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Ocular following response to sampled motion

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ABSTRACT

We investigate the impact of monitor frame rate on the human ocular following response (OFR) and find that the response latency considerably depends on the frame rate in the range of 80–160 Hz, which is far above the flicker fusion limit. From the lowest to the highest frame rate the latency declines by roughly 10 ms. Moreover, the relationship between response latency and stimulus speed is affected by the frame rate, compensating and even inverting the effect at lower frame rates. In contrast to that, the initial response acceleration is not affected by the frame rate and its expected dependence on stimulus speed remains stable. The nature of these phenomena reveals insights into the neural mechanism of low-level motion detection underlying the ocular following response.

1. Introduction

While earlier studies on vision used analog hardware, it is nowadays common practice to use computer-generated stimuli presented on a monitor. This raises an inherent but often unrecognized problem: Are the measured responses biased by artifacts due to the digital nature of stimulus generation and presentation? Psychophysical experiments show that if the sampling frequency of a stimulus is above a certain threshold, digital stimuli appear indistinguishable from corresponding analog versions (Burr, Ross, & Morrone, 1986a, 1986b; Cropper & Badcock, 1994; Fahle, Biester, & Morrone, 2001; Landis, 1954; Simonson & Brozek, 1952; Watson, Ahumada, & Farrell, 1986). Thus, one might be inclined to assume that with monitor frame rates above this threshold the experimental results also apply to the natural situation where motion is continuous.

In our present study we wish to extend the fund of evidences from the perceptual domain to the domain of reflexive eye movements in response to a moving digital stimulus. Reflexive eye movements are particularly interesting because they are less affected by cognitive processes than perception, and are dominated by a "bottom-up" type of information processing, particularly when restricted to the open-loop period. This is the time interval when the eye movements are solely based on the visual information about the initial phase of the moving stimulus and not on information about the eye's self-motion. Hence, during the open-loop period there is a purely feed-forward information flow which is much easier to treat than a closed-loop situation where feedback processes influence motor behavior.

Besides the "smooth pursuit" response to a small moving target, which at least requires some degree of attention by the subject towards the target, there is another more reflexive type of eye movement, the ocular following response (OFR) which is evoked by the coherent motion of a large part of the visual field. The OFR does not require attention, cannot be suppressed and is highly automated, and is therefore very well suited for the study of low-level vision. Discovered and studied by Miles and coworkers in primates (monkey: Kawano & Miles (1986), Miles & Kawano (1986), Miles, Kawano, & Optican (1986); human: Gellman, Carl, & Miles (1990)), the OFR is commonly regarded as being part of a more complex mechanism, the "optokinetic nystagmus", whose assumed main purpose is to stabilize the visual world against self-motion (Ilg, 1997; Miles, 1997). There is convincing evidence that low-level "energy-based" rather than high-level "feature-based" motion detection (Krekelberg, 2008, chap. 2.09; McCool and Britten, 2008, chap. 2.10) is driving OFR (Chen, Sheliga, Fitzgibbon, & Miles, 2005; Hayashi, Miura, Tabata, & Kawano, 2008; Masson, Yang, & Miles, 2002; Miura et al., 2006; Sheliga, Chen, Fitzgibbon, & Miles, 2005; Sheliga, Chen, FitzGibbon, & Miles, 2006).

Throughout the past decade, the methods of investigating motion induced eye movements have changed from using analog to digital equipment for visual stimulation. The objective of the present study is to investigate in how far the temporal resolution of sampled motion affects human OFR. We use two different parameters of the response, i.e. latency and initial eye acceleration, to characterize the dependence of the OFR on stimulus speed and frame rate. We find that a moving random dot pattern evokes OFR in a graded manner, depending not only on stimulus velocity

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(as expected) but also on the monitor frame rate, even for values far above the flicker fusion limit. We therefore conclude that for the study of OFR in humans it is of vital importance whether true or sampled motion is used, and in the latter case, at what specific sampling rate the stimulus is displayed. Our findings might also be relevant for studies on other types of eye movements, e.g. smooth pursuit, and for studies on perception. Besides the methodical implications, our findings reveal interesting aspects about motion vision and the oculomotor pathway contributing to OFR. In particular we find different dependencies of latency and eye acceleration on speed and monitor frame rate. We offer a straightforward explanation of the experimental results on the basis of spatiotemporally oriented receptive fields early in the visuo-motor pathway.

2. Methods

2.1. Visual stimulation

The stimulus consists of a moving random pattern of black dots ($0.05\ \mathrm{cd/m^2}$) on white ground ($107.6\ \mathrm{cd/m^2}$), with an average density of 2 dots per $\mathrm{cm^2}$, each dot having a diameter of 3 pixel $\hat{=}$ 0.12 cm $\hat{=}\ 0.1508^\circ$ viewing angle. We decided against the usual random dot pattern with white dots on black ground because on our CRT monitor they show a (faint) tail when they move, which might have an influence on the ocular response. It is possible that sampling artifacts have a stronger impact on the visual system when using black-on-white stimuli. This circumstance does not, however, touch the consequences we draw from our results. The dots are distributed across the entire screen. When a 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 CRT monitor (Iiyama Vision Master 506) 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° viewing angle. (The angles have been calculated using the exact formula, though.)

Random dot patterns are displayed at three distinct velocities and at three distinct monitor frame rates. Because it was only possible to manually change the monitor frame rate, we separated the experiment into three subsequent sessions with three monitor frame rates 80, 120 and 160 Hz, in random order per subject. The stimulus speeds were randomly shuffled during each session. Since the ocular following response is more pronounced when it is executed shortly after a saccade (monkey: Kawano & Miles (1986); human: Gellman et al. (1990)) – an effect called *post-saccadic enhancement* – it is common to use an appropriate paradigm: An initial saccade triggers the motion onset of the pattern after a certain post-saccadic delay. For our experiments we chose it to be 50 ms. In the frame following this delay the random dot pattern was displaced for the first time.

The temporal sequence of the stimulus is as follows: (1) A random dot pattern appears together with a fixation spot which is displaced 10° randomly to the left or right of the center. (2) 100 milliseconds after the subject fixates the spot, it disappears and re-appears in the center. (3) 50 milliseconds after the subject fixates the central spot, it disappears and the pattern moves for 500 ms at a randomly chosen constant velocity randomly to the left or right. (4) The screen is blanked (white) for 500 ms and the sequence restarts. Note that the time periods given here refer to the instructions for the programmed stimulus sequence. The visual display was updated in the next frame following any of these four steps. The temporal axis was defined to start at stimulus motion onset, that is, at the first frame showing the displaced stimulus.

2.2. Data acquisition

The gaze position of the right 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 postprocessing took place offline and was carried out with MATLAB™.

2.3. Subjects

There were six subjects at the age of 20–40, one being a colleague of the authors familiar with the rationale of the experiment, and the other being recruited students naive to the rationale. All subjects had normal or corrected-to-normal binocular vision and were seated in a darkened chamber with their head resting on a chin-and-forehead support in the eye tracking column, watching the monitor at a distance of 57 cm. Because the integrated corneal-reflex detection of the eye tracking system compensates small involuntary head movements to an extent sufficient for the purpose of our study, we did not apply any other head fixation apart from the chin-and-forehead support.

2.4. Data analysis

In order to reduce measurement noise, the recorded gaze position data were filtered by a zero-phase second-order running average over 10 samples corresponding to 20 ms. From the gaze position $e(t)$ we obtained the gaze velocity $\dot{e}(t)$ and acceleration $\ddot{e}(t)$ by digital derivation. Since we want to analyze pure ocular following responses only, trials containing saccades in the time interval $(0, 200)$ ms after stimulus motion onset were discarded. The criteria for saccade detection were a speed of more than 20 deg/s or an acceleration of more than $2000\ \mathrm{deg/s^2}$.

2.5. Response latency

One of the characteristic features of the ocular following response is its latency, that is, the time it takes for the oculomotor system to react to stimulus motion. There are two main strategies to extract this feature from a set of responses to the same stimulus: (1) determine the latency of the mean response obtained by averaging over the individual responses, or (2) determine the latency of each individual response and calculate the average over these values. We have tested both strategies against each other and opted for the latter because it leaves more options for the statistical evaluation.

We have tested different latency detection methods and also varied the parameters of the corresponding algorithms, and we have decided for a method similar to the one used by Carl and Gellman (1987) and Krauzlis and Miles (1996), because it yielded the most reliable results (see Fig. 1 for illustration). 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 three standard deviations from the baseline. The intersection of these two lines gave the estimate of the response onset. The two fittings involved are more stable if reasonable constraints are defined. The baseline $f_1(t) = a_1 + b_1 t$ is fitted by constraining the parameter for post-saccadic drift a_1 to $(-2, 2)$ deg/s and the parameter for post-saccadic acceleration

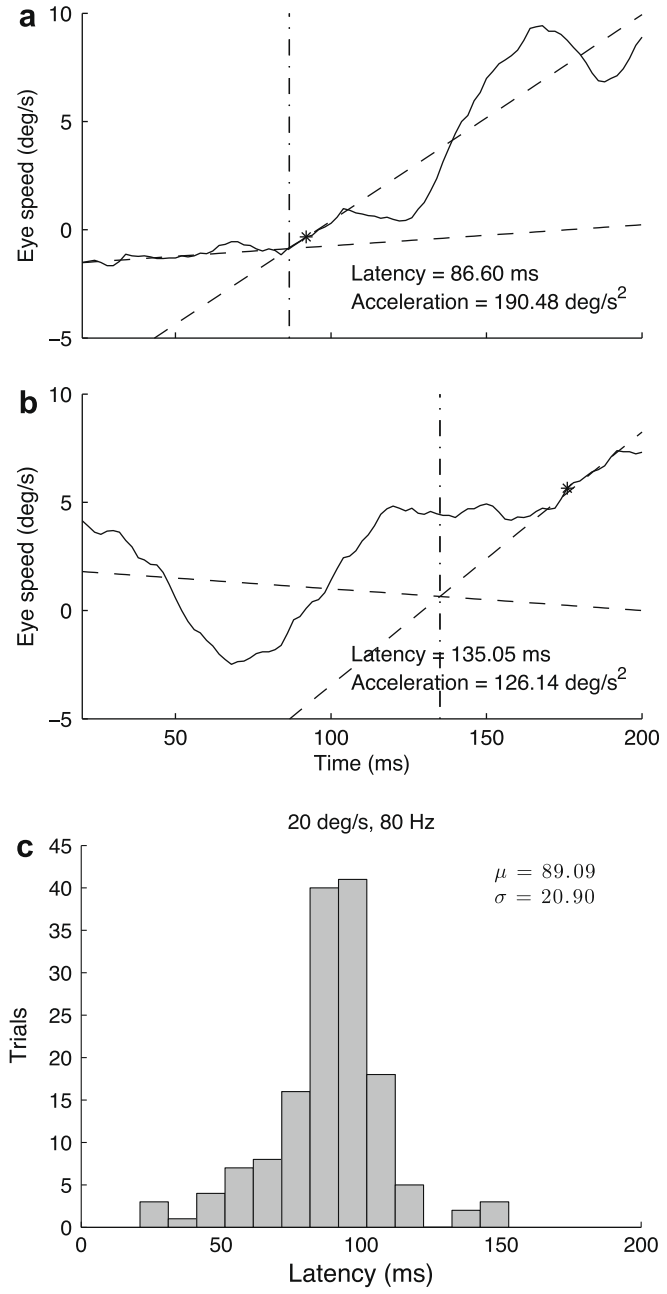

Fig. 1. (a), (b) Examples of how the latency determination algorithm works on individual eye traces. In (a) the algorithm finds a plausible response onset, while in (b) it obviously fails and returns a physiologically highly implausible value. Trials of the latter type are excluded from the statistics. (a) Subject MS, stimulus speed 20 deg/s, frame rate 80 Hz. (b) Subject MS, stimulus speed 10 deg/s, frame rate 80 Hz. The indicated acceleration values are estimates of the initial peak acceleration. (c) Histogram of latency values of subject MS for 80 Hz frame rate and 20 deg/s stimulus speed. When the implausible values outside the range of (50,120) ms are excluded, the mean and standard deviation become $\mu = 89.46$ ms and $\sigma = 14.68$ ms, respectively.

b_1 to $(-10, 10)$ deg/s^2. The response line $f_2(t) = a_2 + b_2 t$ is fitted by restricting a_2 to negative values and b_2 to positive values. Nonetheless, there are cases where the algorithm returns physiologically highly implausible results (Fig. 1b). The histogram of returned latency values shows that those implausible results are cumulated left and right from a central Gaussian-shaped distribution (Fig. 1). This indicates that the "outliers" are due to an instability of the algorithm rather than due to typical measurement noise or biological variability. Since these outliers contaminate the analysis of latency effects, we decided to discard them from the statistics. Comparing different histograms (not shown here), we have chosen the range of accepted values to be $(50, 120)$ ms. After this post-selection, the histograms better approximate a Gaussian shape. The percentage of discarded trials was 8%, 5.5%, 17.6%, 15.7%, 13.9%, and 10.0% for subject FS, LB, MA, MS, MdL, and ND, respectively. Our measurements revealed a mean latency of 70–90 ms, which is in agreement with the literature (Gellman et al., 1990; Ilg, 1997).

2.6. Response acceleration

Another characteristic of the ocular following system is how strongly it reacts to stimulus motion. Among the many ways to quantify this strength we have chosen the initial peak acceleration derived from a 40 ms interval after response onset. To cope with the enhanced measurement noise in the acceleration data, a 5-sample running average filter is applied before determining the acceleration peak.

2.7. Statistics

There were nine stimulus conditions consisting of three stimulus speeds of 10, 20 and 30 deg/s, and of three monitor frame rates of 80, 120 and 160 Hz. There were 150 trials per stimulus condition and subject. Some trials were discarded due to saccades in the initial interval $(0,200)$ ms after stimulus motion onset. Afterwards, there were at least 100 trials left per condition and subject. For each subject and stimulus condition we calculated the mean response latency and acceleration by averaging over the values obtained in the corresponding trials. We then took these mean values obtained per subject and calculated the means, the confidence intervals, the t-tests and the ANOVAs based on a sample size of $N = 6$ subjects. The error bars shown in the figures indicate the 95% confidence interval.

We performed two-tailed paired t-tests on the latency and acceleration data using a significance level of $\alpha = 0.05$. To give an example, we tested the latency for a dependence on the monitor frame rate by grouping the latency data according to stimulus speed and performing a paired t-test on each of the three possible pairings of frame rates (Fig. 5a). Since there are multiple (in this case, three) tests per grouping, a statistical correction was applied resulting in a more conservative significance criterion; we have chosen the Holm–Bonferroni correction method. Since each subject was tested on all conditions, it was possible to apply *paired* t-tests which are more sensitive than standard (unpaired) t-tests. The pairs of numbers (n, m) shown in Fig. 2 and 5, 6 indicate significant pairs, where each number $n = 1, 2, 3$ refers to the nth column in the group. Note how in some cases the 95%-confidence intervals overlap although the corresponding paired t-tests indicate significance.

We also applied ANOVAs on the data whose p-values are shown in Figs. 2 and 5, 6. An ANOVA tests each group of data sets against the null hypothesis of having the same mean. However, it is less sensitive than a paired t-test. Note how in some cases the ANOVA reports no significance although some of the pairs are indicated by the paired t-test as being significantly different.

3. Control experiments

To keep the mean luminance constant when the monitor frame rate is reduced, the monitor displays each individual frame at higher luminance. However, the compensation is not perfect: We measured the luminance of a white displayed rectangle averaged over 3 s using a Minolta LS-110 luminance meter for all three frame rates and found it to be slightly decreasing (about 8%) for lower frame rates. At 80, 120 and 160 Hz the luminance was $99.16 \pm 0.05, 103.43 \pm 0.05$ and 107.90 ± 0.08 cd/m^2, respectively. It therefore might

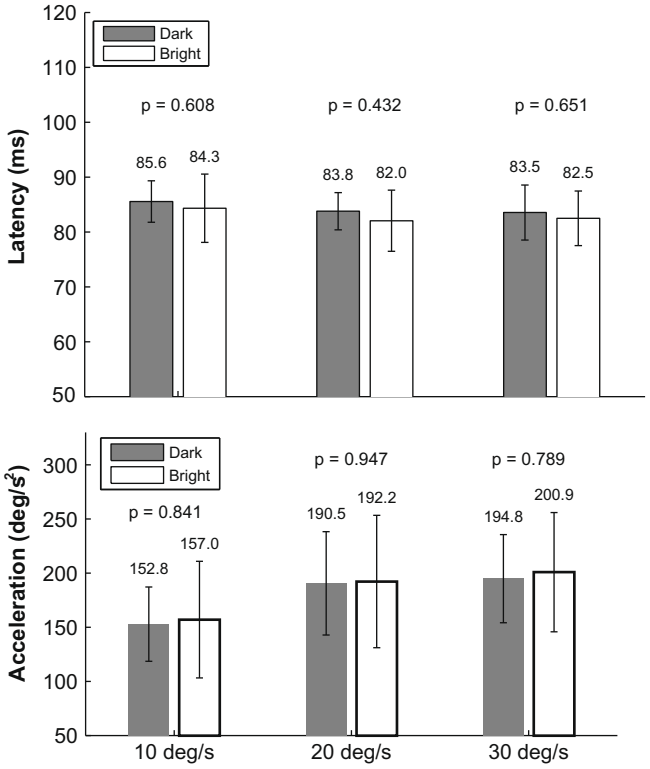

Fig. 2. Control experiments performed on 4 of the subjects (FS, MA, MS, MdL) at a monitor frame rate of 120 Hz: Comparison between the experiment performed at normal luminance level and 50% reduced luminance. A paired *t*-test yields no significant differences with respect to the two luminance conditions. Standard *t*-tests (unpaired) also yield no significant differences (see *p*-values). This applies to both the response latency (top) and acceleration (bottom). Since the cross-subject variability of response acceleration was quite large, we also analyzed the data of each individual subject on basis of the trials. Also this analysis did not reveal a significant effect.

be that the reported dependence of response latency on monitor frame rate is to some extent caused by the decreased mean luminance at lower frame rates. This is not very plausible, though, because the visual system adapts to such small luminance differences within seconds, whereas the monitor frame rate was changed between single sessions each lasting 15 min.

We performed control experiments on four of the subjects (FS, MA, MS, MdL) using a fixed monitor frame rate of 120 Hz and with the mean luminance altered between the normal value of 103.40 ± 0.05 and a 50% reduced control value of $51.00 \pm 0.04\ \mathrm{cd/m^2}$. Apart from the change in mean luminance, the control experiments were identical to the main experiments.

We found that the mean luminance had no significant effect on response latency (Fig. 2 top). Also the response acceleration was not significantly affected (Fig. 2 bottom). Since the acceleration values were quite variable among subjects, we also performed an analysis on the individual subjects, using single trial values for the statistics (data not shown here). Also this analysis revealed no significant effect of the luminance change on response acceleration.

In view of these results, we conclude that a possible contribution of the much smaller luminance differences in the main experiments to the reported latency and acceleration differences can be neglected.

4. Results

We analyzed ocular following responses with respect to the dependence of latency and initial peak acceleration on monitor frame rate and stimulus speed. The four resulting dependency pairs yield insights into the underlying mechanisms of motion detection, as we will lay out in Section 5.

Already by taking a glimpse at the mean gaze velocity traces grouped by stimulus speed (exemplarily shown for subject LB in Fig. 3a), one notices a striking influence of monitor frame rate on response latency. The step from 80 to 120 Hz has more impact than that from 120 to 160 Hz. There is no obvious dependence of latency on stimulus speed, as Fig. 3b reveals, where the eye traces have been grouped by monitor frame rate. The opposite situation arises for the initial peak acceleration. The different slopes of the traces obtained for the different speeds indicate that response acceleration depends on stimulus speed, while there is no obvious dependence on monitor frame rate (exemplarily shown for subject LB in Fig. 4).

These findings obtained by mere visual inspection of the mean time-dependent response traces averaged over all subjects are substantiated by the following statistical analysis.

4.1. Response latency and monitor frame rate

The ANOVA on the response latency values reveals that there is a significant effect of monitor frame rate on response latency. The effect is directed (Fig. 5a), so that a higher frame rate implies a lower latency. Applying paired *t*-tests reveals that the effect is significant for each of the two steps from 80 to 120 Hz and from 120 to 160 Hz.

4.2. Response latency and stimulus speed

The ANOVA on the latency data fails to reveal a significant effect of stimulus speed on response latency (Fig. 5b). However, the paired *t*-tests reveal a significant partial effect. For the low monitor frame rate (80 Hz) and the high stimulus speed (30 deg/s), the latency is significantly higher than on the other two conditions, whereas for the high monitor frame rate, the latency is significantly higher for the low stimulus speed than on the other two conditions (see number pairs in Fig. 5b). We will address and explain this seemingly paradoxical result in Section 5.

4.3. Response acceleration and monitor frame rate

Neither the ANOVA nor the paired *t*-tests reveal a significant effect of monitor frame rate on the initial response acceleration (Fig. 6a).

4.4. Response acceleration and stimulus speed

The ANOVA reveals a significant global influence of stimulus speed on response acceleration (Fig. 6b). The effect is directed, so that higher stimulus speed implies higher response acceleration. The paired *t*-tests draw a more differentiated picture: For the middle and high frame rate, the step from 10 to 20 deg/s evokes a significant difference in response acceleration, while the step from 20 to 30 deg/s does not. This finding indicates a saturation effect of stimulus speed on response acceleration above 20 deg/s.

5. Discussion

Our findings are summarized into four main results:

1. Response latency decreases with monitor frame rate.
2. Response latency is partly affected by stimulus speed. For low monitor frame rate, the latency slightly increases with stimulus speed, for high monitor frame rate, the latency slightly decreases with stimulus speed.

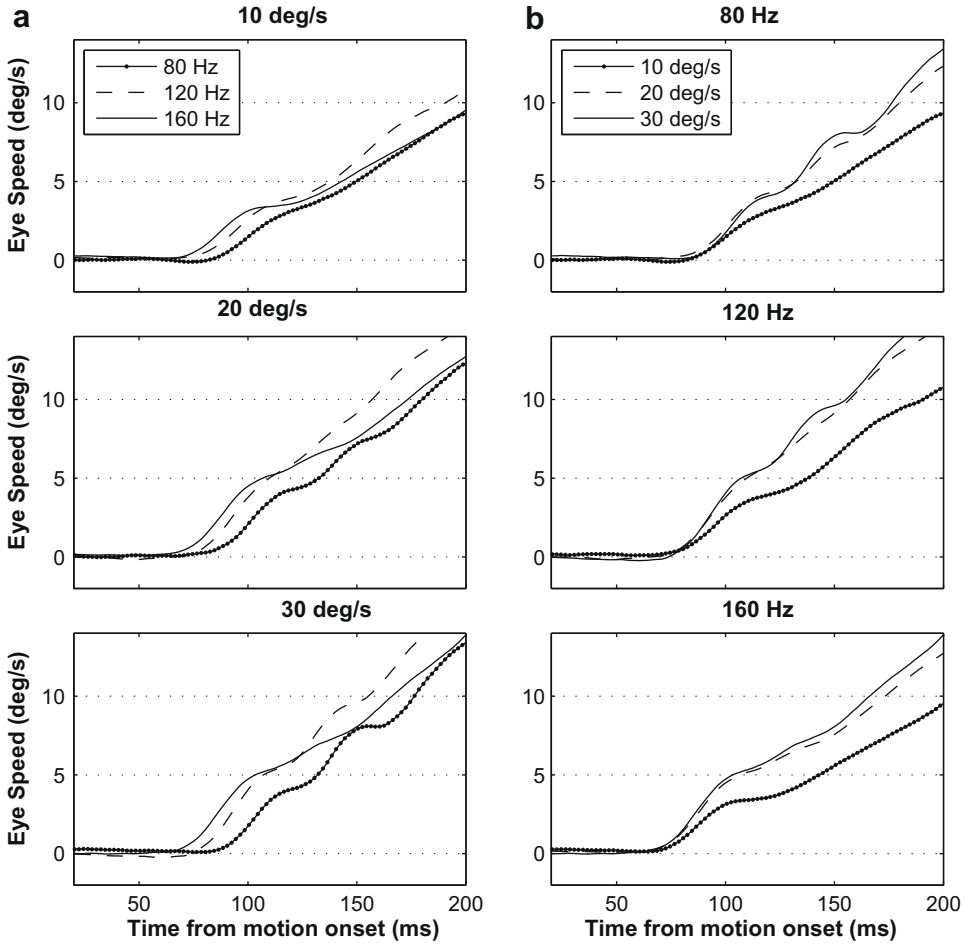

Fig. 3. (a) Mean gaze velocity traces of subject LB, grouped by stimulus speed. The latency differences at different monitor frame rates are obvious, while the initial response acceleration appears to be unaffected. Number of trials: 122–143. (b) Mean gaze velocity traces of subject LB, grouped by monitor frame rate. There are no visible latency differences for the different stimulus speeds, but the initial response acceleration (slope) is clearly affected. For this subject (LB) on the 160 Hz condition (straight lines), there is a peculiar reduction in eye acceleration ~ 30 ms after response onset, in contrast to the other five subjects (not shown here). In fact, the detailed dynamics of the responses considerably differ across subjects, while the effect of frame rate on latency remains a consistent feature.

3. Response acceleration increases with stimulus speed.
4. Response acceleration is unaffected by monitor frame rate.

5.1. Response latency

At first sight it might be surprising that monitor frame rates far above the flicker fusion limit (which is about 15–60 Hz, depending on several factors, see Landis, 1954; Simonson & Brozek, 1952) have such a strong impact on the ocular following response latency. It is known from past investigations that the perceptual system does not distinguish between stimuli presented at sample rates above the flicker fusion limit from continuous stimuli (Landis, 1954; Simonson & Brozek, 1952). However, this is actually only valid for static stimuli. When a stimulus moves, sampling artifacts may become visible. A good explanation for this phenomenon was first provided by Watson, Ahumada and Farrel. They introduced the concept of a "window of visibility" (Watson, Ahumada, & Farrell, 1983; Watson et al., 1986), which is a cuboid in the (2 + 1)-dimensional spatiotemporal frequency domain, so that only that part of the stimulus is processed by the visual system, whose spatiotemporal Fourier transform lies inside the window. The authors derived a formula for the critical sampling frequency above which a sampled stimulus of a certain velocity cannot be distinguished from a non-sampled version of the stimulus. The formula linearly depends on the stimulus velocity, so that faster stimuli imply higher critical frequencies. Just to give some numbers: Their subject ABW had a critical frequency for static stimuli (flicker fusion limit) of 40 Hz. For a stimulus moving at a modest speed of 10 deg/s, his critical frequency was already above 150 Hz. For their subject JEF the flicker fusion limit was about the same, but the critical frequency at 10 deg/s was below 100 Hz. These values illustrate both the strong dependence of the critical frequency on stimulus velocity, and the strong cross-subject variability. The linear relationship between stimulus velocity and critical frequency derived by Watson and coworkers was confirmed by studies of other groups (Burr et al., 1986a; Burr, Ross, & Morrone, 1986b; Cropper & Badcock, 1994; Fahle et al., 2001).

The investigation of apparent motion and sampled motion has led to the development of very successful models of primate vision involving spatiotemporally tuned receptive fields, most notably by Adelson and Bergen (Adelson & Bergen, 1985) who coined the term "motion energy" which is a feature of the spatiotemporal structure of the stimulus extracted and processed by the visual system. Burr and coworkers have pointed out that from the perspective of motion energy models it is no longer meaningful to distinguish between the visual processing of a static stimulus and a moving stimulus (Anderson & Burr, 1985; Burr et al., 1986b; Burr et al., 1986a; Burr & Ross, 1986). These two traditionally separated concepts should be combined into a unitary concept of low-level

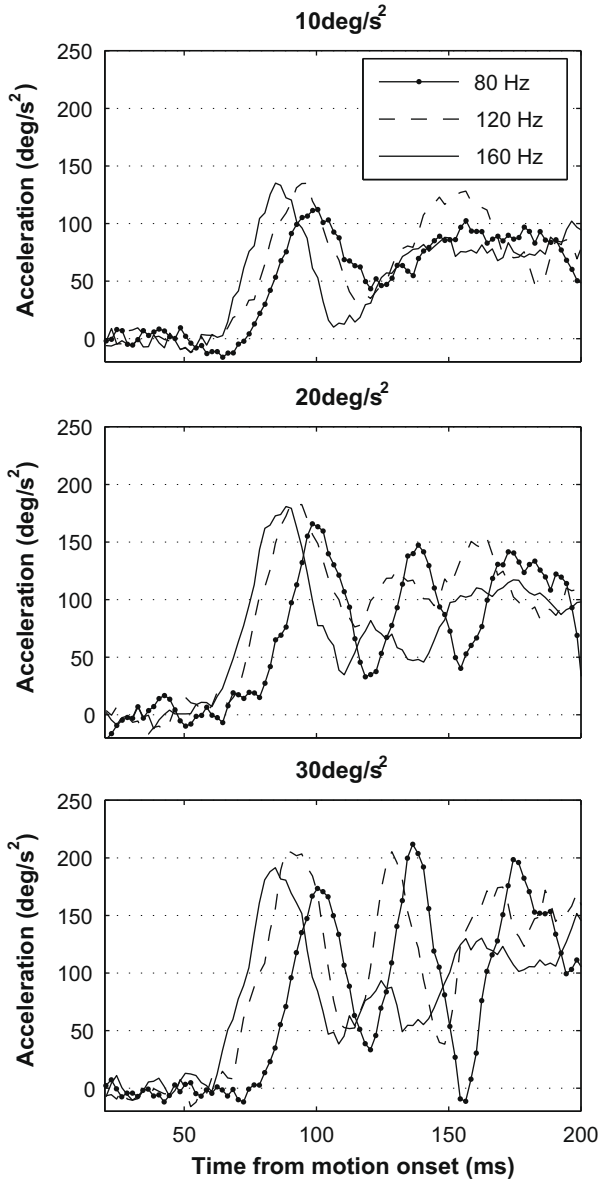

Fig. 4. Mean gaze acceleration traces of subject LB grouped by stimulus speed. The differences in latency and peak acceleration at different stimulus speeds is obvious. Additionally, for this subject (LB) there appears to be a weak dependence of peak acceleration on monitor frame rate. However, this dependence is neither systematic nor consistent across subjects. Statistical analysis (see text) does not reveal a significant effect of frame rate on peak acceleration.

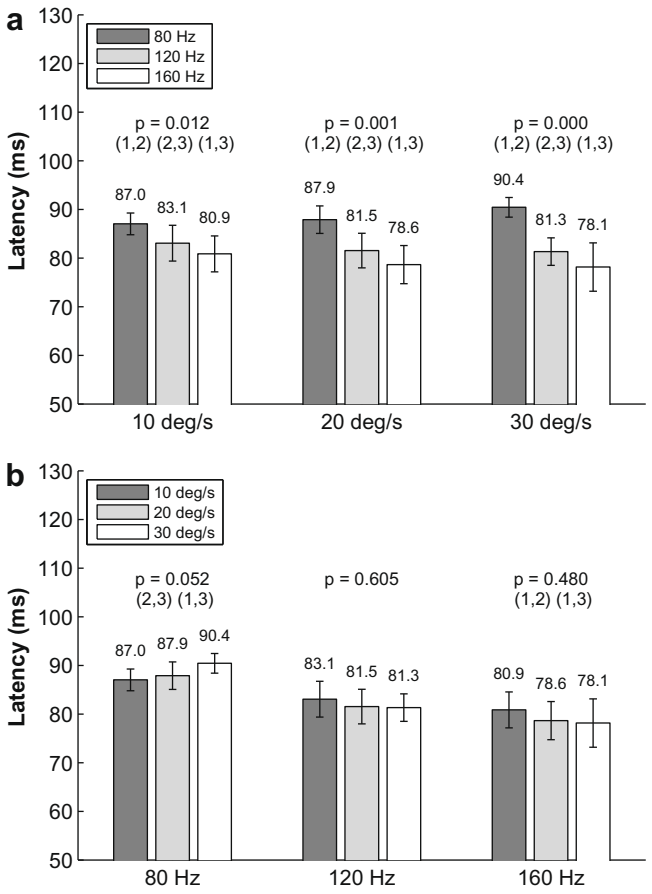

Fig. 5. (a) Response latency data grouped by stimulus speed. All paired *t*-tests report a significant influence of monitor frame rate (see number pairs), and also the ANOVAs report significance (see *p*-values). Error bars are 95% confidence intervals. (b) Response latency data grouped by monitor frame rate. While the ANOVA revealed no global significant influence of stimulus speed (see *p*-values), the paired *t*-tests report two significant partial effects showing in opposite directions (see number pairs). For 80 Hz the latency slightly increases with speed, for 160 Hz it slightly decreases.

vision. There, a visual scene is analyzed by elementary Gabor-like shaped receptive fields oriented in space and time, which therefore respond not only to spatial frequency and orientation (form) but also to temporal frequency and orientation (motion). Burr and coworkers were able to reconstruct the explicit shape of spatiotemporally tuned receptive fields in humans from psychophysical experiments, and these indeed had a Gabor-like shape (Burr et al., 1986a). Physiological studies on monkeys confirm the existence of spatiotemporally oriented receptive fields in the primary visual cortex (V1) (McCool & Britten, 2008; Priebe, Lisberger, & Movshon, 2006). These V1 neurons project into higher areas of the brain, notably the nucleus of the optic tract (NOT) and the middle temporal area (MT) and from there into the medial superior temporal area (MST) (Ilg, 1997). Lesion studies in the monkey suggest that NOT and MST are both part of the OFR system (Inoue, Takemura, Kawano, & Mustari, 2000; Takemura, Inoue, & Kawano, 2002a).

In the following, we will show how spatiotemporally oriented receptive fields can explain all of our findings in a simple and intuitive way.

The ocular following system receives input from a population of neurons in V1, each having a spatiotemporally oriented receptive field restricted to a certain area of the visual field. Such a neuron is maximally activated by illumination in the form of a Gabor patch of the preferred spatial orientation and frequency, moving at the preferred speed in the preferred direction orthogonal to the preferred spatial orientation. A differently-shaped stimulus, such as a dot, may still activate the cell, but not maximally. A system of such neurons encodes the entire spatiotemporal structure of the stimulus.

A computer-generated stimulus has a grainy spatiotemporal structure. The sampled motion of a single dot corresponds to a line of dots in space-time. All neurons with receptive fields that match this trajectory, give excitatory input into the ocular following system. A moving dot sampled at higher rate has a trajectory that is more dense in space-time, hence activating more strongly the matching neurons (Fig. 7a1,a2). In the limit of true (non-sampled) motion we have a continuous line which maximally activates the matching receptive fields (Fig. 7a3). So the higher the sample rate the stronger the output of the matching V1 neurons. Therefore, the downstream neurons of the OFR system receive a stronger input from the V1 cells when the frame rate is higher.

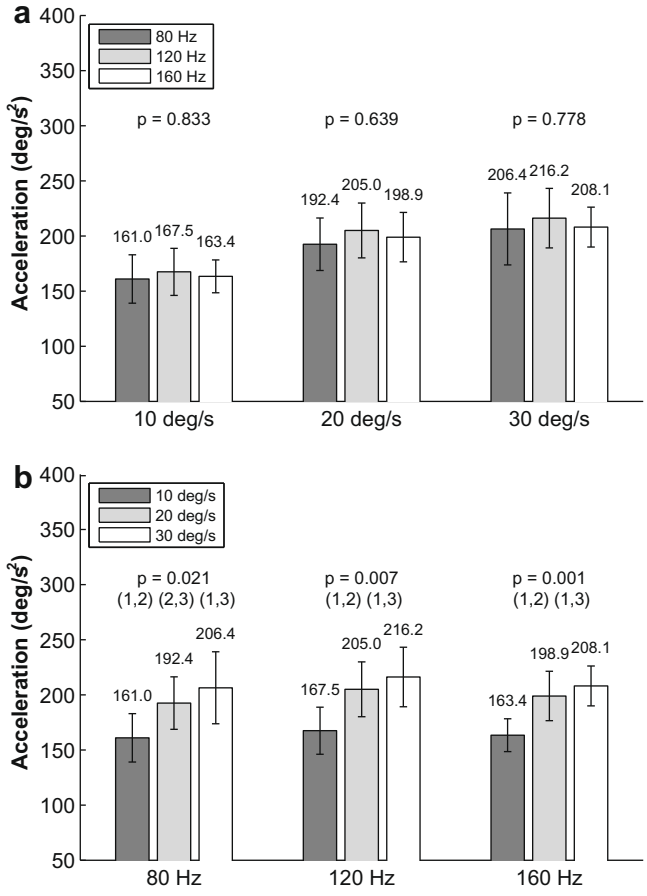

Fig. 6. (a) Response acceleration data grouped by stimulus speed. Neither the paired *t*-tests reveal a significant influence of monitor frame rate (no number pairs), nor do the ANOVAs (all *p*-values much higher than 0.05). (b) Response acceleration data grouped by monitor frame rate. The ANOVAs report a highly significant influence of stimulus speed (see *p*-values), while not all of the paired *t*-tests reveal significance (see number pairs). For 120 and 160 Hz, the step from 20 to 30 deg/s stimulus speed evokes significantly less difference in latency than the step from 10 to 20 deg/s.

It has been argued by Warzecha and Egelhaaf (2000) that an increased synaptic input, here induced by a higher monitor frame rate, can lead to a shorter latency for two reasons. First, a stronger excitatory input reduces the membrane resistance and thus the time constant of the dendrite. Hence, the membrane introduces shorter signal transmission delays (Koch, 1999) which result in shorter response latencies. Second, stronger synaptic input leads to steeper rise times of the postsynaptic potential, and if the projected cell is equipped with a threshold nonlinearity as is the case for spiking neurons, then the transmission delay will further be shortened. Although Warzecha and Egelhaaf (2000) originally intended to explain latency effects in the visual system of the blowfly, their reasoning concerns basic neurophysiological considerations and thus also applies to the primate visual system. In the present case, a higher frame rate would introduce shorter response latencies of neurons downstream of V1 and hence also of the final eye movement. This is what we found. In addition to such a mechanism that could explain the latency differences at different frame rates, it might be relevant that action potentials in V1 cells of monkeys as well as visually evoked potentials in humans that are largely driven by the activity in V1 phase-lock to frame rates up to at least 100 Hz (Williams, Mechler, Gordon, Shapley, & Hawken, 2004). It is, however, unclear if and how this phase-locking contributes to the effects found in the present study.

Now let us turn to the apparently paradoxical result that at the low frame rate (80 Hz) the response latency increases with stimulus speed and at the high frame rate (160 Hz) it decreases (Fig. 5b). The latter observation coincides with former studies on humans and monkeys (Gellman et al., 1990; Miles et al., 1986; Kawano, Shidara, & Yamane, 1992; Kawano, Shidara, Watanabe, & Yamane, 1994). Notably, those studies have been performed using analog hardware, thus generating true stimulus motion. We were able to reproduce the previously described latency dependence on stimulus speed only for the high frame rate (160 Hz). At the middle frame rate (120 Hz) we found no (significant) dependence, and at the low frame rate (80 Hz) the dependence was inverted. This finding strongly points to a sampling phenomenon which we seek to explain as follows:

The trajectory of a moving dot sampled at a fixed rate becomes less dense with higher speed (Fig. 7b), hence the activation of matching V1 neurons decreases with speed. Thus, the output of the entire neuron population decreases with speed for a given frame rate. According to the considerations above, response latency therefore tends to increase with stimulus speed. This tendency, which is merely due to the temporal discreteness of the stimulus, is opposed to the tendency of the latency to decrease with stimulus speed, as is observed for continuously moving stimuli in the studies already mentioned. The neuronal basis for the latter tendency is yet unknown; a possible reason might be a stronger output by those neurons encoding for higher speeds, which therefore would induce shorter latencies in downstream cells for the already discussed reasons. The two opposite tendencies roughly cancel each other at the middle frame rate (120 Hz), and one of it wins against the other at the lower and higher frame rate (80 and 160 Hz).

The measured dependence of latency on stimulus speed is rather weak over the range of chosen stimulus speeds. At 160 Hz monitor frame rate, the latency decreases from 80 to 78 ms for stimulus speeds of 10 and 30 deg/s, respectively. These findings are in good agreement with Gellman et al. (1990) who found a latency decrease from 79 to 76 ms within the same speed range, using continuous motion (their Fig. 4). The similarity of their and our latency estimates indicates that for our highest monitor frame rate of 160 Hz we may approach the critical frequency at which motion induced eye movements in response to digital stimuli become undistinguishable from those to analog stimuli. In their monkey study, Miles et al. (1986) found a considerably stronger relationship between latency and stimulus speed. For example, the latency decreased from 64 to 54 ms for random dot patterns continuously moving leftwards at speeds of 10 and 30 deg/s, respectively (their Fig. 5). Hence, possibly not only the absolute latency differs between humans and monkeys but also the dependence of latency on speed.

5.2. Initial response acceleration

It is not surprising that the initial response acceleration increases with stimulus speed from a functional point of view. When the stimulus moves faster, the eyes should accelerate more strongly to reach the target velocity in time. Other studies also reported a positive dependency of initial response strength on stimulus speed (Gellman et al., 1990; Kawano et al., 1992; Kawano et al., 1994), although the used measures vary from study to study. It might be interesting to note that the velocity step from 10 to 20 deg/s induced a stronger rise of initial peak acceleration than the step from 20 to 30 deg/s, indicating a beginning saturation of the mechanism underlying the motion-sensitivity of the OFR.

It may be surprising that the initial response acceleration does not depend on the frame rate. From our previous

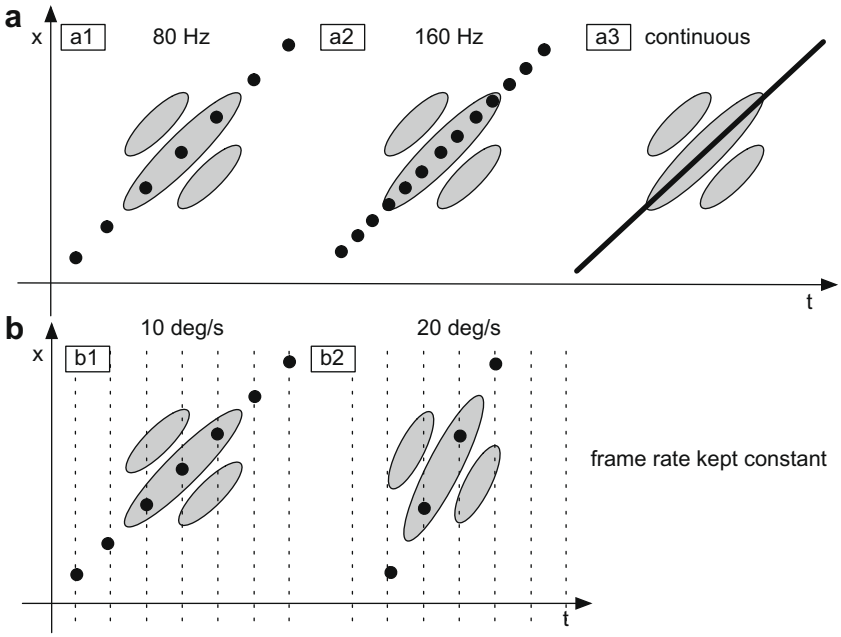

Fig. 7. (a) Sampled motion of a single dot crossing a spatiotemporally oriented receptive field of a motion-sensitive neuron. For higher frame rates (a1–a2) the receptive field is stimulated more strongly. For the continuous case (a3) the receptive field is maximally stimulated. The polarity of the receptive field components is not indicated. (b) Sampled motion of a single dot with constant frame rate. When the stimulus speed increases (b1–b2), the spatiotemporal dot density decreases. Hence, for higher stimulus speeds the matching receptive fields are stimulated less strongly.

considerations we have argued that a poor sampling rate results in a weaker activation of V1 cells and hence in a weaker excitation of downstream cells. Considered that this excitation is translated into the activation of eye muscles which generate the final rotational acceleration of the eye ball, one might expect an influence of stimulus sampling rate on response acceleration. That such is not the case has implications for the physiological mechanism mediating OFR. Obviously, the strength of the output of the motion-sensitive neurons is not directly translated into muscle contraction, as it is the case in the fly visuo-motor system, where a stronger activation of motion-sensitive neurons leads to stronger following responses (Egelhaaf & Borst, 1993; Warzecha & Egelhaaf, 1996). An overall weakening of the population output due to poor sampling rates would result in a reduction of overall output strength but not in a shift of the population mean. Hence, it must be this population mean which determines the final eye acceleration and not the overall output strength. This consequence is also supported by conclusions derived from neurophysiological studies on MT and MST in monkeys (Churchland & Lisberger, 2001; Priebe & Lisberger, 2004; Takemura, Kawano, Quaia, & Miles, 2002b). Moreover, already in their seminal work on the OFR, Miles et al. (1986) postulated two mechanisms, one for triggering and one for motion integration. Their model predicts different effects of stimulus speed on latency and response acceleration, in line with our results. In any case, all such mechanisms require adequately elaborate neural circuitry such as gain control (e.g. Simoncelli & Heeger, 1998). It is interesting to see that even a rather simple reflexive mechanism like the ocular following response is realized in a rather sophisticated manner.

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