considerable differences resulting from this measure.

In the above described method, the artificial eye remains stationary, so what about measurement noise induced by eye motion due to motion smear? The exposure time of the camera falls below 1 ms. In our experiments, the eye speed stayed below 10 deg/s, so motion smear would fall below 0.01 deg which undercuts the spatial resolution of the eye tracker. It is therefore rather unlikely that eye movements increase the tracker noise. Nonetheless, we measured the noise with the artificial eye being put into sinusoidal motion by a digital function generator and a Galvo motor. The viewing angle is swept over a range of 5 deg with a temporal frequency of 1 Hz, thus covering the range of measured viewing angles and eye speeds occurring in our experiments. In accordance to our theoretical considerations, we did not find any systematic dependence of measurement noise on eye speed.

The effective noise terms of the oculomotor response are time-dependent, so how shall we compare these to the time-independent effective noise from the psychophysical task? We could simply take the end of the open-loop phase. At this point in time the stimulus motion is completely processed by the oculomotor system. However, the OFR system might reach its optimal estimation

performance at some instance before or after the end of the open-loop phase, depending on the speed and efficiency of the neuronal processes involved in speed estimation and motor control. Consequently, we calculate the speed discrimination performance of the OFR system at several time points and then take the optimum value. In the following considerations let us suppress the explicit time dependence of the effective noise values while keeping in mind that we take the minimum over a series of values obtained in the interval [0,200] ms after stimulus motion onset. The minimum of the curve is taken as the measured effective noise $\tilde{\sigma}_{ocm}$ of the oculomotor system, including measurement noise,

$$\tilde{\sigma}_{ocm} = \min_{t\in[0,200]\ ms}\{\tilde{\sigma}_{ocm}(t)\}. \tag{8}$$

The time point t_{opt}, where this minimum value is taken yields the time point, where oculomotor and psychophysical discrimination performance are compared,

2.4.4. Noise sources

We now seek to identify and quantify the effective contribution of different noise sources along the oculomotor pathway. By "effective contribution" we mean here that the individual contributions of internal noise sources are taken to be (1) statistically independent and (2) additive. Consequently, the square of the total effective noise is the sum of the squares of the individual effective noise contributions,

$$\tilde{\sigma}_{total}^2 = \sum_i \tilde{\sigma}_i^2. \tag{9}$$

In our experimental situation the total effective noise is the measured effective oculomotor noise $\tilde{\sigma}_{ocm}$ from the OFR system, as obtained from the oculometric function. The contributions come from the sensory noise $\tilde{\sigma}_{sens}$ in the visual system, the motor noise $\tilde{\sigma}_{mot}$ in the post-sensory (motor) part of the oculomotor system, and the tracker noise $\tilde{\sigma}_{track}$ in the eye tracker:

$$\tilde{\sigma}_{ocm}^2 = \tilde{\sigma}_{sens}^2 + \tilde{\sigma}_{mot}^2 + \tilde{\sigma}_{track}^2. \tag{10}$$

On the other hand, the noise $\tilde{\sigma}_{psy}$ of the perceptual system, obtained from the psychometric function, is determined by the sensory noise in the visual system, $\tilde{\sigma}_{sens}$, and the "decision noise" $\tilde{\sigma}_{dec}$ in the neuronal structure that transforms the output of the visual system into the final decision:

$$\tilde{\sigma}_{psy}^2 = \tilde{\sigma}_{sens}^2 + \tilde{\sigma}_{dec}^2. \tag{11}$$

The decision noise is influenced by hardly controllable factors like the degree of concentration, training, general ability and daily form. Since the decision noise is in any case greater or equal to zero, we have

$$\tilde{\sigma}_{psy}^2 \geqslant \tilde{\sigma}_{sens}^2, \tag{12}$$

and thus, with the true effective oculomotor noise $\tilde{\sigma}_{oc}$ given by

$$\tilde{\sigma}_{oc} = \sqrt{\tilde{\sigma}_{ocm}^2 - \tilde{\sigma}_{track}^2}, \tag{13}$$

it follows that the motor noise of the OFR system is bounded from below by

$$\tilde{\sigma}_{mot} \geqslant \sqrt{\tilde{\sigma}_{oc}^2 - \tilde{\sigma}_{psy}^2}. \tag{14}$$

2.4.5. Psychophysical data

The 2AFC paradigm is evaluated by plotting the proportion of responses "test stimulus appears faster" against the speed of the test stimulus (see Fig. 7). The data points are fitted with a cumulative Gaussian function, the *psychometric curve*. The fitting function is forced to approach 0 and 1 for negative and positive infinity,

respectively. The effective noise $\tilde{\sigma}_{psy}$ is then defined by the width of the fitted cumulative Gaussian.

2.4.6. Eye tracker data

Since we wanted to record uncontaminated ocular following responses, trials containing saccades in the analysis interval [0,200] ms after onset of stimulus motion have been discarded. This post-selection affects only a relatively small fraction of the data (below 5%). The chosen criteria for saccade detection are a speed of more than 20 deg/s or an acceleration of more than 1000 deg/s². These relatively strict criteria have been chosen to also account for micro-saccades. In order to reduce measurement noise, data were filtered by a running average over five samples corresponding to 20 ms. Eye speed data were obtained by digital derivation of the filtered gaze position data.

As already stated, the direction of stimulus motion – either to the left or to the right – has been randomly chosen for each stimulus presentation in order to prevent anticipatory eye movements. In about 50% of the trials, therefore, the reference stimulus moved opposite to the test stimulus. These cases are potentially problematic as our data revealed (see Section 3). Consequently, we have discarded these trials from the statistics and only kept those, where test and reference stimulus moved in the same direction.

Due to these rather massive post-selections, of originally 160 trials per subject and experimental condition (stimulus speed) there remained 70–80 trials per subject and experimental condition which is sufficient for our statistical analysis.

2.4.7. Response latency

One of the characteristic features of ocular responses in general is their *latency*, that is, the time it takes for the oculomotor system to react to stimulus motion. We applied a latency determination method already used in a former study (Boström & Warzecha, 2009). Basically, we determined the latency of each individual response and calculated the average over these values. A baseline was fitted through the eye velocity data within a 40 ms interval starting 20 ms after stimulus motion onset. A second line was fitted through the data within a 40 ms interval starting at the point, where the eye velocity exceeded 3 standard deviations from the baseline. The intersection of these two lines gave the estimate of the response onset. If the algorithm does not find a response onset within the interval [0,200] ms, the trial is discarded.

2.4.8. Correlation

The chosen experimental paradigm allows us to investigate the correlation between the perceptual decision and the oculomotor response on a trial-by-trial basis. We checked the significance of the correlation by a *t*-test, as explained in the following. At time t_{opt}, when the oculomotor discrimination performance is optimal, the eye velocities in response to reference and test stimulus are compared. This yields an oculomotor decision in favor of the stimulus which elicited a faster eye movement. This way, perceptual and oculomotor decision can both be represented by binary random variables X and Y, respectively. The joint outcome of X and Y is governed by the joint probability distribution $p(x,y)$ for $x,y \in \{0,1\}$ with the marginal distributions $p_X(x) = \sum_y p(x,y)$ and $p_Y(y) = \sum_x p(x,y)$. If the *null hypothesis* is true then X and Y are statistically independent, i.e. the joint probability distribution factorizes, $p(x,y) = p_X(x)p_Y(y)$. If the null hypothesis is not true, then there will be a difference between $p(x,y)$ and $p_X(x)p_Y(y)$. The statistical significance of this difference is quantified by a two-tailed *t*-test, similar to the procedure applied by Stone and Krauzlis (2003). Generally, the estimator $\hat{p}$ for a probability obeys a Bernoulli statistics with the confidence interval

$$u = t_{s,N} \cdot \sqrt{\frac{\bar{p}(1-\bar{p})}{N}}, \tag{15}$$

where $\bar{p}$ is the estimated probability value, $t_{s,N}$ is the student t-factor corresponding to $N-1$ degrees of freedom, and s is the significance level. In the present study we have chosen $s = 0.95$, and the number N of trials is about 70–80, depending on the occasional removal of trials due to saccades in the relevant time interval. We estimated two probabilities: the true coincidence probability $\hat{p}_{\text{true}} = \hat{p}(0,0) + \hat{p}(1,1)$ and the chance coincidence probability $\hat{p}_{\text{chance}} = \hat{p}_X(0)\hat{p}_Y(0) + \hat{p}_X(1)\hat{p}_Y(1)$. Both probabilities are significantly different at level s, if

$$|\bar{p}_{\text{true}} - \bar{p}_{\text{chance}}| \geqslant \sqrt{u_{\text{true}}^2 + u_{\text{chance}}^2}. \tag{16}$$

On the condition, where test and reference stimulus are equal ($v_{\text{test}} = v_{\text{ref}} = 10$ deg/s), we know *apriorily* that the chance probability equals $\bar{p}_{\text{chance}} = 0.5$, so we can use this value instead of the chance probability estimated from the data and hence get a more sensitive significance criterion with $u_{\text{chance}} = 0$.

3. Results

3.1. Ocular responses

Fig. 1 exemplarily shows the eye speed of subject KJB while observing the stimulus in 140 trials. After some latency the eye starts to follow the motion reaching velocities between about 2 and 5 deg/s 150 ms after stimulus motion onset. Obviously, there is a large variability even though the stimulus is the same across trials. A straightforward measure of variability is the standard deviation of the eye velocity (Fig. 2). By looking at the time course of the variability, one recognizes a slight increase of variability shortly after the onset of the ocular following response. Moreover, by relating the overall variability to stimulus motion (see legend in Fig. 2), one recognizes a slight increase of variability with stimulus velocity. These two observations hold for all subjects, albeit to a different extent. The fact that we were able to measure weakly stimulus-dependent noise also indicates that the (uncorrelated) tracker noise is sufficiently small.

Despite the large variability, the mean ocular responses a clearly structured (Figs. 3 and 4). The faster the stimulus moves, the stronger the ocular response. Also, the responses are stronger
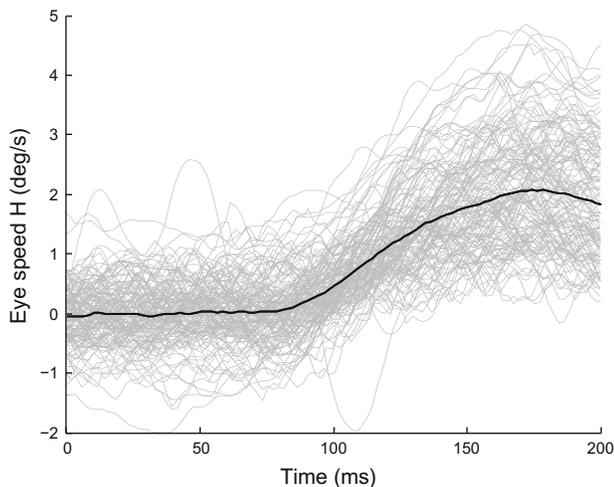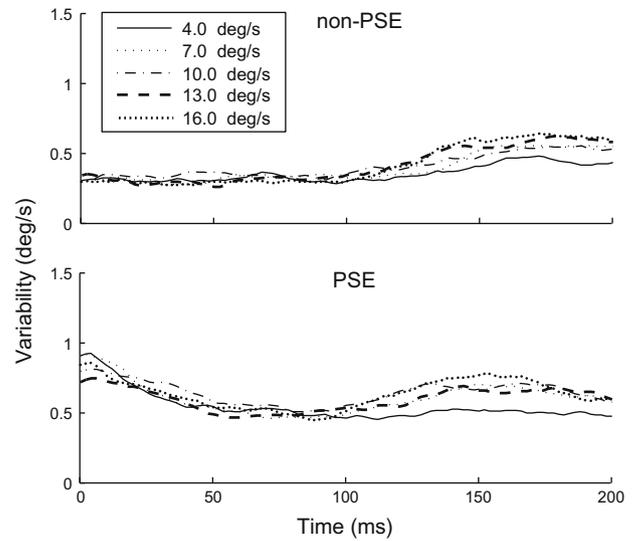
Fig. 2. Variability in terms of the standard deviation of the oculomotor responses of subject KJB as a function of time in ms after stimulus motion onset, on the non-PSE and PSE condition.

on the PSE condition (Fig. 4) as compared to the non-PSE condition (Fig. 3) which confirms the effect of post-saccadic enhancement.

3.2. Direction of stimulus motion and eye movements

On the PSE condition, the subject performs an initial saccade from the left to the center of the screen. If the stimulus moves in the same direction, i.e. rightwards, the strength of the ocular following response might be different than in the case that the stimulus moves against the initial saccade. Indeed, our data show that for all subjects there are statistically significant differences in response strength when the stimulus motion is parallel or opposite to the initial saccade (see Fig. 4). Surprisingly, even on the non-PSE condition there were for some subjects significant differences in response strength depending on the direction of eye movements. In this case, there was a drift component in the eye movements which was present even during fixation (see Fig. 3).

3.3. Response latency

Our measurements (see Table 1) revealed mean latencies of 70–87 ms, which is in agreement with the literature (Gellman et al., 1990).

The stimulus is visible for 75 ms, thus some subjects started to move their eyes in some trials shortly before the stimulus disappeared. This overlap might potentially affect the motion information processing for those trials. However, the overlap is very short in comparison to the overall stimulus duration and the eye speed is very small at the beginning of eye movement.

3.4. Discrimination performance of oculomotor system

From the eye speed data we constructed oculometric curves at chosen time points $t = t_i$, as is exemplarily shown in Fig. 5 for subject KJB at $t = 130$ ms. From the oculometric curves at these time points t_i we calculated the effective noise values $\bar{\sigma}(t_i)$ and hence obtain an estimate for the time course of the speed discrimination performance (Fig. 6). The minimum of the curve yields the value for the estimated effective oculomotor noise $\bar{\sigma}_{ocm}$ (see Eq. (8)). A glimpse at the curves for the individual subjects (Fig. 6) reveals

Fig. 1. 140 Eye velocity traces (gray) of subject KJB in response to the reference stimulus on the non-PSE condition, overlaid with the corresponding mean trace (black). The stimulus starts to move at $t = 0$ ms with 10 deg/s and disappears at $t = 75$ ms.
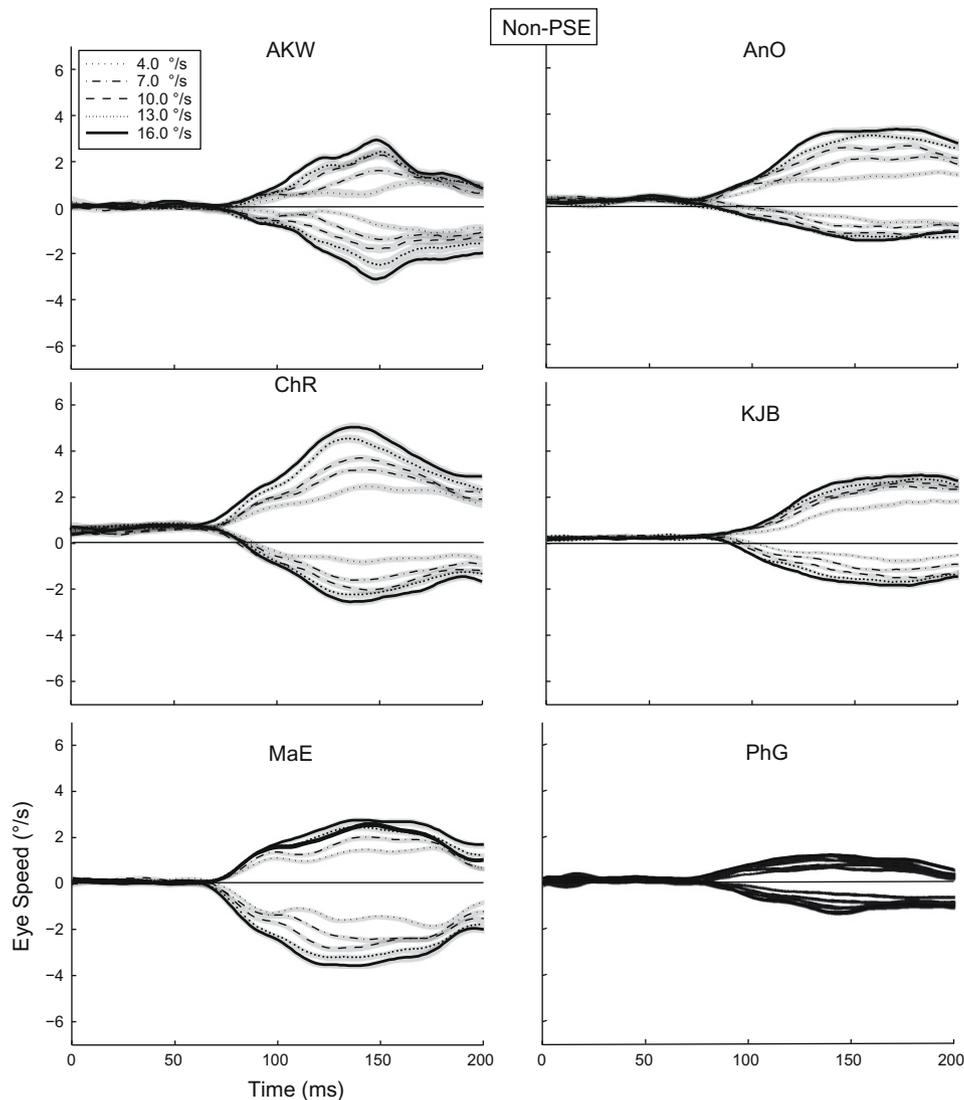
Fig. 3. Mean responses of all subjects on the non-PSE condition, that is, without initial saccade. Even though there is full left–right symmetry in the stimulus, for some subjects (AnO, ChR and KJB) there is a significant difference between left and right eye movements due to a slow drift (<1 deg/s) which is present even in the first 50 ms when the stimulus is not yet being translated into eye movement. This drift makes those trials impossible to evaluate, where test and reference stimulus move in opposite directions. The shaded areas correspond to the 95% confidence interval.

that the best performance is generally reached between 100 and 150 ms after stimulus motion onset.

3.5. Psychophysics

The psychophysical data from the speed discrimination task define a psychometric function as exemplarily shown in Fig. 7 with the data of subject KJB. The derived effective noise values $\tilde{\sigma}_{psy}$ for all subjects and conditions are shown in Table 2. Weber fractions can be obtained by division through the reference stimulus speed of 10 deg/s.

3.6. Comparison of oculomotor and psychophysical performance

For the comparison of psychophysical and oculomotor performance we take the optimum value of the oculomotor discrimination performance curve (see Eq. (8)). Using Eq. (13), we then obtain from this value the effective oculomotor noise $\tilde{\sigma}_{oc}$, which is shown in Table 2, together with the effective tracker noise $\tilde{\sigma}_{track}$, and the effective psychophysical noise $\tilde{\sigma}_{psycho}$. Importantly, for all subjects the psychophysical discrimination performance is

better than the oculomotor performance. Moreover, although the tracker noise is not completely negligible, it does not override motor noise.

There is a considerable variability across the subjects with respect to their perceptual performance, which could be due to each subject's individual ability to perceive motion, to concentrate on the task, to memorize the stimuli and compare them in mind, and also due to the daily form of the subject. Also, as we have seen during the course of the experiments, many naive subjects find the task extremely difficult and seem to confuse stimulus speed with apparent stimulus duration. Because of these factors the perceptual discrimination performance as determined in our experiments is a lower bound on the ideal value that could be obtained under optimal conditions. On the other hand, the oculomotor discrimination performance obtained in our experiments can be expected to be more confident given that the oculomotor response is highly reflexive. Despite this fact we find a considerable variability of oculomotor responses across subjects.

Using Eq. (14), the values for psychophysical and oculomotor noise uniquely determine a lower bound for the motor noise introduced in the post-sensory (motor) part of the oculomotor pathway.
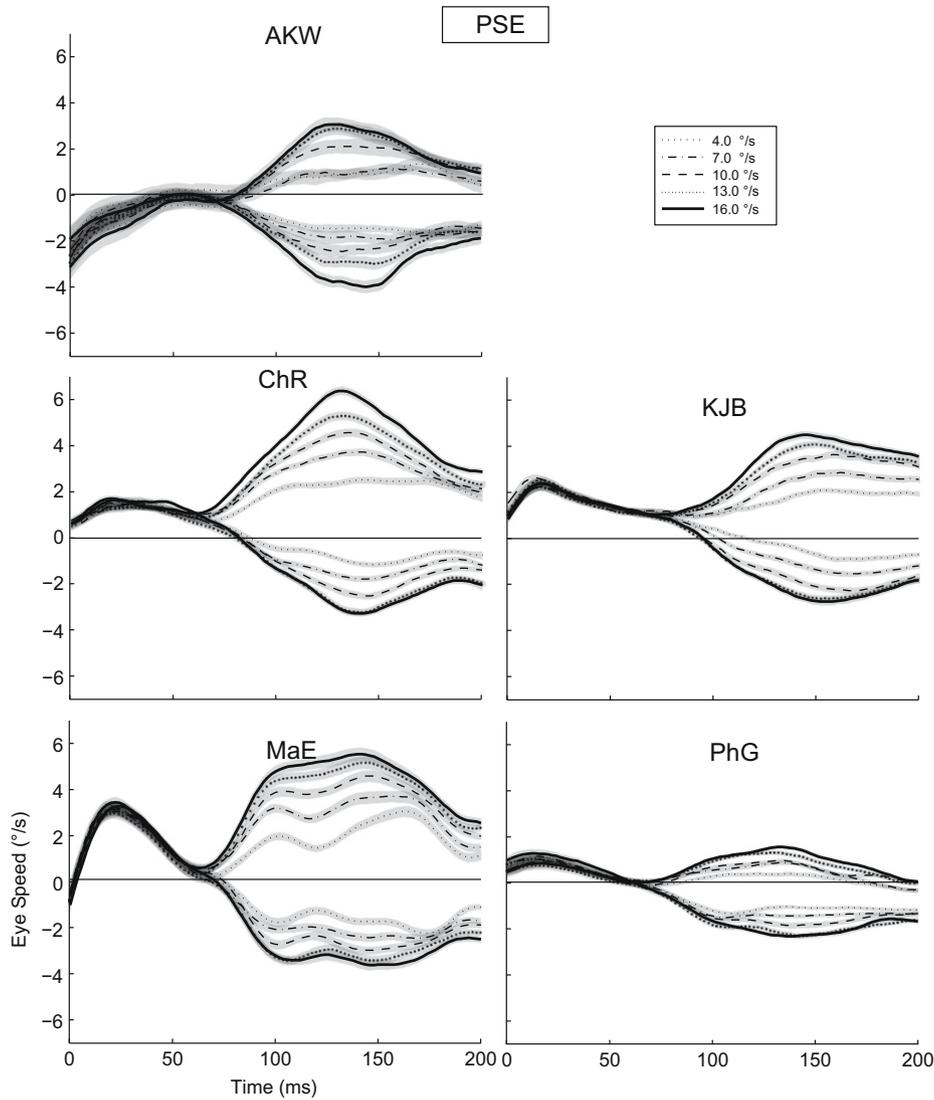
Fig. 4. Mean responses of all subjects on the PSE condition, that is, shortly after an initial saccade. The responses to the right (positive velocity values) are in the same direction as the initial saccade and are significantly stronger than the responses to the left, except for subject AKW and PhG. This effect makes those trials impossible to evaluate, where test and reference stimulus move in opposite directions. The shaded areas correspond to the 95% confidence interval. Subject AnO did not participate in the PSE sessions.

Table 1
Estimated latency values in ms of all subjects on the PSE and the non-PSE condition and for all stimulus speeds. (Subject AnO did not participate in the PSE experiments.) The 95% confidence intervals range between ±2 and ±4 ms.

Subject	non-PSE (deg/s)					PSE (deg/s)				
	4	7	10	13	16	4	7	10	13	16
AKW	83	82	84	82	82	86	80	80	83	79
ChR	77	77	76	76	76	78	74	74	76	71
KJB	83	85	86	84	84	86	87	83	80	85
MaE	75	77	72	71	71	77	81	72	70	71
PhG	76	76	80	79	79	70	76	74	75	74
AnO	80	81	83	84	85	–	–	–	–	–

Table 2 demonstrates that the motor noise $\tilde{\sigma}_{mot}$ is of about the same magnitude as the other two natural noise sources, and is hence not negligible.

3.7. Correlation

If we assume that both the perceptual and the oculomotor system share the same sensory sources, and both systems do not add too much noise of their own, then their responses should be correlated. Errors due to noise in the shared sensory system should lead to correlated errors in the perceptual and oculomotor responses. If this is not the case then either both systems rely on different sensory subsystems or they introduce so much noise on their own that the correlation is destroyed.

Recall that the "oculomotor judgment" is defined by the choice of the stimulus that elicits a higher eye speed at the point in time when oculomotor discrimination performance is optimal. On the basis of both perceptual and oculomotor judgment for the same pairs of stimuli, we determine the trial-by-trial correlation between the judgments. The results of our analysis evaluated for all subjects are shown in Fig. 8. The actual coincidence probabilities and those expected by chance are very similar. The data point in the center at $v_{test} = 10$ deg/s is of particular interest, because here the stimuli are indistinguishable and hence all decisions are based on noise only. If there is a correlation between the perceptual and oculomotor responses due to a common noise source then it should be most prominent on this condition. However, our data reveal a 95%-significant deviation from chance coincidence only for one subject (AnO). Moreover, for this subject
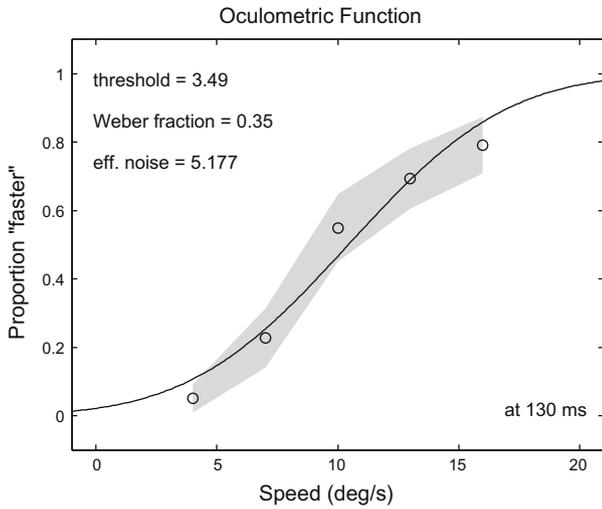
Fig. 5. Oculometric function of subject KJB on the PSE condition, calculated at $t = 130$ ms after stimulus motion onset, where the oculomotor discrimination performance was optimal. The shaded area represents the 95% confidence interval from the Bernoulli statistics of the estimated probabilities.

Fig. 6. The time course of the effective noise of the oculomotor response for all subjects on the non-PSE and PSE condition. The x-axis is the time in ms from stimulus motion onset, the y-axis is the time-dependent effective oculomotor noise $\bar{\sigma}_{ocm}(t)$ in deg/s.

and stimulus combination we find *less* coincidences than expected by chance, which speaks against the hypothesis of a com-

Fig. 7. Psychometric function of subject KJB on the PSE condition. For several test speed values the proportion of answers "test stimulus appears faster than reference stimulus" is experimentally determined. These data points (circles) are fitted with a cumulative Gaussian (straight line). The difference between the 0.5 and 0.75 quantiles defines the perceptual threshold, the ratio of threshold and reference value (here 10 deg/s) defines the Weber fraction, and the width of the cumulative Gaussian defines the effective noise $\bar{\sigma}_{psy}$. The shaded area represents the 95% confidence interval estimated from the Bernoulli statistics of the estimated probabilities.

Table 2
Effective noise values in deg/s, for all subjects on the PSE and the non-PSE condition. (Subject AnO did not participate in the PSE experiments.) From the oculomotor noise $\bar{\sigma}_{oc}$ the tracker noise has already been removed using Eq. (13). The value $\bar{\sigma}_{mot}$ is the resulting lower bound for the effective noise from the post-sensory (motor) part of the pathway, obtained by Eq. (14). Note that the effective noise does not reflect the absolute amount of noise but rather represents an inverse signal-to-noise ratio. Hence the absolute tracker and motor noise of subject PhG was not exceptionally large but his mean eye movements particularly small (see Figs. 3 and 4).

Subject	Non-PSE				PSE			
	$\bar{\sigma}_{psy}$	$\bar{\sigma}_{oc}$	$\bar{\sigma}_{track}$	$\bar{\sigma}_{mot}$	$\bar{\sigma}_{psy}$	$\bar{\sigma}_{oc}$	$\bar{\sigma}_{track}$	$\bar{\sigma}_{mot}$
AKW	4.49	6.10	0.81	**4.12**	4.19	6.94	1.36	**5.53**
ChR	3.74	5.81	1.31	**4.45**	2.94	5.09	1.14	**4.17**
KJB	2.71	5.75	2.84	**5.07**	2.76	5.00	1.35	**4.17**
MaE	2.27	6.73	1.20	**6.34**	2.79	9.73	1.00	**9.32**
PhG	5.83	12.08	10.17	**10.58**	2.93	7.63	4.88	**7.06**
AnO	5.86	10.47	1.49	**8.68**	–	–	–	–

mon noise source, and which makes it more likely that this particular deviation is due to random fluctuations. Indeed, a two-tailed *t*-test at the 95%-level for all test speeds yields only two occurrences of significance, indicated by an asterisk above the tested value: AnO on the PSE condition (already mentioned) and MaE on the non-PSE condition. Since the level of significance is 95% and there are $(6 + 5) \times 5 = 55$ different significance tests, up to three false alarms are allowed by the laws of probability to not reject the null hypothesis. Thus altogether we do not find significant correlation between perceptual decision and oculomotor response.

3.8. Different integration methods

As already mentioned in Section 2.4.1, we have focused throughout the paper on one out of three temporal data integration methods, that is, we have focused on taking into account the eye velocity at discrete time points *t*. Because the data have been filtered beforehand by a running average over 20 ms, the discrete time point actually corresponds to a time window of that size.
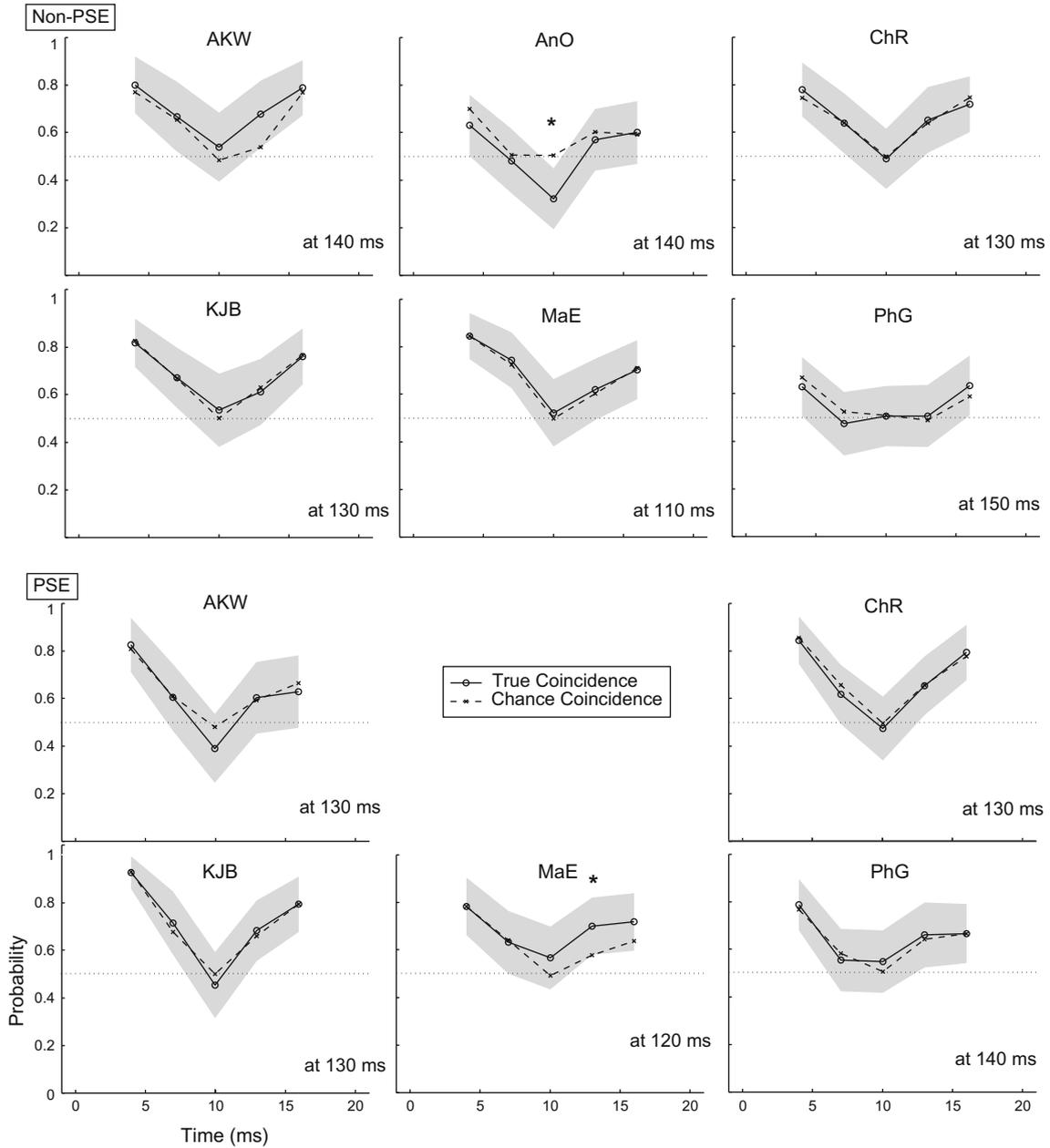
Fig. 8. Coincidence probability (solid curve) and chance coincidence probability (dashed curve) of oculomotor and perceptual judgments as a function of test stimulus speed for all subjects on the non-PSE (upper two rows) and PSE condition (lower two rows). The shaded region indicates the distance between true and chance probability necessary for significance at the 95%-level, an asterisk indicates significance. The correlation is calculated with respect to the eye velocity data taken at the time t_{opt} of optimal oculomotor discrimination performance. Subject AnO did not participate in the PSE sessions.

The two other integration methods did not improve the oculomotor performance, the third method even diminished it considerably. The values $\tilde{\sigma}_{mot}$ for the effective motor noise are shown in Table 3. The second integration method tends to yield higher values of $\tilde{\sigma}_{mot}$, indicating a worse oculomotor performance. The third integration method yields an even worse oculomotor performance. For the sake of comparison, the resulting curves of $\tilde{\sigma}_{ocm}(t)$ are exemplarily shown for subject ChR on the PSE condition in Fig. 9. Altogether, the first integration method, which involved a window of 20 ms, yields the best value for the oculomotor performance.

We have also analyzed the correlation based on the other two integration methods (not shown here) and also found no significant correlation.

Table 3
Effective motor noise values $\tilde{\sigma}_{mot}$ in deg/s, for all subjects and three different integration methods. The first method involves a running average over 20 ms, the second method involves a running average over 100 ms, and the third method involves a cumulative integration from stimulus motion onset. The first method is the default integration method throughout the paper, and the shown values correspond to the values of $\tilde{\sigma}_{mot}$ in Table 2.

Subject	Non-PSE			PSE		
	20 ms	100 ms	Cumulative	20 ms	100 ms	Cumulative
AKW	4.12	5.27	10.19	5.53	7.95	15.57
ChR	4.45	4.52	8.64	4.17	4.46	8.25
KJB	5.07	5.48	7.47	4.17	5.93	10.27
MaE	6.34	5.48	6.54	9.32	9.51	18.63
PhG	10.58	12.72	17.68	7.06	9.43	12.58
AnO	8.68	6.78	10.04	–	–	–

4. Discussion

We have compared human ocular following responses and simultaneously measured speed perception in order to gain insight into the potential sources of response variability. Our main findings comprise two issues. First, the open-loop speed discrimination performance of the perceptual system is systematically better than that of the oculomotor system. Second, the responses of perceptual and oculomotor system do not significantly correlate.

Under the assumption that perceptual and oculomotor system share the same sensory subsystem (see Fig. 10a), we have calculated the amount of noise in the post-sensory (motor) part of the oculomotor pathway and found it to be of about the same magnitude as the noise from the sensory part. Furthermore and on the same assumption, the lack of correlation between perceptual and oculomotor responses implies that the amount of post-sensory noise is large enough to destroy the correlation.

We have determined higher psychophysical thresholds than similar studies (De Bruyn & Orban, 1988; Rasche & Gegenfurtner, 2009; Watamaniuk & Duchon, 1992). This may be due to shorter training phases in particular in comparison to the extensive training performed in the study by De Bruyn and Orban (1988). Moreover, our stimuli were considerably shorter than those used in most other studies and extremely short stimulus durations have been shown to affect perceptual threshold (De Bruyn & Orban, 1988). Whatever the reasons for the higher psychophysical thresholds, their being too high rather strengthens our main hypothesis, because even a not optimally performing perception evidently outperformed the oculomotor system in terms of speed discrimination. If the perceptual performance of our subjects would have been better (due to enhanced training, say) then likewise the distance to the oculomotor performance and thus the derived amount of motor noise would have become even larger.

For the following discussion of other studies that have compared perceptual and oculomotor performance or have otherwise derived conclusions about the origin of noise that limits the performance of the human motion vision system, it is important to note that to our knowledge there is no equivalent study with respect to the ocular following response. Therefore, discrepancies between our findings and that of other groups might be due to the different types of oculomotor response. Nevertheless we continue with a discussion of possible reasons for discrepancies because there is ample evidence that perception, smooth pursuit and ocular following response share a common pathway up to MT/MST (Britten, 2004; Britten et al., 1996; Dürsteler & Wurtz, 1988; Liu & Newsome, 2005; Newsome et al., 1989, 1985; Orban & Vanduffel, 2004; Petit & Haxby, 1999; Takemura et al., 2007).
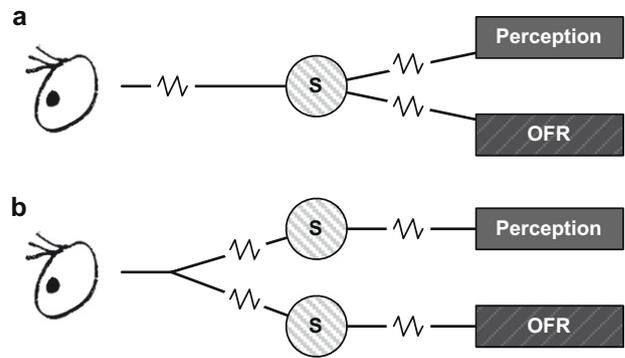
Fig. 10. Two possible schemes for the motion information pathway running from the eye through one or more sensory subsystems (S) to either the perceptual or the OFR system. In each branch of the pathway there is a certain amount of noise (wiggles). (a) The same sensory subsystem gives input to the perceptual and oculomotor pathway. This scheme is favored based on the literature. If the noise in the sensory subsystem dominates later noise sources, perceptual and oculomotor decision should be similarly reliable and correlated. If there are substantial noise sources after the separation of the pathways of perception and OFR, either one may perform better than the other and both systems do not need to correlate. (b) Perceptual and oculomotor pathway diverge early so that each is contaminated separately by early and late noise sources. If this processing scheme would apply we cannot with our approach derive conclusions about the relative contribution of sensory and motor noise.

Some studies find, like us, a considerably lower discrimination performance of the oculomotor system as compared to the perceptual system, albeit with respect to a different stimulus property (direction of motion, as in Beutter & Stone, 2000; Watamaniuk & Heinen, 1999) or a different type of oculomotor response (smooth pursuit, as in Beutter & Stone, 2000; Kowler & McKee, 1987; Rasche & Gegenfurtner, 2009). Although their data actually confirm our findings, some of these groups (Beutter & Stone, 2000; Watamaniuk & Heinen, 1999) conclude that perceptual and oculomotor performance are limited by a common sensory noise source within the motion processing pathway. They argue that the discrimination threshold of the oculomotor response is higher because the oculomotor system multiplies the noise that the visual system passes to it. Thus, there would be an increase of threshold although there are no additional noise sources in the oculomotor system. We are, however, not convinced by this argument. If the oculomotor system multiplies the noise coming from the visual system, then it also multiplies the signal. Hence, the signal-to-noise ratio is maintained and there should be no change of threshold. In other words, the system does not lose information by multiplication of the sensory output. In our discretion, the higher oculomotor threshold can only be explained by an additional
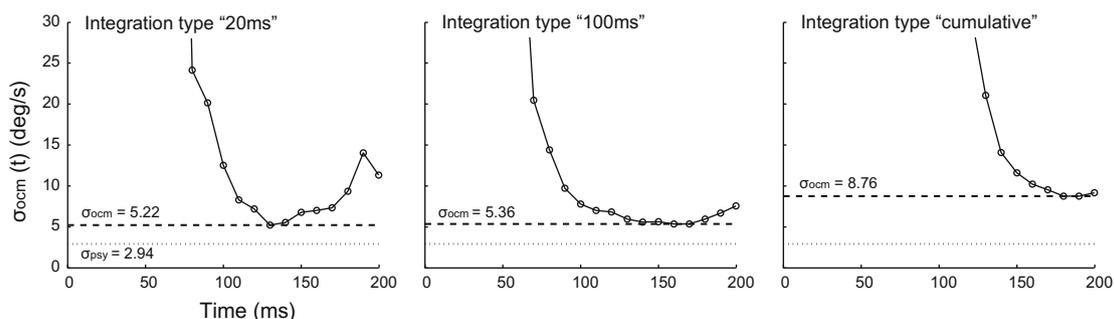
Fig. 9. The time course of the effective noise of the oculomotor response for subject ChR on the PSE condition, using the three different integration methods. The x-axis is the time in ms from stimulus motion onset, the y-axis is the time-dependent effective oculomotor noise $\bar{\sigma}_{ocm}(t)$ in deg/s. The lower bound for the effective oculomotor noise $\bar{\sigma}_{ocm}$ is taken as the minimum of the curve over the interval [0, 200] ms, indicated by the dashed line. The psychophysical performance $\bar{\sigma}_{psy}$ is indicated by the dotted line. From the lower bound for the effective oculomotor noise $\bar{\sigma}_{ocm}$ the lower bound for the effective motor noise $\bar{\sigma}_{mot}$ is derived via Eq. (14), whose values are given in Table 3.

amount of noise introduced in the post-sensory part of the oculo-motor pathway.

In their study, Rasche and Gegenfurtner (2009) applied methods similar to ours to the human smooth pursuit response (SP). Their results are qualitatively the same, with the oculomotor noise also being substantially higher than the perceptual noise. The authors conclude, like us, that there must be non-negligible additional noise in the post-sensory part of the pathway. In direct compari-son, the measured oculomotor thresholds for the SP at the end of the open-loop phase (for the SP this is about 300 ms after stimulus motion onset) are about half as large as those measured by us for the OFR. (Compare their Fig. 4 at $t = 300$ ms with our values for $\tilde{\sigma}_{oc}$ in Table 2.) Thus, during the open-loop period the SP seems to be more accurate than the OFR. This appears comprehensible in view of the higher latency of the SP, which is about twice as large as that of the OFR. The SP system has twice the time to ana-lyze the visual data and to generate adequate eye movements. Lastly, the variability in terms of the standard deviation of the eye velocity measured by Rasche and Gegenfurtner (2009) approx-imately coincides with that of our measurements (compare their Fig. 1 with our Fig. 2), which indicates that our measurement de-vice introduces about the same amount of noise.

If the hypothesis that sensory noise dominates the oculomotor and perceptual performance were true, which is put forward partic-ularly in the studies by Osborne et al. (2007, 2005), and by Huang and Lisberger (2009), then the noise in the post-sensory part of the pathway would be effectively irrelevant. Consequently, the per-ceptual system, which is assumed to also receive its input from the sensory system, should show no better discrimination performance than the oculomotor system. If the discrimination performance of the perceptual system is close to that of the oculomotor system then the perceptual responses should correlate with the oculomo-tor responses, because according to the assumption both systems share the same input and do not add noise of their own. However, experimentally we find that (1) the discrimination performance of the perceptual system is higher than that of the oculomotor system and (2) the perceptual and oculomotor responses are not corre-lated. These findings are incompatible with the sensory noise hypothesis and rather support the complementary hypothesis that there is a considerable amount of additional noise in the post-sen-sory pathway which suffices to lower the oculomotor performance and to destroy the correlation with the perceptual system. The evi-dence in support of the sensory noise hypothesis (Huang & Lisber-ger, 2009; Osborne et al., 2007, 2005) is not compelling to us and others (e.g. Rasche & Gegenfurtner, 2009). In the study by Osborne et al. (2005) only oculomotor performance was analyzed and not compared to perceptual performance. Moreover, their analysis was based on assumptions (picking three eigenvectors out of a con-tinuum, associating these eigenvectors with sensory estimates of the stimulus) that may but do not need to apply to the oculomotor pathway. Similarly, the finding by Osborne et al. (2007) that motor noise does not change when the motor task (direction of stimulus motion) changes does not disagree with our finding of considerable motor noise contributing to oculomotor performance. It merely shows that direction discrimination performance is not noticeably affected by changing the direction of stimulus motion. Moreover, since no anisotropy has been found experimentally (Churchland et al., 2003), there is no obvious reason for the acuity of eye move-ments varying between different directions.

Not only behavioral experiments have been interpreted in favor of the sensory noise hypothesis. Model simulations of an entire population of MT-neurons that take into account experimentally determined neuronal correlations indicate that no post-sensory noise is needed to explain motor performance (Huang & Lisberger, 2009). It needs to be analyzed further whether there are differ-ences between SP and OFR with respect to the contribution of post-sensory noise, since Huang and Lisberger characterized neu-ronal responses partly using relatively large random dot stimuli that could also have driven OFR (Barthelemy, Vanzetta, & Masson, 2006). Moreover, since their model can reproduce a wide range of behaviors based on different physiologically plausible parameters, their simulations are as compatible with the opposite hypothesis (favored by us) that some of the variability is due to post-sensory (motor) noise.

Several experimental findings indicate that ocular following re-sponse and perception share a common neuronal pathway at least on a coarse anatomical scale: research on monkeys provides strong evidence that area MT, which is known to be involved in motion per-ception (Britten, 2004; Britten et al., 1996; Liu & Newsome, 2005; Newsome et al., 1989), is also involved in all sorts of short-latency tracking eye movements (Dürsteler & Wurtz, 1988; Miles, 1998; Takemura et al., 2007). However, it cannot be excluded with cer-tainty that oculomotor and perceptual system involve different neu-ronal sub-populations within these areas. Therefore, it is also possible to interpret our findings as evidence for effectively separate pathways leading to OFR and speed perception, as shown in Fig. 10b. The oculomotor system relies mainly on an adequate estimation of stimulus speed, while the perceptual system in the given task needs to discriminate between stimuli. Discrimination and estimation are functionally different and thus might engage different neuronal sub-populations (Jazayeri & Movshon, 2006, 2007).

We, however, do not see sufficiently convincing evidence that the sensory pathways for OFR and perception are effectively sepa-rate, and therefore we favor the formerly mentioned explanation that there is a considerable amount of post-sensory noise entering the oculomotor pathway from area MT onwards.

Acknowledgments

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