Demonstration of an eye-movement-induced visual motion illusion (Filehne illusion) in Rhesus monkeys

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During pursuit eye movements, the world around us remains perceptually stable despite the retinal-image slip induced by the eye movement. It is commonly held that this perceptual invariance is achieved by subtracting an internal reference signal, reflecting the eye movement, from the retinal motion signal. However, if the reference signal is too small or too large, a false eye-movement-induced motion of the external world, the Filehne illusion (FI), will be perceived. A reference signal of inadequate size can be simulated experimentally by asking human subjects to pursue a target across backgrounds with externally added motion that are perceived as moving. In the present study we asked if non-human primates respond to such manipulation in a way comparable to humans. Using psychophysical methods, we demonstrate that Rhesus monkeys do indeed experience a percept of pursuit-induced background motion. In this study we show that an FI can be predictably induced in Rhesus monkeys. The monkey FI shows dependencies on the size and direction of background movement, which is very similar to the ones characterizing the human FI. This congruence suggests that the perception of self-induced visual motion is based on similar inferential mechanisms in non-human and human primates.

Keywords: spatial cognition, perceptual organization, eye movements


**Introduction**

One of the cardinal problems in perception is the discrimination of sensory stimuli elicited by activities of the subject from others originating in the external world. Inferential theories of perception assume that the necessary disambiguation is accomplished by comparing the sensory stimulus with an internal reference signal, optimally reflecting the sensory consequences of the action (Haarmeier, Bunjes, Lindner, Berret, & Thier, 2001; Wertheim, 1994). In its simplest form, such a reference signal may be conceived as a replica of the motor command responsible for the action, referred to as an “efference copy” or a “corollary discharge” (Sperry, 1950; von Holst & Mittelstaedt, 1950). For instance, perceptual stability in the case of smooth-pursuit eye movements, where the image of the stationary world moves across the retina at the velocity of the eyes, might be accomplished by subtracting a copy of the eye movement motor command from the retinal motion signal. If the two cancel each other, visible structures, which do not move, will be perceived as non-moving, even though their images move on the retina as a consequence of the eye movement. However, an inferential mechanism based solely on an efference copy is likely to fail under most
conditions since one and the same eye movement may have very different sensory consequences, depending on
the composition of the visual environment in which the
movement unfolds. In fact, rather than relying on a simple
reference signal such as the efference copy, the visual
system should instead rely on a much more elaborate
reference signal, able to take the sensory consequences of
the action into account. In order to do so such a reference
signal would have to take the sensory environment into consideration and make appropriate adjustments.
In fact, recent psychophysical work on motion perception
during smooth-pursuit eye movements has provided
evidence that the human visual system indeed uses an
adaptable reference signal (Haarmeier et al., 2001).
However, irrespective of the specific properties of this
reference signal, previous work suggests that there is a
wide variety of conditions in which the reference signal
does not have the magnitude required to completely cancel
the self-induced retinal-image slip during smooth-pursuit
eye movements executed across stationary objects in the
background (Filehne, 1922; Freeman, 1999; Freeman &
Banks, 1998; Mack & Herman, 1973; Wertheim, 1994).
The existence of uncompensated self-induced retinal-
image slip was first noted by Filehne (1922). He reported
that smooth-pursuit eye movements made by humans
elicit the percept of a small, yet significant, illusory
movement of stationary objects, which is usually in a
direction opposite to that of the eye movement, and
termed the Filehne Illusion (FI) after him. This deviation
from perfect perceptual stability, however, is so small
under everyday viewing conditions that it usually goes
unnoticed. Hence, interest in the Filehne illusion is not so
much generated by its ecological relevance—which is
probably negligible—but by the hope that the under-
standing of the mechanisms underlying the illusion will
unravel the brain circuits generating perceptual stability
during self-induced motion and, more specifically, will
shed light on the properties of the reference signal and the
mechanisms leading to its adjustment.

The evidence for a flexible reference signal alluded to
earlier is based on the demonstration of an exaggerated
Filehne illusion in human subjects (Haarmeier et al., 2001;
Haarmeier & Thier, 1996, 1998) evoked under experi-
mental conditions creating gross imperfections of the
reference signal. Imperfections are simulated experimen-
tally by moving a large-field visual background across
which subjects pursue a visual target in a consistent
manner trial after trial. The psychometric data on the
perception of background motion obtained in such experi-
ments suggests that the visual system acts on the
assumption that the visual environment, represented by
the large-field background, across which the eyes pursue
the visual target, is stationary rather than moving and is
perceived as moving because it is evaluated with an
imperfect reference signal. Accordingly, the visual system
adjusts the reference signal in a manner suitable to reduce
the percept of background movement. The adjusted
reference signal is unsuitable for a physically stationary
background, presented on occasional catch trials; the latter
will prompt a strong illusion of background motion. Our
long-term goal is to understand the neuronal mechanisms
underlying the generation of perceptual stability during
pursuit eye movements and self-induced motion at large
at the level of single cells. This requires the establish-
ment of a suitable animal model. Rhesus monkeys have
been amply and successfully used as suitable primate
model of the human visual system in many earlier
studies on the neural underpinnings of visual perception.
In fact, previous work has not singled out any significant
difference between the visual systems of humans and
Rhesus monkeys. However, do Rhesus monkeys also
experience a Filehne illusion and does it show similar
dependencies as the human Filehne illusion? Only if
these questions could be answered in the affirmative,
would it become possible to get a handle on the neural
mechanisms of perceptual stability during pursuit eye
movements.

Recent psychophysical evidence on motion perception
during smooth-pursuit eye movements has delivered
evidence that the human visual system indeed uses an
adaptable reference signal (Haarmeier et al., 2001; for a
different view, see Freeman, 2007). In fact, preliminary
findings suggest that the inferential mechanism involving
an adaptive reference signal does not seem to be specific
to the human visual system. Rather, psychophysical
observations on two rhesus monkeys used in previous
electrophysiological work on the cortical processing of
self-induced visual motion suggested that similar princi-
pies also apply to the monkey visual system (Dicke,
Chakraborty, & Thier, 2008). This conclusion is fully
supported by the results of the detailed analysis of the
perception of pursuit-induced retinal-image slip in non-
human primates presented here.

**Materials and methods**

Four male rhesus monkeys (*Macaca mulata*), A, E, T,
and Z participated in this study. Two of the animals (E
and T) had contributed to our study of the cortical basis
of pursuit-induced retinal-image slip (Dicke et al., 2008).
Head movements were prevented by using a chronically
implanted head post that enabled easy and painless
stabilization of the head. Sceleral search coils were
implanted chronically in order to record eye position at
high temporal (1 kHz) and spatial resolution (Judge,
Richmond, & Chu, 1980). All monkey procedures includ-
ing implantation of search coils and head posts followed
standard surgical protocols (Thier & Erickson, 1992),
complied with the NIH Guide for Care and Use of
Laboratory Animals, and were approved by the local
animal care committee.
Determining the Filehne illusion in monkeys

In human studies, the Filehne illusion has usually been quantified by determining the amount of external background motion needed to balance out the pursuit-induced Filehne illusion, i.e., by identifying the background velocity that renders the background subjectively stable (Haarmeier et al., 2001; Haarmeier & Thier, 1996, 1998; Mack & Herman, 1973, 1978; Wertheim, 1994). In other words, the velocity of the background motion at this point of subjective stationarity (PSS) is the inverse of the Filehne illusion. The same approach was used here to measure the Filehne illusion of monkeys.

Stimuli were presented on a 50-cm computer monitor (Mitsubishi, frame rate 72 Hz, 1280 × 1024 pixels) placed 40 cm in front of the monkeys. The monkeys were required to keep their eyes within an eye-position window of 4° × 4° centered on the fixation target, a red dot of 3-arcmin diameter. The fixation target first appeared in the center of the screen, remained stationary for 500 ms, then jumped to an eccentric position on the left and moved to the right at a constant speed (12°/s for monkeys E and T) or 10°/s for monkeys Z and A), until it reached the same eccentricity on the right. While the monkeys pursued the target steadily on its way from left to right, a random dot pattern covering 25° × 25° was presented for 300 ms (monkeys E and T) or 500 ms (monkeys Z and A), temporally centered at the time the target reached the center of the screen (Figure 1). The background pattern consisted of 350 white dots (dot diameter = 15 arcmin, dot luminance = 14.6 cd/m²) randomly presented on the otherwise dark screen. The dot pattern moved coherently at a constant velocity either to the left or to the right. At the end of the trial, monkeys were asked to report the direction of the background motion by making indicative saccadic eye movements. Two green dots (diameter = 15 arcmin) served as response targets located 7.5° above or below, respectively, the center of the screen. Responses were accepted if eye position fell into the response window of 4.5° × 4.5° centered on the response targets. Animals were trained to make saccades to the upper target if they had perceived a rightward background motion and, conversely, to the lower target if they perceived a leftward motion.

The velocity of the background pattern was varied according to 3 independent and randomly interleaved strategies (Figure 2A). The 3 strategies were used for different purposes and had different proportions of trials in a given session.

The majority of the trials (85%) comprised trials of strategies 1 and 2, both having equal proportions of trials and consisting of constant background velocities. Strategy 1 involved the presentation of a constant background velocity intended to create large retinal-image slips (Figure 2A). To ensure an adequate stimulus driving recalibration of the reference signal, strategy 1 trials had to dominate a given experimental block and hence had a comparatively higher proportion (42.5%). To avoid a response bias (see below), another 42.5% of the trials consisted of a background, which always moved at a constant low speed of 3°/s (strategy 2) opposite to the direction of background motion of strategy 1. Although the velocity of the background of strategy 2 was much smaller than that of strategy 1, it was well above threshold, as reflected by usually close to 100% correct decisions by the subjects. A reward of liquid was given for correct responses to the recalibration background (strategy 1) and its complement (strategy 2), i.e., the monkeys got correct feedback concerning their responses. The trained monkeys were correct close to 100% of the time. A sequence of five correct responses allowed the monkeys to receive double the amount of reward and this amount was delivered until an incorrect answer was given.

Strategy 3 (15% of the trials) consisted of backgrounds in which the velocity was varied according to an adaptive staircase procedure (Parameter Estimation by Sequential Testing (PEST); Lieberman & Pentland, 1982; Taylor & Creelman, 1967). Trials of strategy 3 converged on the velocity where the subjects gave right and left responses with equal probability, reflecting random responses to a background, i.e., perceived as being stationary (point of subjective stationarity (PSS); Figure 2A).

Without introduction of strategy 2, the share of strategy 1 trials would have been twice as large, prompting monkeys to respond to 85% of trials for the direction of the strategy 1 background and only in those few trials for the opposite direction, on which strategy 3 (PEST) had chosen a background moving opposite to strategy 1. The
dominance of decisions in the direction of the strategy 1 background might have been expected to increase the tendency of the monkey to prefer this response direction in the case of close to threshold PEST strategy trials, in other words, introducing a response bias shifting the PSS.

To yield a better estimate of the subject’s perception, we subjected the strategy 3 trials (PEST strategy) to a probit analysis (McKee, Klein, & Teller, 1985) in order to estimate the background velocity at PSS (Figure 2B). The probit analysis fits a sigmoidal function to the psychometric data, using a least-square algorithm. The parameters characterizing the probit function are its turning point and the slope at that point. The turning point of the probit function defines the background velocity that yields equally probable right and left decisions, taken to reflect subjective stationarity of the background.

Figure 2A illustrates the trials from different strategies and the time course of one typical measurement session. In this example, the background velocity of strategy 1 was 15°/s (leftward) while the monkey was pursuing the target moving to the right at 10°/s. The complementary strategy 2 background having equal proportion of trials moved rightward at 3°/s. The monkey received a drop of liquid/juice as reward for each successful response.

The PSS was derived from the responses to strategy 3 trials (Figure 2A). Strategy 3 started from two different
starting levels (−6°/s and 6°/s) using two independent PEST strategies. As can be seen in Figure 2A, both PEST strategies converged to a similar background velocity and are in good agreement with the PSS derived from the probit analysis (Figure 2B). For the example shown in Figure 2B, the background velocity at which the monkey perceived the stimulus as stationary was −1.27°/s. The negative sign indicates leftward movement, i.e., the background was perceptually stationary for the monkey when it actually moved at 1.27°/s toward the left while the monkey was pursuing the target moving rightward at 10°/s. For trials with strategy 3 backgrounds, the monkeys were rewarded at random. This was necessary in order to prevent the formation of decision strategies based on internal states of the monkey, rather than on background motion, whose velocity was close to the perceptual threshold for most of the strategy 3 trials.

The monkeys obviously cannot tell us what they perceive; all they do is to respond in a fashion they think is appropriate given the feedback they have been provided. In any case the monkeys will try to optimize the overall amount of reward they earn in the experiment. Hence, the question is if the feedback the monkeys get would allow them to resort to a response strategy not reflecting their percept of background motion and still achieve a favorable outcome in terms of reward optimization. In the case of strategy 1 and strategy 2 stimuli, monkeys' responses closely corresponded to the physical direction of motion as indicated by the fact that success rates were typically considerably larger than 90%. As we cannot see any alternative to using a perception-based strategy providing such good success rates, it may be firmly concluded that the monkeys actually relied on their percept of motion. However, as rewards for strategy 3 stimuli were provided at random, one might assume that monkeys decided to also respond at random rather than paying attention to the percept of motion prompted by strategy 3 stimuli. There are 2 reasons we think that monkeys actually preferred a response strategy reflecting the percept of background motion. (1) The strategy 3 stimuli were based on two independent PEST strategies starting from two different velocities (−6°/s and 6°/s), which nevertheless always converged at the same PSS velocity. This would not be expected if monkeys had responded at random. (2) As will become clear from the results, we observed very specific modifications of the reference signal, determined by the responses to strategy 3 stimuli, depending on the speed and direction of strategy 1 stimuli. However, this would not be expected to be the case if strategy 3 stimuli were interpreted by the monkeys independent of the dominating strategy 1 and strategy 2 stimuli, which, as argued earlier, were based on their perceptual quality. These considerations suggest that the monkeys stuck to the percept-based response strategy appropriate for the strategy 1 and strategy 2 stimuli because these stimuli dominated the overall sequence by large.

Our paradigm is characterized by completely predictable speed, direction, and duration of target motion guiding the pursuit eye movement. On the hand, the motion of the strategy 3 background whose direction of movement had to be determined by the monkey was completely unpredictable as the speed and direction were chosen at random, hence lacking any cues that might have allowed monkeys to avoid assessing the given background motion by predicting future stimuli.

### Data analysis

Psychophysical and the eye-position data were stored for further offline analysis. All data analyses were performed by applying in-house custom written routines (MATLAB 6.5, The Maths Works, MA). Eye velocity was obtained by differentiation of the eye-position data. Occasional saccades were removed by using an acceleration threshold and smooth-pursuit velocity was linearly interpolated during saccades.

### Results

#### Experiment 1: Modulation of the Filehne illusion as a function of strategy 1 background velocity

The first set of experiments tested the assumption that the perception of pursuit-induced background movement in a given trial depends on the perception of background movement in earlier trials, an observation central to previous studies on human subjects (Haarmeier & Thier, 1996, 1998). To this end, the Filehne illusion was measured in three monkeys (E, T, and Z) by systematically varying the speed of the background of strategy 1 stimuli in different experimental sessions. As explained in the Materials and methods section, strategy 2 stimuli were moving at 3°/s, always in the direction opposite to those of strategy 1.

Stimuli moving in the same direction as the eyes reduce the resulting retinal-image motion and, therefore, mimic a reference signal over-compensating the reduced retinal-image flow. We will, therefore, refer to this as the “reference signal too high” (RS_large) condition. Conversely, stimuli moving in the opposite direction to the eyes enhance the resulting retinal-image motion and, therefore, mimic a reference signal under-compensating the enhanced retinal-image flow. Accordingly, we will refer to this as the “reference signal too low” (RS_small) condition.

We measured the PSS for experiments with various different strategy 1 background velocities, some moving in the direction of the pursuit eye movement (to the right) and others moving in the opposite direction (to the left). Varying
the velocity of strategy 1 backgrounds led to changes in the retinal-image slip of strategy 1 background measured as the difference between strategy 1 background velocity and eye velocity (positive signs for rightward movement and negative signs for leftward movement). Varying the retinal-image slip had a profound effect on the Filehne illusion as measured by the PSS (Figure 3A). In monkeys T and E, the PSS increased with positive, i.e., rightward, background motion of strategy 1. This increase was observed for a range of retinal-image slip velocities from about −30°/s to about +10°/s (corresponding approximately to about −20°/s to +20°/s if the PSS is plotted as a function of strategy 1 background velocity) with saturation emerging for velocities surpassing these limits in either direction. In monkey Z, saturation was not prominent; rather a drop of the PSS values immediately after the peak at retinal-image slip velocities of about −25 and +5°/s, respectively, was observed (Figure 3A, only the retinal-image slip velocity range from −25 and +5°/s for monkey Z is shown). Note that the plot for monkey Z had to be based on an ideal measure of retinal slip of the image of the strategy 1 background as given by the difference of background velocity and target velocity, assuming that eye and target velocity would be the same. On the other hand, for monkeys T and E, the corresponding plots were based on the actual retinal slip of the strategy 1 backgrounds, considering the actual mean eye velocity at the time of background presentation. Unfortunately, a consideration of the actual retinal slip was not possible for monkey Z as eye-position data were not available for post-hoc analysis, although eye position had been carefully monitored during the experiment using the same criteria as for the other two monkeys. As shown in Figure 4, monkey T exhibited a pursuit gain that was completely independent of background velocity, whereas monkey E showed a slight but significant increase of gain with increasing velocity of the strategy 1 background. Yet, the plots of PSS as a function of strategy 1 background image slip shown in Figure 3A are basically the same for these two monkeys, indicating that the slight differences in pursuit gain did not matter. We cannot exclude that the changes in the corresponding plot for monkey Z may have possible contribution from profound changes in pursuit gain prompted by the presentation of the background as described in several previous studies (Keller & Khan, 1986; Kodaka, Miura, Suehiro, Takemura, & Kawano, 2004; Mohrmann & Thier, 1995). In any case, small differences between the individual animals notwithstanding all 3 monkeys showed very similar dependencies of their percept as reflected by the fact that the data of all monkeys could be approximated well by a linear function with the velocity of the strategy 1 background image slip as an independent variable.

It is important to note that the percept of the monkeys changed in a way appropriate to ameliorate perceptual stability: Conditions with consistent strategy 1 background motion to the right (RS_large) induced high Filehne illusions, i.e., low reference signals as indicated by positive background velocities at PSS. Conversely, conditions with consistent leftward background motion (RS_small) induced low, i.e., inverted, Filehne illusion, resulting from high reference signals. In other words, in both conditions (RS_large, RS_small) the reference signal changed in a way that made the strategy 1 background more stable perceptually.

Figure 3B shows similar results for two human subjects. Both the pattern of PSS change as function of background motion and the range in which the values of PSS fall appear to be comparable to the monkey subjects.

**Experiment 2: Is the modulation of the Filehne illusion due to motion adaptation?**

As discussed earlier, the profound effect of the repeatedly presented background motion on the PSS may
reflect a modification of the reference signal (e.g., Haarmeier et al., 2001). However, an alternative explanation is also possible. Rather than changing the reference signal, repeated background motion might modify the afferent signal via mechanisms usually referred to as “motion adaptation”. It is well established that following prolonged image motion in the visual field, a stationary pattern appears to move in a direction opposite to the adapting stimulus (Barlow & Hill, 1963; Mather, Vestraten, & Anstis, 1998; Thompson, 1880). Accordingly, repeated exposure to moving background stimuli in our experiments might shift the PSS because of motion adaptation. For example, repeated presentation of backgrounds moving to the left might produce motion adaptation to the left and correspondingly a motion aftereffect to the right. An aftereffect to the right would reduce the visual motion signal evoked by pursuit eye movement to the right and result in a leftward shift of the PSS—as indeed observed. Previous work on human subjects argued against motion adaptation as an explanation for the modification of the Filehne illusion (Haarmeier et al., 2001; Haarmeier & Thier, 1996). The goal of Experiment 2 was to test if visual motion adaptation influenced the percept of self-induced background motion in the monkeys.

**Experiment 2a: Influence of background presentation time**

The motion aftereffect depends on the duration of stimulus presentation (Mather et al., 1998). A motion aftereffect typically decays exponentially in time with a time constant of 5–10 s (Keck & Pentz, 1977; Verstraten, Fredericksen, Grüsser, & van der Grind, 1994). In order to induce strong motion aftereffects, usually presentation times of a few seconds are thought to be necessary. To further minimize the potential impact of motion aftereffect, we ran an additional set of experiments, in which the duration of presentation of the background was reduced. Therefore, if motion aftereffect played a role, the modification of the PSS should depend on the presentation time of the strategy 1 background. In Experiment 1, the background presentation time of strategy 1 was 300 ms (monkeys E and T) and 500 ms (monkey Z), respectively. To look for an influence of motion adaptation, we tested monkeys T and Z with
additional presentation times (monkey T: 150 ms; monkey Z: 300 ms). The observed PSS values were compared to the standard experiment (Experiment 1). In Figure 5 the PSS observed in monkey T is plotted against the retinal velocity of the image of the strategy 1 background for two different presentation times (300 ms and 150 ms). The basic dependency of the PSS on the retinal-image motion was the same for both presentation times as indicated by the fact that data points for both presentation times overlapped considerably (Figure 5a). This impression was further supported by the results based on fitting the individual plots by linear functions and then showing that the slopes of the two functions have similar values (see Figure 5a).

In monkey Z we compared the PSS values between two durations of background presentation (500 ms and 300 ms) for only two different strategy 1 velocities (+10°/s: RS_large, and −10°/s: RS_small). As clearly evident from Figure 5b, the modification of the PSS did not depend on presentation time (t-test, p > 0.05; Bonferroni corrected). In summary, background presentation time had no influence on the modification of the Filehne illusion, at least not for the range of durations tested in our experiments. However, one may argue that even the very short durations used in this experiment may have had the potential to induce a motion aftereffect not further differentiating between duration of 150 ms and 500 ms. In fact, a recent study by Kanai and Verstraten (2005) on human subjects has demonstrated a rapid motion aftereffect for short duration adaptation stimuli (corresponding to our stimuli durations), which decayed after a blank period of 2–3 s. However, in our experiments, there were at least 2.5–3 s between subsequent presentations of backgrounds (the sum of the fixation period, pursuit without background, time for the response plus intertrial intervals). Hence, a rapid motion aftereffect in our experiments akin to the one reported by Kanai and Verstraten seems very unlikely.

**Experiment 2b: Motion-balanced strategy 1 stimuli**

In monkeys Z and A, we carried out another set of experiments to determine the role of motion adaptation in modifying the PSS. The main idea of this experiment was to avoid motion adaptation by minimizing net retinal-image motion in strategy 1 trials by balancing leftward and rightward stimuli (Haarmeier et al., 2001). In this experiment, the monkeys’ pursuit eye movements alternated between left and right whereas the direction of the strategy 1 backgrounds was kept fixed relative to the direction of pursuit, either always in the same or opposite direction of pursuit. The PSS was determined only for rightward pursuit. More specifically, in the RS_large condition, all rightward pursuit trials involved background stimuli moving at 10°/s toward the right and all the leftward pursuit trials involved background stimuli moving at 10°/s...
towards the left. Conversely, in the RS_small condition, all rightward pursuit trials involved backgrounds moving at 10°/s toward the left and all the leftward pursuit trials involved backgrounds moving at 10°/s towards the right. As in both conditions, the trials were equally balanced in terms of the direction of background movement; there was no resulting retinal net motion. If motion adaptation were to be responsible for the modification of the PSS, then this modification should drop to zero in the present configuration. Contrary to this prediction, we found that the observed PSS values for RS_large and RS_small were significantly different from each other. This was true for both monkeys tested (t-test, p < 0.05 each; Figure 6).

**Experiment 3: Does the modification of the Filehne illusion depend on a consistent mismatch between pursuit velocity and strategy 1 background velocity?**

Experiments 1 and 2 support the notion that the modification of the reference signal by the strategy 1 background stimuli reflects an inherent plasticity of the reference signal, and we have argued earlier that this plasticity may be needed in order to allow its optimization. Optimization needs feedback on the adequacy of the optimized variable, which should be both fast and reliable. For instance, if visually guided hand reaching has to be adapted to changes of the visual input, the adaptation will only take place if the feedback is consistent (Burge, Ernst, & Banks, 2008). In order to provide further support for the notion of reference signal plasticity and optimization, therefore in a final set of experiments we tried to manipulate the consistency of the visual information thought to drive the adaptation. Specifically, we asked whether the modification of the Filehne illusion depended on the consistent pairing of a given pursuit eye movement with a non-matching background (retinal image) velocity, i.e., the consistency of this mismatch. To answer this question, background velocity during strategy 1 was either constant for all trials (like in all previous experiments) or, in additional measurements, could have one of two preset values changing randomly from trial to trial. During strategy 1 background velocity was set to be 10°/s and 15°/s, respectively, to reduce the mismatch consistency. Accordingly, in the RS_large condition, instead of having single (+10°/s or +15°/s) strategy 1 velocity we had two constant strategy 1 velocities (+10°/s and +15°/s) presented randomly interleaved. Likewise, in the RS_small condition, strategy 1 velocities would alternate between −10°/s and −15°/s and the resulting modification was again compared to conditions for which strategy 1 velocity was constant throughout all trials (−10°/s or −15°/s, respectively). Strategy 3 was used in the same way as in previous experiments, and pursuit target velocity was kept constant at 10°/s (to the right). Two monkeys (Z and A) participated in this experiment.

In Figure 7, the PSS values are plotted for the different velocity combinations. The PSS values shown for the different conditions are averages (±standard errors) of at least 5 separate experiments in each monkey. Firstly, the figure shows that negative strategy 1 velocities (RS_large) induce shifts of the PSS in a leftward direction, and conversely, positive velocities (RS_small) result in PSS values shifted toward the right. Second, the respective shifts are stronger for higher velocities (+15°/s and −15°/s as compared to +10°/s and −10°/s, respectively). While these two observations are replications of Experiment 1, the important comparison here was whether a combination of two different velocities had an impact on the Filehne illusion. The PSS values for the configuration combining the two strategy 1 velocities should fall between those two involving only one single background velocity (10°/s or 15°/s). Conversely, if the modification of the Filehne illusion required a consistent mismatch, then the shift of the PSS values would be expected to be even smaller than the one observed for the lower velocity in the standard experiment. As a result, we observed in both monkeys that the absolute PSS values resulting from a combination of two different strategy 1 velocities were smaller as compared to the conditions involving only one single background velocity (10°/s or 15°/s). In other words, PSS values did not fall inside the range of PSS values spanned by the standard configurations. Notably, in monkey A, the PSS values did not deviate from zero at all suggesting a theoretically perfect percept of the world without any modification resulting from combining two strategy 1 stimuli.

![Figure 6](https://jov.arvojournals.org/)
This result is yet another argument against a significant contribution of motion adaptation to the modification of the PSS by the strategy 1 backgrounds in Experiment 1. If this modification was indeed a consequence of motion adaptation, one would expect the PSS values generated by the mixture of the 10°/s and 15°/s strategy backgrounds in Experiment 3 to fall in between those prompted by the individual strategy 1 backgrounds.

Discussion

Our study shows that it is possible to estimate the Filehne illusion, a subjective experience of background motion associated with smooth-pursuit eye movements, in monkeys by measuring the amount of external background motion required to cancel the pursuit-induced illusion. The psychophysical measurements in monkeys further support the concept that the perception of visual motion is based on a comparison of an afferent signal encoding retinal-image velocity with a reference signal predicting the consequences of the eye movement (Wertheim, 1994). According to this concept the two signals are subtracted from each other and the result of this subtraction is directly translated into a percept of motion. Changes of the size of the reference signal for a given amount of retinal-image slip will therefore yield different percepts of motion. Our experiments in monkeys show that the size and the direction of motion perceived during pursuit eye movements can be altered consistently and—depending on the choice of parameters—dramatically, if subjects repeatedly perform eye movements across a visual background that moves at a constant, predictable velocity. The changes induced by these constant velocity backgrounds are qualitatively similar to the ones previously reported in studies of human observers (Haarmeier et al., 2001; Haarmeier & Thier, 1996).

In principle, the observed modification of the percept of motion as measured by corresponding changes in the size of the PSS could have three possible reasons: response bias, visual motion adaptation, and reference signal recalibration. The first one, a response bias whose size and direction might depend on the strategy 1 background, can explain the changes observed here. A response bias might be expected to result from the fact that perceptual decisions prompted by high velocity strategy 1 backgrounds should come more easily and reliably than those prompted by their counterpart, the low-speed strategy 2 backgrounds, which are usually closer to the perceptual threshold. For instance, a strategy 1 background moving to the left will evoke close to 100% consistent leftward decisions, whereas the corresponding strategy 2 background may be expected to prompt a smaller percentage of rightward decisions. Hence, the monkey may generate a bias for rightward decisions in order to compensate for the smaller number of perceptually driven rightward decisions. However, the strength of the response bias should not depend on the absolute velocity of the strategy 1 background for velocities well above the perceptual threshold. However, as shown in Experiment 1, the PSS depends parametrically on strategy 1 background velocity. A further argument against a relevant role of this mechanism comes from the experiment with motion-balanced strategy 1 background presentation, where eye movement direction alternated between left and right and correspondingly, the strategy 1 background motion direction alternated between right and left, yielding equal numbers of trials with high-speed backgrounds to the left and to the right. Hence, any putative response biases for either side should have cancelled each other and consequently eliminated any modification of the PSS. However, this was clearly not the case as we observed...
consistent changes in the PSS that depended on the choice of the specific condition (RS_small vs. RS_large; Figure 6).

The second alternative explanation, passive visual adaptation resulting from prolonged exposure to visual background motion, can be discarded as well. Several observations clearly indicate that the modification of the Filehne illusion is not a consequence of visual motion adaptation. First, motion adaptation increases with longer presentation times and shorter time intervals between the adapting stimulus and the test stimulus, the latter because motion adaptation decays exponentially in time with a time constant of 5–10 s (Keck & Pentz, 1977; Verstraten et al., 1994). Therefore, to induce strong motion adaptation, usually presentation times of the order of a few seconds are thought to be necessary. Results from our experiments with varying presentation time are at odds with the notion of passive motion adaptation since shortening of presentation times by up to 50% left the Filehne illusion unchanged. This observation is in agreement with the fact that an increase of intertrial intervals in humans did not attenuate the modification of the Filehne illusion (Haarmeier & Thier, 1996). A second argument against motion adaptation is offered by the experiments balancing out the net retinal flow of motion resulting from the modifying stimuli. As a result of these experiments—again consistent with previous studies on humans (Haarmeier et al., 2001)—we found that the Filehne illusion can be altered even under conditions lacking any directional retinal motion asymmetry. Finally, the combination of two different strategy 1 stimuli (Experiment 3) shows that repeated retinal-image motion per se does not necessarily lead to a change in motion perception. Rather, it is the consistency between pursuit eye movement and related image motion, which has to be considered as the necessary condition for perceptual modification. We, therefore, interpret the present animal data as totally in line with the concept of the third option, a recalibration process directed to optimize the size of the reference signal.

Why should the reference signal be modified at all? One possible answer is that the inherent plasticity of the reference signal may be needed to cope with the variability of visual information on the one hand and of the variability of the oculomotor periphery on the other hand. The neuronal reflections of retinal-image slip are not faithful replicas of image slip on the retina but depend on a number of factors other than velocity such as luminance, contrast, pattern size, and structure, which will all modify both the size as well as the latency of the neuronal responses. Conversely, one and the same oculomotor command will have very different effects, depending on the efficacy of the oculomotor plant, which may change as a consequence of disease, aging, or simply fatigue. In order to achieve the perfect match needed, the brain should continuously adjust the size of the reference signal in a way so as to precisely predict the visual signal resulting from the ongoing eye movement. As shown in our final experiment (Figure 7), the recalibration process critically depends on the availability of a consistent mismatch between the two compared signals. This requirement of consistency in the modification of the perception of self-induced visual motion is reminiscent of the need for a consistent error driving motor learning (Burge et al., 2008). In this context it may not be surprising that a recent functional imaging study demonstrated BOLD responses in the lateral cerebellar hemispheres correlating with the size of the reference signal (Lindner, Haarmeier, Erb, Grodd, & Thier, 2006). That the cerebellum may indeed be involved in the cancellation of self-induced sensory signals and, most notably, in the adjustment of sensory predictions has been shown convincingly in elaborate studies on the electric fish (e.g., Bell, 2001). Our current knowledge on the neural underpinnings serving perceptual stability in humans is limited and relies most of all on non-invasive neuro-imaging techniques (Goltz, DeSouza, Menon, Tweed, & Vilis, 2003; Haarmeier & Thier, 1998; Lindner et al., 2006; Thier, Haarmeier, Chakraborty, Lindner, & Tikhonov, 2001; Tikhonov, Haarmeier, Thier, Braun, & Lutzenberger, 2004). By demonstrating that human and non-human primates share the same underlying principles, we think that we are now in a better position to answer many of the impending questions. Lesion, stimulation, and single unit recording studies can be employed on monkeys to characterize the brain areas involved in perceptual stability during pursuit eye movement and to search for a direct correlate of the inferential principle in the awake behaving animal.

PSS = Point of subjective stationarity
PEST = Parameter Estimation by Sequential Testing
RS_small = Reference signal too small
RS_large = Reference signal too large

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