Insufficient compensation for self-motion during perception of object speed: The vestibular Aubert-Fleischl phenomenon

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To estimate object speed with respect to the self, retinal signals must be summed with extraretinal signals that encode the speed of eye and head movement. Prior work has shown that differences in perceptual estimates of object speed based on retinal and oculomotor signals lead to biased percepts such as the Aubert-Fleischl phenomenon (AF), in which moving targets appear slower when pursued. During whole-body movement, additional extraretinal signals, such as those from the vestibular system, may be used to transform object speed estimates from a head-centered to a world-centered reference frame. Here we demonstrate that whole-body pursuit in the form of passive yaw rotation, which stimulates the semicircular canals of the vestibular system, leads to a slowing of perceived object speed similar to the classic oculomotor AF. We find that the magnitude of the vestibular and oculomotor AF is comparable across a range of speeds, despite the different types of input signal involved. This covariation might hint at a common modality-independent mechanism underlying the AF in both cases.

Introduction

Accurately estimating the speed of moving objects and self-motion with respect to the world is an important task for the nervous system which supports safe locomotion and interaction with the environment. This crucial ability depends on transformations between different reference frames, including retinal, head, and world coordinate systems. Extraretinal signals about eye movements must be taken into account to transform retinal signals into a head-centric reference frame and estimate object speed relative to the head (von Holst & Mittelstaedt, 1950). Similarly, when the head moves, vestibular and neck-muscle information must be used to transform signals from head-centered to body- and world-centered reference frames.

The estimates resulting from these transformations can be biased, yielding phenomena such as the Filehne illusion in which stationary objects appear to move during smooth pursuit eye movements (Filehne, 1922). An analogous vestibular phenomenon is the oculogyral

illusion, in which a head-fixed visual target seems to move during physical self-rotation relative to the observer in the direction of angular acceleration (Graybiel & Hupp, 1946).

The Filehne illusion is thought to arise from differences in the perceptual estimates of retinal and oculomotor speed (Freeman, Champion, & Warren, 2010; Furman & Gur, 2012; Haarmeier & Thier, 1996; Souman, Hooge, & Wertheim, 2005, 2006; Wertheim, 1981, 1987). This mismatch leads also to a related bias in perceived speed called the Aubert-Fleischl phenomenon (AF), in which pursued targets are perceived to move more slowly than nonpursued ones (Aubert, 1886). The underestimation of object speed during oculomotor pursuit was originally attributed to an erroneous estimate of eye velocity via an extraretinal signal, whereas retinal motion estimates were hypothesized to be veridical (Mack & Herman, 1973; Raymond, Shapiro, & Rose, 1984). Subsequent work cast doubt on this hypothesis by showing that the AF and Filehne illusion can be reversed, i.e., retinal velocity may become underestimated compared to oculomotor velocity, depending on the spatial frequency of the stimulus (Freeman & Banks, 1998; Wertheim, 1987). In other words, the strength and direction of the AF depends on the relationship between retinal and oculomotor speed estimates, with the former being a function of the stimulus. If both signals are linearly related to speed, then their ratio captures the behavior of phenomena such as the AF and Filehne illusion (Freeman, 2001; Furman & Gur, 2012; Souman et al., 2006).

In addition to eye movement, head and body movement also lead to motion at the retina, so the question arises how other reference frame transformations, e.g., into body or world coordinates, influence the perception of object speed. When the head moves, head-centric estimates can be transformed into a world-centric coordinate system using additional cues, i.e., signals from the vestibular system. These carry information about linear and angular accelerations and thereby allow for estimation of head motion.

In summary, estimation of object motion when the observers move their eyes, head, and body can be recovered by integrating the speed of the object on the retina, the speed of the eyes with respect to the head, and the movement of the head in space. Previous studies have focused on the perception of object speed in experimental conditions where the head was held still while the eyes were either fixating a stationary target or pursuing a moving target (Dichgans, Wist, Diener, & Brandt, 1975; Freeman, 2001; Freeman & Banks, 1998; Freeman et al., 2010; Powell, Meredith, McMillin, & Freeman, 2016; Raymond et al., 1984; Souman et al., 2006; Wer-

theim, 1987). The present study, in contrast, investigates the impact of vestibular signals on the perception of perceived object motion in the world during passive whole-body rotations.

There are some previous studies that have investigated the impact of vestibular signals on perception of object motion (e.g., Dyde & Harris, 2008; Jaekl, Jenkin, & Harris, 2005). However, these studies were not conducted under conditions that allowed for direct comparison between vestibular and oculomotor compensation which was our intention here. To preview our findings, we observe a phenomenon analogous to the classical (oculomotor) AF, in which objects that are pursued with a whole-body rotation, appear to move more slowly than nonpursued objects. We call this the vestibular AF. Our results show that the oculomotor and vestibular AF effects are similar in magnitude and can be described by a simple linear model of the signals involved.

Methods

Participants

Nine observes (four male, five female) with normal or corrected-to-normal vision participated in the experiment. They were aged 21 to 27 years (average age = 23.2 years) and had no history of neurological, visual, or vestibular disorders. Participants gave informed consent before taking part in the study. All but two (the experimenters) were naïve to the purpose of the study. The experiment was approved by the ethics committee of the University Hospital of Munich and conducted in accordance with the ethical standards of the Declaration of Helsinki.

Equipment

The experiment was conducted in a virtual reality setup consisting of a 6-degree-of-freedom hexapod motion platform (Moog© 6DOF2000E; MOOG, East Aurora, NY) and a stereo screen (JVC© GD-463D10, Refresh rate: 60 Hz; JVC, Yokohama, Japan) with dimensions 101.8 × 57.3 cm. Participants were seated in a racing seat mounted on top of the platform at a viewing distance of 47 cm. They wore custom-made welding goggles, restricting the field of view (FOV) to prevent them from seeing the edges of the screen (effective FOV: ~ 90° × 60° visual angle). The goggles enabling display of stereoscopic images contained a pair of circular polarized filters, a clockwise filter in one eye, and a counterclockwise filter in the other eye to match the polarization of each eye's image. The goggles also contained a blurring film to blend neighboring pixels, thereby weakening accommodative cues to screen
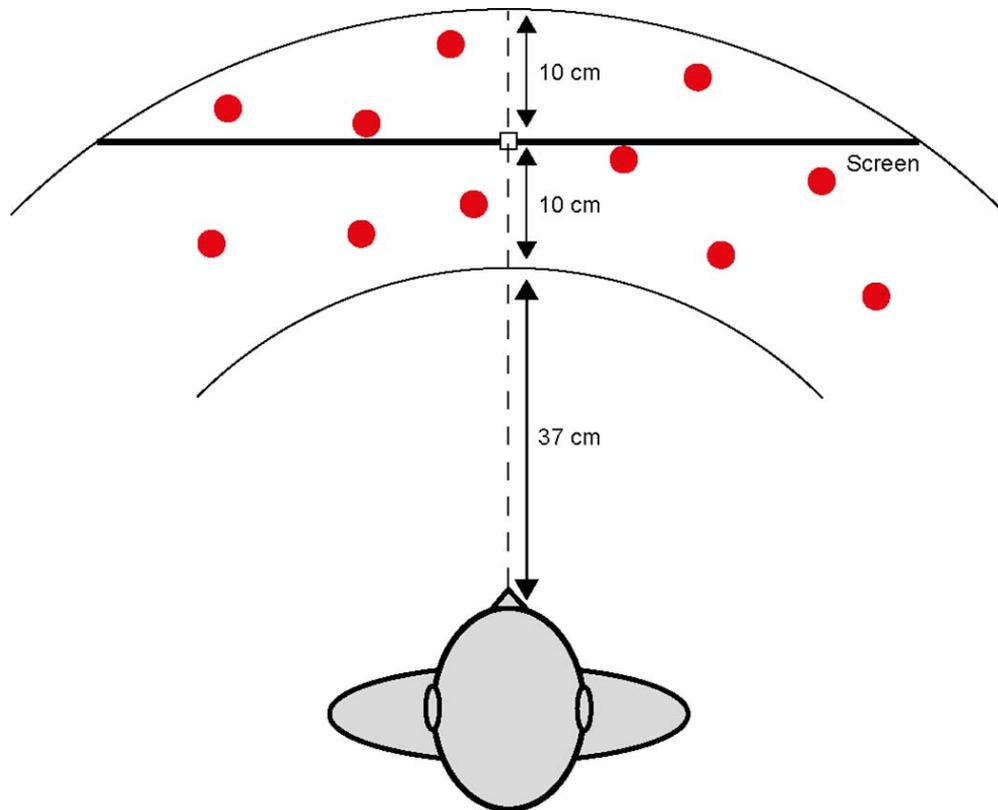
Figure 1. Experimental setup. Participants seated at a viewing distance of 47 cm watched a three-dimensional volume of randomly placed red spheres on a black background. Only spheres within the annulus of 10 cm in front of and behind screen depth were visible.

distance. The visual scene rendered via OpenGL© and Psychtoolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) consisted of a volume of randomly placed red spheres (radius = 0.4 cm) at a density of 0.004 spheres/cm^3 on a black background. To avoid spheres from obstructing the fixation point during rotation, only spheres located 4 cm above and below the white fixation point were visible. In addition, spheres located at a radial distance closer than 37 cm and further away than 57 cm from the eyes were not visible. Thus, the visual scene only contained spheres within the annulus of 10 cm in front of and behind screen depth (Figure 1).

During the experiment, the head was kept fixated with two padded restraints at the temples to minimize any movement of the head. Participants wore noise-cancelling headphones through which white noise was played to mask the sounds of the active platform. Responses in the experiment were collected using a response box with two buttons.

Experimental procedures and conditions

Participants performed a two-interval forced-choice (2IFC) task during which they indicated with a button press in which of the two intervals the annulus rotated more (displacement), faster (velocity), or stronger (acceleration) in the world (Figure 2). Displacement, velocity, and acceleration scaled together, and participants were explicitly informed that they could make judgments based on any of these. Anecdotally, subjects report having an intuition about the judgment without knowing whether they were judging displacement, velocity, or acceleration. For simplicity, we will only refer to velocity or speed in the following.

Depending on condition, different cues were available to estimate annulus speed. In retinal motion intervals (R), participants were instructed to fixate a white head-fixed fixation point at screen depth while the rotation of the annulus of red spheres induced retinal flow. This condition nulled eye movements and maximized retinal motion. In the eye pursuit intervals (Figure 2, left upper panel, E) the fixation point was moving at the same speed as the annulus. Here, eye movements were maximized and retinal flow minimized.

In the vestibular pursuit intervals (Figure 2, left lower panel, V), participants were passively rotated on the motion platform around the center of the head while the fixation point and annulus were stationary on
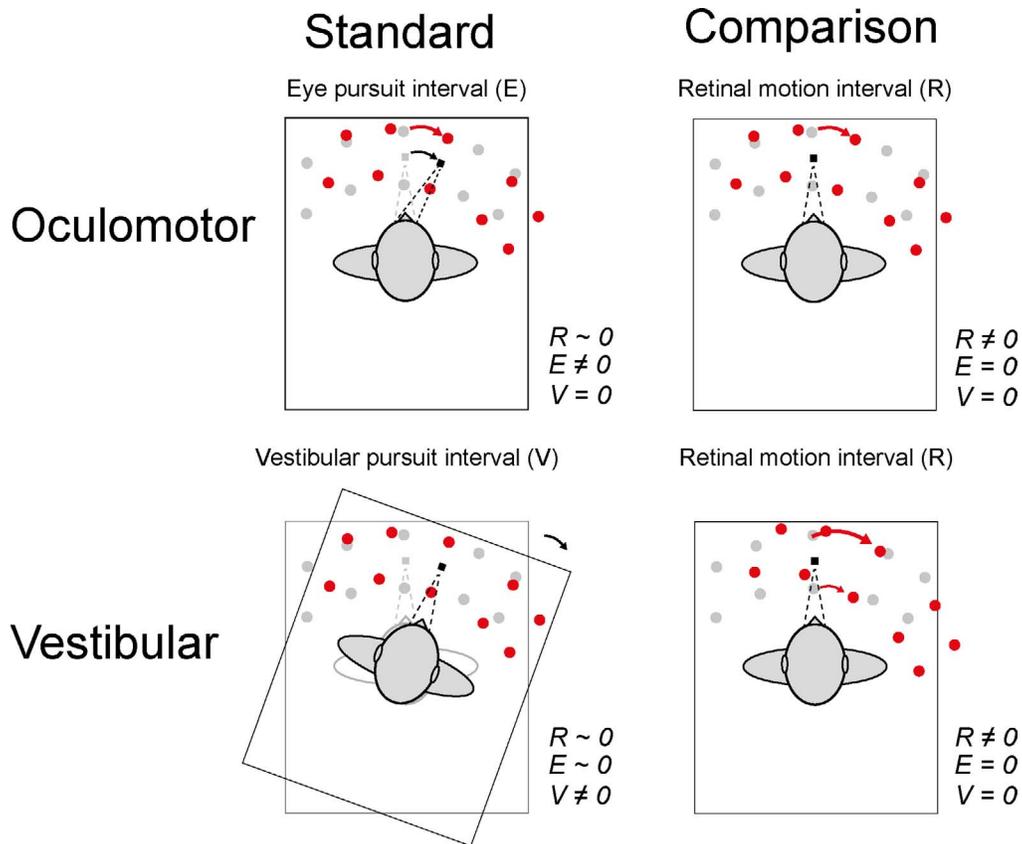
Standard   Comparison

Figure 2. Experimental conditions. On each trial, participants experienced a standard pursuit interval (left) and a comparison retinal motion interval (right) and indicated which rotation (around the center of the head) was larger, faster, and stronger (2IFC). The order of standard and comparison intervals was randomized across trials. The annulus elements are shown in red, the fixation point in black, the dashed lines indicate oculomotor fixation, and the rectangular outline indicates the motion platform. In the oculomotor condition (top), the pursuit was executed by following the fixation point with the eyes (dashed lines). In the vestibular condition (bottom), the pursuit was executed by maintaining fixation while the platform and annulus rotated together. These conditions were run in separate blocks. Equations to the lower right of each panel indicate if the stimulus velocity (R: retinal motion; E = eye pursuit; V = vestibular pursuit) was held constant (=0), approximately constant (~0), or varied ($\neq$0).

the screen. Here, the judgment about how fast the annulus had rotated in the world was dominated by vestibular signals. Participants were explicitly told that the annulus and fixation target remain stationary on the screen so that they rotate at the same speed in space as the participant.

Every trial consisted of a standard stimulus interval (either oculomotor or vestibular, Figure 2, left column) and a retinal-motion comparison interval (Figure 2, right column). The speed of the latter was adjusted from trial to trial according to a staircase procedure (Palamedes toolbox, Prins & Kingdom 2009) consisting of two interleaved staircases (2up-1down, 1up-2down) with a step size of 0.2 natural logarithms. The order of standard and comparison stimulus was randomized. Physical and visually simulated yaw rotation was about a vertical axis passing through the midpoint of the interaural axis of the head. Each movement had a

raised cosine velocity profile:

$$v(t) = \frac{D}{T}\left[1 - cos\left(\frac{2\pi t}{T}\right)\right]$$

with a duration (*T*) of 1 s, such that displacement (*D*), velocity (*V*), and acceleration scaled together.

The experiment consisted of two conditions that were run separately. In the (classical) oculomotor AF condition (E-R), the eye pursuit interval (E) was the standard and the retinal motion interval (R) the comparison. In the vestibular perceived speed condition (V-R), the oculomotor pursuit was replaced by a passive vestibular whole-body pursuit (V) while the retinal motion interval (R) still served as the comparison. The direction of rotation (left vs. right) across trials was randomized but both rotations within each trial were in the same direction and were separated in time by a pause of 0.5 s. At the end of each trial, a tone
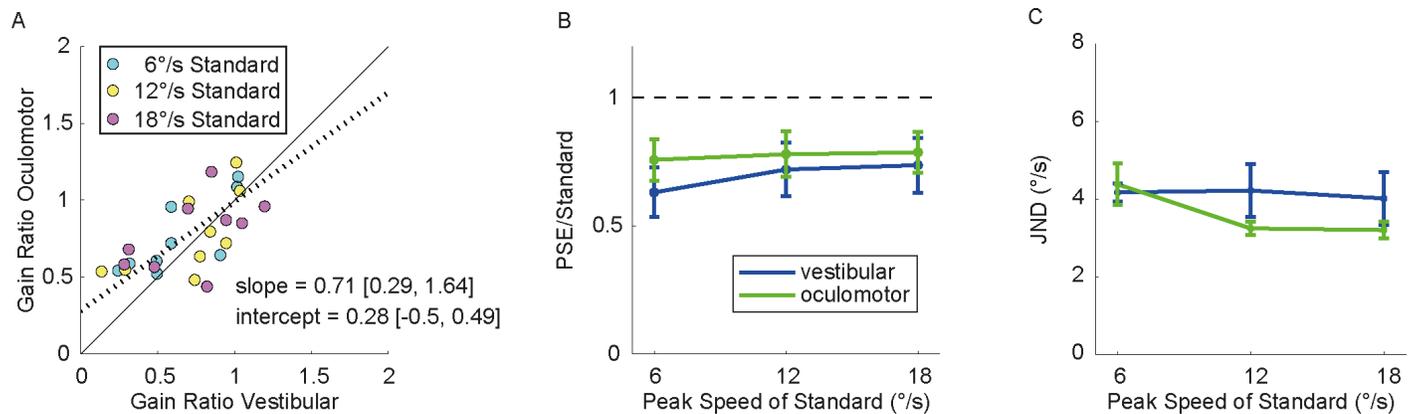
Figure 3. Results, (A) Oculomotor and vestibular gain ratios of all participants for three peak speeds of standard (6°/s, 12°/s, and 18°/s); the black line represents unity slope, the black dotted line indicates a total least squares fit with confidence intervals of slope (0.71) and intercept (0.28) in brackets. (B) Mean ratios of retinal to oculomotor (R/E, green) and retinal to vestibular (R/V, blue) speed at PSE for the three peak speeds of standard are shown. Gain ratios smaller than 1 represent an underestimation of oculomotor or vestibular pursuit speed with respect to retinal speed. Error bars indicate the standard error of the mean. (C) Mean JNDs for oculomotor (green) and vestibular (blue) conditions for the three peak speeds of standard. Error bars indicate the standard error of the mean.

of 0.2 s served as a signal for participants to respond using the button box.

Both conditions were tested at three speeds (standard peak velocity V_{max} of 6°/s, 12°/s, or 18°/s) with 75 trials per staircase, condition, and speed level, resulting in 900 trials in total. Ten practice trials with verbal feedback at the start of each condition ensured that participants had understood the task correctly. Each condition was divided into blocks of 75 trials with short breaks in-between to maintain participants' attentiveness.

Statistical analyses

Using MATLAB (version R2010b; MathWorks, Natick, MA) and the Palamedes toolbox (Prins & Kingdom, 2009), each participant's data for every condition was fit by cumulative Gaussians using a GLM with a probit link and a maximum likelihood fitting routine. The mean of the cumulative Gaussian fit was taken as the point of subjective equality (PSE), i.e., the stimulus intensity that elicits 50% "comparison faster than standard" responses. Significant deviation of the PSE from the standard was interpreted as a bias, i.e., incomplete compensation for eye or body motion. The standard deviation of the cumulative Gaussian fit was taken as the just-noticeable difference (JND), i.e., the change in stimulus intensity relative to the PSE that results in 84% comparison faster judgments.

To estimate the size of the AF in the two conditions, we calculated the ratio of retinal speed at the PSE to oculomotor or vestibular speed of the standard stimulus, i.e., R/E or R/V respectively. We call this the "gain ratio" in keeping with definitions in the literature (see Furman & Gur, 2012, for a review). If the perceived speed of retinal motion is greater than either the oculomotor or the vestibular standard, then the comparison interval would need to be slowed down to achieve the speed-match at the PSE. In this case, R/E or R/V < 1, as in the classic AF. If, on the other hand, oculomotor or vestibular standards appeared faster, then R/E or R/V > 1.

Results

The mean gain ratios shown in Figure 3B suggest similar AF effects in the oculomotor and vestibular conditions. In fact, gain ratios from both conditions are significantly correlated ($\rho = 0.65$, $p < 0.001$) and the confidence intervals of slope and intercept of a total-least squares fit contain 1 and 0, respectively (see Figure 3A), supporting the high similarity between both AF effects.

A two-way, repeated-measures ANOVA did not reveal any main effects of self-motion condition, $F(1, 8) = 1.19$, $p = 0.31$, nor was there a main effect of peak standard speed, $F(2, 16) = 2.67$, $p = 0.10$, which suggests that the AF effects can be described reasonably well by a linear model in which the signals estimating retinal, oculomotor, and vestibular speed depend on the relevant physical speed of movement times some fixed gain factor (Freeman, 2001; Furman & Gur, 2012; Souman et al., 2006). In support of this hypothesis, the ANOVA did not reveal any interaction between factors, $F(2, 16) = 1.01$, $p = 0.39$.

Since there was no significant main effect of speed, gain ratios from all speed levels were pooled to test both AF effects. A one-sample t test showed the mean gain ratio in the oculomotor condition ($M = 0.77$, $SD = 0.24$) was significantly less than 1, $t(26) = -4.90$, $p < 0.001$, which is consistent with the classic AF. Another one-sample t test revealed the mean gain ratio in the vestibular condition ($M = 0.70$, $SD = 0.30$) was also significantly less than 1, $t(26) = -5.28$, $p < 0.001$, which supports our hypothesis of a vestibular analogue of the classic AF.

JNDs are shown in Figure 3C. A two-way, repeated-measures ANOVA did not show any main effect of self-motion condition, $F(1, 8) = 3.11$, $p = 0.12$, nor was there a main effect of speed, $F(2, 16) = 1.09$, $p = 0.36$, i.e., JNDs were approximately the same for all peak standard speeds, similar to previous findings by Freeman et al. (2010). The ANOVA did not show any interaction between speed and condition, $F(2, 16) = 1.19$, $p = 0.33$.

Discussion

Targets are typically perceived to move more slowly when pursued by eye (Aubert, 1886; Dichgans et al., 1975; Freeman, 2001; Freeman & Banks, 1998; Freeman et al., 2010; Raymond et al., 1984; Souman et al., 2006). This so-called Aubert-Fleischl phenomenon (AF) reveals differences in perceptual processing of signals encoding image motion and those encoding eye movement. Here, we found the same was true for extraretinal signals that originate from the vestibular system. Objects that are physically pursued via whole-body rotations appear to move more slowly than nonpursued objects. The ratio of vestibular pursuit speed to the perceptually equivalent retinal speed during the nonpursuit interval was significantly smaller than 1, demonstrating a vestibular analogue of the AF.

Vestibular and oculomotor AF compared

It is remarkable that similar gain ratios were observed in the oculomotor and vestibular conditions (Figure 3A and B). In both cases, the estimate of object speed based on the extraretinal signal, whether oculomotor or vestibular, was reduced relative to the estimate of speed based on retinal motion with stationary eyes and head. In the vestibular condition, a head-fixed fixation target ensured that the eyes remained stationary with respect to the head, implying that the vestibulo-ocular reflex (VOR) was suppressed. Gauthier and Vercher (1990) have argued that VOR suppression mainly results from smooth pursuit signals.

This argument raises the possibility that both oculomotor and vestibular AF are driven by the same underlying mechanism, namely smooth pursuit. Additional evidence for the importance of VOR suppression signals for the (illusory) perception of object motion comes from a study by Evanoff and Lackner (1987) showing that the magnitude of the oculogyral illusion depends on the suppressed VOR signals during fixation of a head-stationary target. Heckmann, Post, and Deering (1991) could also show that the amount of illusory self-motion perception induced by fixating a target on a moving background can be manipulated. Deviation of the fixation point in the same direction as the background motion reduced induced motion while deviation in the opposite direction enhanced induced motion. These findings support the hypothesis by Whiteside, Graybiel, and Niven (1963) that the oculogyral illusion and related phenomena such as induced motion may be due to an overriding mechanism of reflexive compensatory eye movements to maintain fixation of the retinal image.

We also found that the gain ratios did not depend on speed. Thus, a linear model in which the speed estimates defined by the underlying signals are a fixed fraction of speed (e.g., Freeman, 2001; Furman & Gur, 2012; Souman et al., 2006) can also characterize cases in which extraretinal signals originate from the vestibular system.

JNDs were approximately constant for all peak standard speeds. Although not being consistent with Weber's law, this finding is in line with previous reports which show that Weber fractions (i.e., JNDs expressed as a fraction of the standard speed) for speed discrimination over this range of standard speeds become smaller, irrespective of whether stimuli are fixated or pursued (Freeman et al., 2010). As with the linear speed estimates, the noises associated with oculomotor and vestibular signals appear to be remarkably similar.

In the two remaining sections of the discussion, we relate our newly found vestibular AF effect to research on self-motion perception and we discuss a possible common explanation of both oculomotor and vestibular AF.

The AF during self-motion

Whereas previous research investigating the AF effect primarily focused on the perception of object motion in stationary subjects, some studies have shown that the AF effect also occurs for visually induced self-motion (de Graaf, Wertheim, & Bles, 1991; de Graaf, Wertheim, Bles, & Kremers, 1990) when participants experienced an increment in speed of circular vection while the eyes were kept stationary as compared to

periods of optokinetic nystagmus. Our study broadened the scope of the AF effect by asking observers to judge object motion during passive physical self-motion. The existence of both visually induced and vestibular self-motion AF effects can possibly be explained by early visual-vestibular interactions such as the convergence of both vestibular and visual afferents in the medial vestibular nucleus (Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2012).

In contrast to previous studies using very sparse stimuli with a small field of view (Brenner & van den Berg, 1994; Freeman & Banks, 1998; Freeman et al., 2010; Raymond et al., 1984; Souman et al., 2005; Turano & Heidenreich, 1999), observers in our experiment viewed a stereoscopic visual scene with a relatively large field of view. The current results reveal a systematic underestimation of object speed, not only for stationary observers (classic AF), but also for passively moved observers (vestibular AF). The latter implies incomplete compensation for self-motion, which has previously been shown for estimation of object paths (Dokka, MacNeilage, DeAngelis, & Angelaki, 2015). A possible explanation may be an underestimation of self-motion based on vestibular signals during passive movement (Dyde & Harris, 2008) which appears to be reduced when movements are actively generated and efference copy and proprioception are available (Dupin & Wexler, 2013; Dyde & Harris, 2008; Genzel, Firzlaff, Wiegrebe, & MacNeilage, 2016). This suggests that the vestibular AF may be reduced when head movement is actively generated, but this idea remains to be tested.

Another possible explanation for the AF during both eye and head movement is that participants failed to judge object motion in the world reference frame, as instructed. They may have inadvertently combined speed estimates across reference frames (e.g., retinal- and world-centered) as proposed previously (Hogendoorn, Alais, MacDougall, & Verstraten, 2017).

Speed estimation under natural conditions

In real life, moving the eyes to pursue a moving object usually results in relative motion of the object compared to the stationary background. Also during self-motion, fixating a body-fixed target (e.g., looking at a spot on the car window) induces relative motion of the target compared to the background, i.e., retinal flow with respect to the stationary fixation point (or spot on the window). Therefore, our prior experience generally predicts retinal motion of the stationary background in the direction opposite the pursuit movement while the target remains fixated.

In our experiments, the visual stimuli during pursuit intervals were kept as simple as possible to isolate pursuit from any influence of relative motion; there was no relative motion of the background. Here we raise the possibility that the AF we find in our experiment could be partially due to the discrepancy between the prior knowledge about real world statistics of relative motion between fixated object and background and impoverished experimental stimuli where no relative motion signal is available. Revisiting previous studies that investigated the classical AF reveals a general lack of motion of the target relative to the background during pursuit intervals (Dichgans et al., 1975; Freeman et al., 2010; Raymond et al., 1984; Souman et al., 2006). Freeman et al. (2010) tried to rule out this explanation of the AF by testing whether relative motion has an influence on the perceived speed during stationary fixation. Speed perception was compared between conditions with and without a textured background, but no difference was observed. Whereas this speaks against relative motion as an explanation of the AF effects, Brenner and van den Berg (1994) found that under natural conditions, perceived target velocity was accurate (i.e., no AF was observed) if the relative motion between a target and the background was maintained. Further experiments investigating the influence of background motion are needed to determine whether the AF can be partially ascribed to the lack of naturalistic relative motion signals during pursuit.

Keywords: Aubert-Fleischl, speed perception, vestibular, oculomotor, retinal

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