

Task influences on the dynamic properties of fast eye movements

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It is widely debated whether fast phases of the reflexive optokinetic nystagmus (OKN) share properties with another class of fast eye movements, visually guided saccades. Conclusions drawn from previous studies were complicated by the fact that a subject's task influences the exact type of OKN: stare vs. look nystagmus. With our current study we set out to determine in the same subjects the exact dynamic properties (main sequence) of various forms of fast eye movements. We recorded fast phases of look and stare nystagmus as well as visually guided saccades. Our data clearly show that fast phases of look and stare nystagmus differ with respect to their main sequence. Fast phases of stare nystagmus were characterized by their lower peak velocities and longer durations as compared to fast phases of look nystagmus. Furthermore we found no differences between fast phases of stare nystagmus evoked with limited and unlimited dot lifetimes. Visually guided saccades were on the same main sequence as fast phases of look nystagmus, while they had higher peak velocities and shorter durations than fast phases of stare nystagmus. Our data underline the critical role of behavioral tasks (e.g., reflexive vs. intentional) for the exact spatiotemporal characteristics of fast eye movements.

Keywords: main sequence, optokinesis, nystagmus, saccade

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Introduction

Fast eye movements can be characterized by a tight relationship between several of their kinematic parameters. Duration and peak velocity increase with amplitude. This relationship has first been described for voluntary saccades and was termed the *main sequence* (Bahill, Clark, & Stark, 1975). Since then the existence of a main sequence has been shown for different types of saccades including: reflexive saccades (Baloh, Sills, Kumley, & Honrubia, 1975), memory-guided saccades (Becker & Fuchs, 1969; Smit, Van Gisbergen, & Cools, 1987), antisaccades (Smit et al., 1987; Van Gelder, Lebedev, & Tsui, 1997), and catch-up saccades (Van Gelder et al., 1997). However, the individual main sequences for different kinds of saccades show considerable variability. For example, visually guided saccades are faster than memory-guided saccades and antisaccades of identical amplitude (Smit et al., 1987). Concerning other factors like saccade direction the reports in the literature are less consistent. While some studies reported centripetal saccades to be faster than centrifugal ones (Becker & Jürgens, 1990; Hyde, 1959; Pelisson & Prablanc, 1988), others reported the opposite (Garbutt, Han et al., 2003; Robinson, 1964), described differences only for large

amplitudes in a subset of subjects (Boghen, Troost, Daroff, Dell'Osso, & Birkett, 1974), or found no difference at all (Bahill et al., 1975). Another group of fast eye movements that has been shown to adhere to a main sequence is the fast phases of different kinds of reflexive, compensatory eye movements (Garbutt, Han et al., 2003; Garbutt, Harwood, & Harris, 2001; Gavilan & Gavilan, 1984; Mackensen & Schumacher, 1960; Ron, Robinson, & Skavenski, 1972; Sharpe, Troost, Dell'Osso, & Daroff, 1975). Studies comparing saccades and fast phases of the vestibulo-ocular reflex (VOR) reported identical or very similar main sequences (Guitton & Mandl, 1980; Ron et al., 1972; Sharpe et al., 1975), but lower velocities for the VOR have also been reported (Gavilan & Gavilan, 1984). Fast phases of optokinetic nystagmus (OKN) have either been reported to follow the same main sequence as visually guided saccades (Kaminiarz, Königs, & Bremmer, 2009a; Mackensen & Schumacher, 1960; Sharpe et al., 1975) or to be slower than saccades (Garbutt, Han et al., 2003; Garbutt et al., 2001; Gavilan & Gavilan, 1984; Henriksson, Pyykko, Schalen, & Wennmo, 1980). Aside from the type of saccade performed factors like fatigue can influence the main sequence (Bahill & Stark, 1975; Riggs, Merton, & Morton, 1974). Depending on the subjects' attitude regarding the task two kinds of OKN can be distinguished (Ter Braak, 1936). When subjects

watch the stimulus attentively without intentionally foveating any element a so-called stare nystagmus can be observed, which is characterized by small fast-phase amplitudes and high fast-phase frequencies. If subjects intentionally follow single elements of the stimulus they perform a so-called look nystagmus, which is typically characterized by a low frequency but large amplitude of fast phases. The slow phases of look nystagmus have often been linked to voluntary pursuit, but to our best knowledge the fast phases occurring during the different types of OKN have not been classified.

In this study we aimed at disentangling the relative influence of task/cortical control and input/stimulus characteristics on the main sequence by comparing in individual subjects the main sequences of stare nystagmus, look nystagmus, and visually guided saccades. Preliminary results have been published in abstract form (Kaminiarz, Königs, & Bremmer, 2009b).

Methods

Subjects

In total, 18 healthy subjects (6 males and 12 females, 22–30 years, mean age 26.3 (*SD* 4.7)) participated in the experiments. All had normal or corrected-to-normal vision and gave informed written consent. All procedures used in this study conformed to the declaration of Helsinki.

Experimental procedure

All experiments were carried out in a dark, sound attenuated chamber. Eye movements were monitored and recorded at 500 Hz with an infrared eye tracking system (Eye Link II, SR Research). The system was calibrated at the beginning of each session and a so-called drift correction (compensating for potentially occurring small drifts of the eye position signal) was performed before every third (visually guided saccades) or before each trial (other experiments). The subjects' heads were stabilized by a chin rest with their eyes leveled at the center of the screen.

Visual stimuli were projected onto a tangent screen ($70^\circ \times 55^\circ$) via a CRT projector (Marquee 8000, Electrohome) running at 100 Hz and a resolution of 1152×864 pixels. The screen was viewed binocularly at a distance of 114 cm.

OKN

A random dot pattern (RDP) consisting of black dots (size: 2.0 deg, luminance < 0.1 cd/m², mean density: 0.065 dots/deg²) moving across a white background (22.1 cd/m²) for 4 s was used to elicit OKN. In the main experiment dots moved at 10°/s while speeds of 10, 15, and

20°/s were used in a second experiment on the interaction of slow and fast eye movements. Dot lifetime was either infinite or limited to 80 ms. Each dot that reached its maximum lifetime was displaced to a new, randomly assigned position on the screen. During sessions with unlimited dot lifetime subjects were either instructed to intentionally follow single dots with their eyes (look nystagmus) or to watch the screen attentively without tracking individual dots (stare nystagmus).

Visually guided saccades

Each trial started with subjects fixating a central green fixation target for 1000 ms. Afterward, the target jumped purely horizontally to the left or right. Five different step amplitudes were used (1.5, 3, 4.5, 6, and 7.5 deg). Since it has been reported that background characteristics can influence the main sequence (Henriksson et al., 1980) we used a moving RDP with identical spatial properties as in the large field OKN experiment served as background. The RDP moved either left- or rightward at 10 deg/s throughout the trial. Saccades could be either in the same

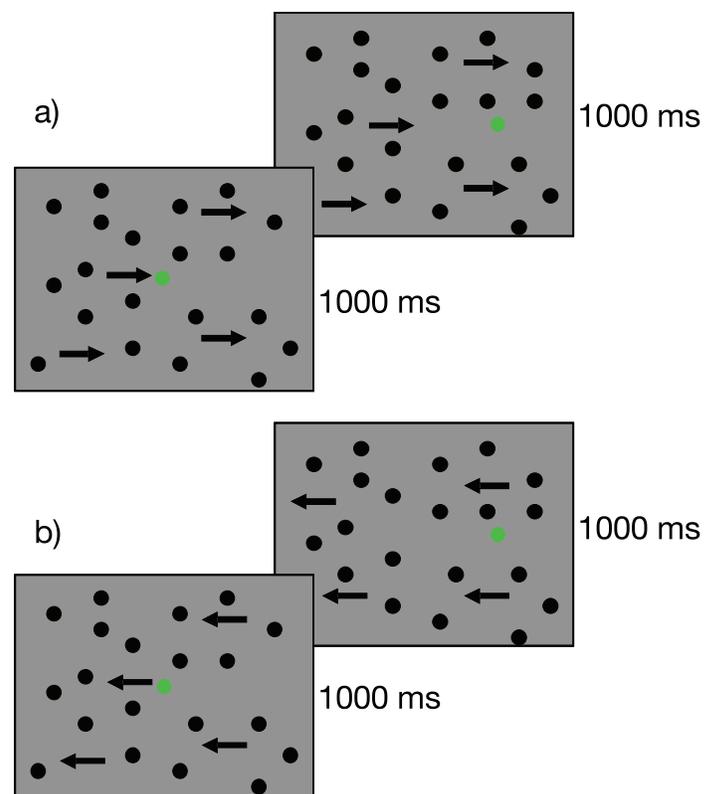


Figure 1. Illustration of the saccade paradigm. Each trial started with subjects fixating a central target for 1000 ms. Then the target jumped either to the left or right ($\pm 1.5, 3, 4.5, 6,$ and 7.5 deg) and remained at the new position for another 1000 ms. A Random Dot Pattern (RDP) consisting of black dots on a gray background was moving at 10 deg/s either in (a) the same or (b) the opposite direction as the target step.

(Figure 1a) or in the opposite direction (Figure 1b) as the background motion. Accordingly subjects could not anticipate the direction of the upcoming saccade. Subjects were instructed to follow the target as fast and accurately as possible by an appropriate eye movement.

Data analysis

Data were analyzed using Matlab R2007b (The MathWorks) and SigmaStat 3.10 (Systat Software).

Eye-position data for all trials were inspected offline. Trials were excluded from further analysis if (1) fast phases/saccades were contaminated by (partially suppressed) blinks that had not been detected automatically, (2) subjects did not perform systematic OKN, or (3) a saccade not directed toward the target was executed in the analyzed time window (experiment on visually guided saccades only). In total 22.6% (ranging from 1.7% to 80.7% for different subjects) of the trials had to be excluded from further analysis.

The first 500 ms of eye movement data recorded on OKN trials were discarded since we cannot exclude that the stimulus-onset influences fast eye movement characteristics. For the experiments on visually guided saccades only the first saccade in a time window from 100 to 500 ms after the target step was analyzed.

Saccade detection

Eye velocity was derived from unfiltered eye position data by discrete differentiation of the raw data set, which had been sampled at 500 Hz. In other words, the speed of sample n was computed as the difference of position samples pos_{n+1} and pos_n ; this difference was then divided by the temporal difference of these two samples $t_{n+1} - t_n = 2$ ms: $v_n = \frac{pos_{n+1} - pos_n}{t_{n+1} - t_n}$. Saccades were detected using a flexible velocity criterion. Mean horizontal eye velocity was calculated for a 40-ms time window (v_{mean}). Whenever eye velocity deviated from v_{mean} (calculated for the preceding 40 ms) by more than 24 deg/s for three consecutive samples (i.e., 6 ms) a saccade onset was detected. Saccade offset was detected when eye velocity dropped below the same threshold for three consecutive samples.

Main-sequence analysis

Peak velocity and duration of the fast eye movements were plotted as a function of their amplitude. The range of fast-phase/saccade amplitudes recorded varied for the different conditions. Lebedev, Van Gelder, and Tsui (1996) showed that fit parameters are substantially influenced by the amplitude range used, even in the same

data set. Therefore we matched the data sets for all comparisons with respect to the fast-phase amplitude. To do so, we calculated the 95 percentiles for the amplitudes of each data set and used the smallest of them as the maximum amplitude for the comparison. We then fitted power functions to the data using least squares procedures according to: $y = ax^b$. Power functions were chosen since they are especially well suited for data sets with small amplitudes (Lebedev et al., 1996).

To test for significant differences between conditions at the single subject level we performed a bootstrap analysis and fitted a power function to each of the new data sets created by this means. Afterward, we calculated the 5% and 95% percentiles of the curves fitted to the bootstrapped data sets. Wilcoxon Signed Rank Tests were used to compare the parameters of the power functions fitted to the data at the population level for significant differences.

Analysis of velocity traces

Mean velocity traces were computed from individual velocity traces after sorting saccades/fast phases in 1 deg wide bins according to their amplitude and aligning the individual velocity traces to saccade/fast-phase onset. Only bins that contained at least ten fast phases/saccades were used for further analysis. From the mean velocity traces we determined the duration of the acceleration and deceleration periods as well as the total duration. The skewness of the velocity traces was calculated as the duration of the acceleration period divided by the total duration of the saccade/fast phase.

Results

Fast phases of look and stare nystagmus (unlimited dot lifetime)

The slow phases of look nystagmus are often compared to smooth pursuit eye movements. In addition, fast phases during look nystagmus aim at specific elements of the moving stimulus and hence are similar to visually guided saccades. Therefore we analyzed fast phases of both stare and look nystagmus since the grade of reflexiveness of these eye movements varies under otherwise identical stimulus conditions due to the subjects' task.

The amplitudes of fast phases executed during look and stare nystagmus trials differed considerably. The 95 percentiles used for amplitude matching had a range of 13.7 deg (2.4 SD) for look nystagmus, 9.23 deg (1.7 SD) for stare nystagmus, and 6.8 (1.6 SD) for stare nystagmus evoked with limited dot lifetime, respectively. During stare nystagmus (unlimited dot lifetime) mean eye position, averaged across subjects, was shifted 7.6 deg

(5.0 *SD*) opposite to the direction of the slow phase (“shift of the beating field”). This shift decreased to 4.1 deg (3.5 *SD*) during stare nystagmus evoked with limited dot lifetime. During look nystagmus we observed a shift in direction of the slow-phase component (3.1 deg (6.4 *SD*)). Slow-phase gain (eye velocity/RDP velocity) was 1.0 (0.03 *SD*) for look nystagmus, 0.90 (0.06 *SD*) for stare nystagmus with unlimited dot lifetime, and 0.60 (0.13 *SD*) for stare nystagmus with limited dot lifetime.

Figures 2a and 2b show duration and peak velocity, respectively, for fast phases as a function of fast-phase amplitude during look (black symbols) and stare nystagmus (red symbols: unlimited dot lifetime, blue symbols: limited dot lifetime) for a representative subject.

As can be clearly seen, stare nystagmus fast phases lasted longer and reached a lower peak velocity than look nystagmus fast phases of identical amplitude. This functional relationship was found in all eight subjects.

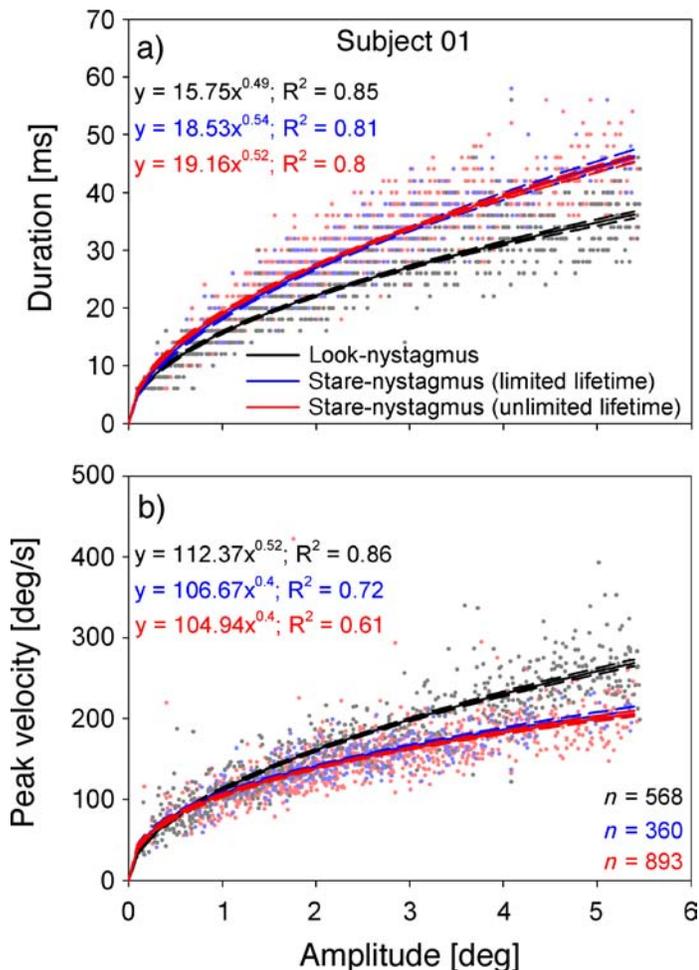


Figure 2. Comparison of main sequences for look and stare nystagmus. The graphs show (a) duration vs. amplitude and (b) peak velocity vs. amplitude relationships for stare (red symbols: unlimited dot lifetime, blue symbols: limited dot lifetime) and look nystagmus (gray, black). Dots represent data from individual fast phases while solid lines depict power functions fitted to the data.

Statistical analysis proved the difference in the scaling factor but not the exponent of the power function to be significant for the duration vs. amplitude relationship and the peak velocity vs. amplitude relationship (duration vs. amplitude: (a) $p = 0.008$; (b) $p = 0.148$; peak velocity vs. amplitude: (a) $p = 0.008$; (b) $p = 0.25$; Wilcoxon Signed Rank Test). Fit parameters for all subjects under both conditions (look nystagmus and stare nystagmus with unlimited lifetime) are displayed in Figure 3.

In a next step we compared the mean velocity traces for fast phases of look and stare nystagmus (unlimited dot lifetime). In Figure 4 these mean velocity traces are depicted for the same subject as before. Solid lines represent data from look nystagmus fast phases while dashed lines represent data from stare nystagmus (unlimited dot lifetime) fast phases. Fast phases of similar amplitudes are color-coded. As already shown in the main sequence plots, stare nystagmus fast phases of a given amplitude were slower and lasted longer than fast phases of look nystagmus with a similar amplitude. For both look and stare nystagmus skewness (duration of the acceleration period/total duration of the fast phase) of the velocity traces increased with amplitude.

The skewness was larger for fast phases of stare nystagmus as compared to fast phases of look nystagmus. The ratio $\text{look}_{\text{skew}}/\text{stare}_{\text{skew}}$ was 1.11 (0.15 *SD*). While for both eye movements the acceleration interval was not significantly different ($p > 0.05$, Wilcoxon Signed Rank Test) the eyes decelerated more slowly during fast phases of stare nystagmus.

Effects of limited dot lifetime

In the experiment described above we demonstrated that stare nystagmus fast phases last longer and have a lower peak velocity as compared to look nystagmus fast phases. Yet, we had not used a limited dot lifetime in the stare nystagmus condition. So, in principle, subjects could have performed a combination of look and stare nystagmus. Such a mixture of eye movements could have resulted in an underestimation of the differences between the two eye movements. Therefore, we decided to record stare nystagmus with limited and unlimited lifetimes as well as look nystagmus in the same subjects.

For fast phases of stare nystagmus evoked with limited lifetime dots we observed the same effect as for those evoked with unlimited dot lifetime (Figure 2, data depicted in blue). As for fast phases of stare nystagmus evoked with unlimited lifetime dots the difference in the scaling factor but not the exponent of the power function was significant for the duration vs. amplitude relationship and the peak velocity vs. amplitude relationship (duration vs. amplitude: (a) $p = 0.016$; (b) $p = 0.383$; peak velocity vs. amplitude: (a) $p = 0.008$; (b) $p = 0.938$; Wilcoxon Signed Rank Test). The ratio $\text{look}_{\text{skew}}/\text{stare}_{\text{skew}}$ was 1.11 (0.18 *SD*) indicating that velocity traces were skewed

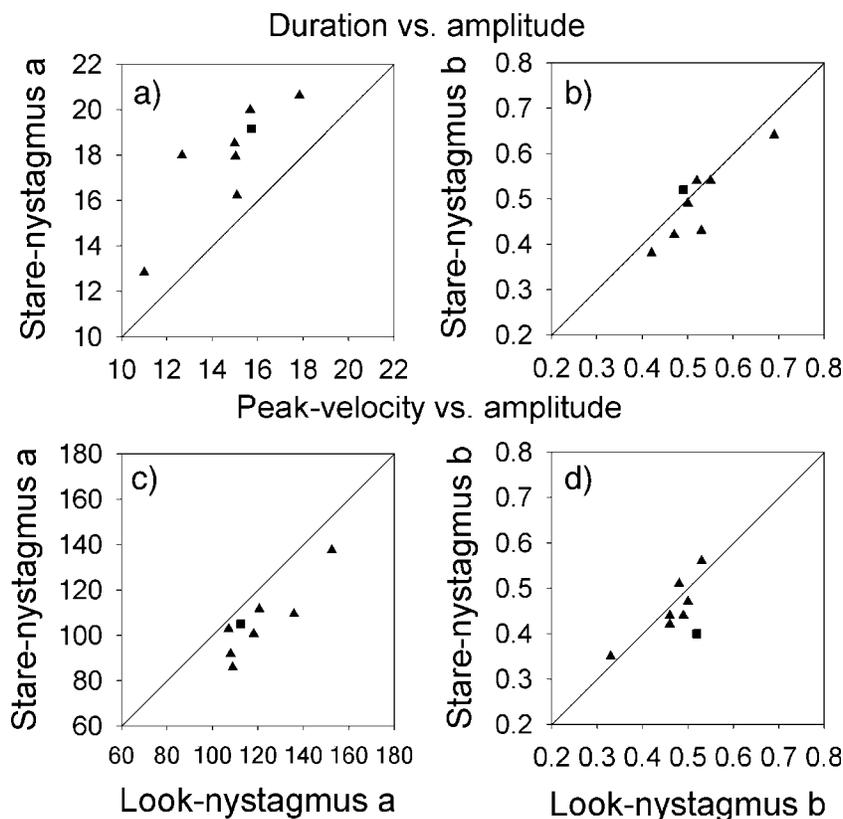


Figure 3. Comparison of fit parameters (a) scaling factor and (b) exponent of the power functions fitted to the main sequences for fast phases of look and stare nystagmus (unlimited dot lifetime). The square represents data from subject 01 (whose data were shown also in Figure 2) while triangles represent data points for all other subjects. The solid black lines represent the identity lines.

more strongly for fast phases of stare nystagmus. The direct comparison of fast phases of stare nystagmus evoked with unlimited and limited dot lifetimes revealed significant differences for the scaling factor of the duration vs. amplitude relationship only (duration vs. amplitude: (a) $p = 0.023$; (b) $p = 0.742$; peak velocity vs. amplitude: (a) $p = 0.109$; (b) $p = 0.578$; Wilcoxon Signed Rank Test).

Effects of fast phase direction/initial eye position

Studies comparing the main sequences of centrifugal and centripetal saccades have reported inconsistent results. Centripetal saccades have been reported to be faster than centrifugal ones by some authors while others reported the opposite (see the Introduction section). We compared the main sequence of centripetal and centrifugal fast phases of look nystagmus. Fast phases consisting of both centripetal and centrifugal components (i.e., fast phases crossing the vertical meridian) were not considered for the analysis. Statistical analysis revealed no significant differences between the power functions fitted to the data ($p > 0.05$, Mann–Whitney Rank Sum Test).

In a second step we asked if the main sequence of centrifugal fast phases depends on the eye position at the

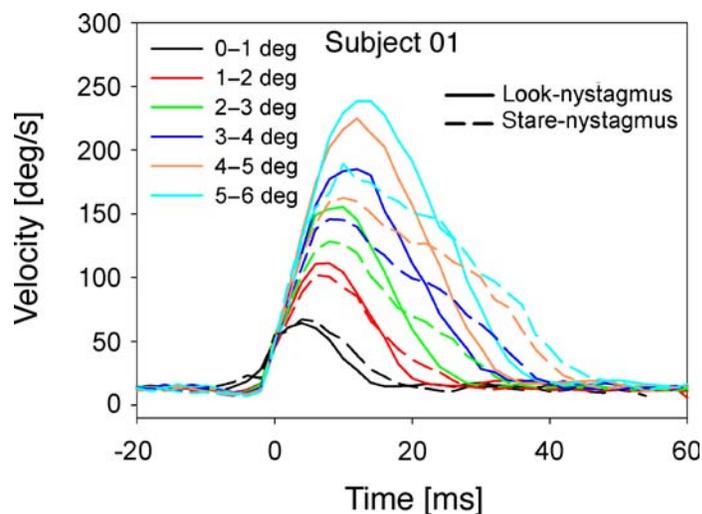


Figure 4. Average velocity traces for fast phases of look and stare nystagmus (unlimited dot lifetime) for subject 01. Velocity is plotted against time from fast-phase onset ($t = 0$ ms). Solid lines represent look nystagmus fast phases while dashed lines represent stare nystagmus fast phases. Fast-phase amplitude is color-coded. Each curve represents the mean of at least 10 individual velocity traces.

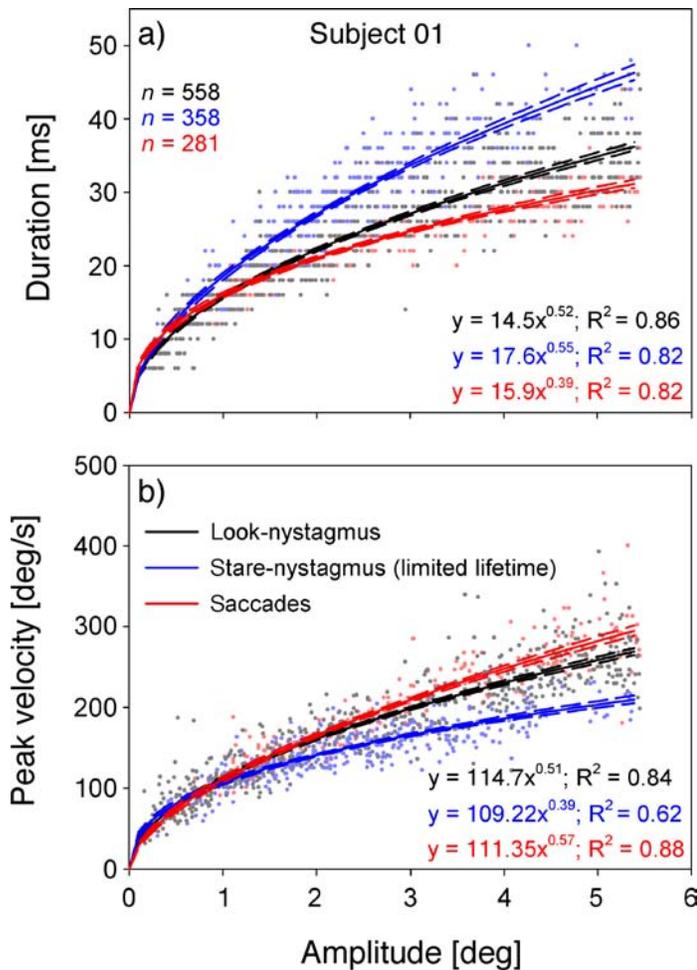


Figure 5. Comparison of main sequences for saccades and fast phases of look and stare nystagmus evoked with limited lifetime dots. The graphs show (a) duration vs. amplitude and (b) peak velocity vs. amplitude relationships for stare nystagmus (blue), look nystagmus (gray, black), and saccades (red). Dots represent data from individual fast phases while solid lines depict power functions fitted to the data.

time of initiation of the fast phase. To do so we performed a median split with respect to the initial eccentricity of the eye at the onset of the fast phase and compared the main sequence for fast phases starting at smaller or larger eccentricities. Statistical analysis revealed no significant differences between the power functions fitted to the data for fast phases of look as well as of stare nystagmus (in all cases: $p > 0.05$, Mann–Whitney Rank Sum Test).

Interaction of fast- and slow-phase eye movements

To quantitatively test for an interaction of the slow and fast phases of OKN we recorded look and stare nystagmus evoked with different stimulus velocities (10°/s, 15°/s, and 20°/s). Five subjects, who already participated in the

previous experiments, served as observers. We observed a slight but statistically not significant increase of fast-phase peak velocity with stimulus velocity for fast phases of look nystagmus only ($p > 0.05$; ANOVA on Ranks).

Fast phases versus saccades

In the past OKN fast phases have often been compared with visually guided saccades. Fast phases were reported to be either similar to saccades or to have lower peak velocities/longer durations. In none of the studies, however, stimuli with limited lifetime had been used. Considering our results it might be the case that in those studies reporting different main sequences subjects had performed pure stare nystagmus while in the studies reporting no differences subjects had performed a mixture of look and stare nystagmus. Therefore we asked subjects to perform visually guided saccades and compared these with fast phases of look and stare nystagmus (limited dot lifetime).

Data for the same subject as before are displayed in Figure 5.

This subject shows relatively similar main sequences for look nystagmus and reflexive saccades while the main sequence of stare nystagmus fast phases was clearly different. Corresponding mean velocity traces are displayed in Figure 6.

Six of the eight subjects exhibited a similar behavior, one subject showed larger similarities between saccades and stare nystagmus as compared to look nystagmus while for the last subject saccades were not similar neither to fast phases of stare nor look nystagmus for the range of amplitudes recorded. Statistical analysis revealed significant differences between saccades and fast phases of stare nystagmus (limited dot lifetime) for the scaling factor but

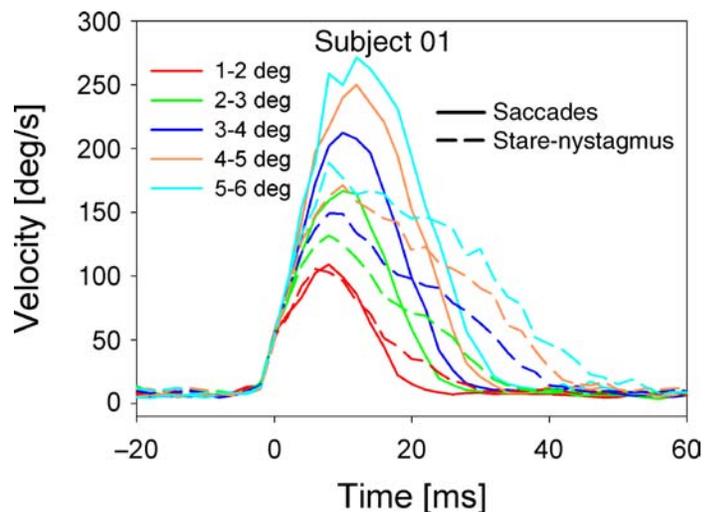


Figure 6. Average velocity traces for fast phases of stare nystagmus (limited dot lifetime) and saccades for subject 01. Velocity is plotted against time from fast-phase onset ($t = 0$ ms).

not the exponent for both the duration vs. amplitude [(a) $p = 0.016$; (b) $p = 1$; Wilcoxon Signed Rank Test] and the peak velocity vs. amplitude relationship [(a) $p = 0.016$; (b) $p = 0.563$; Wilcoxon Signed Rank Test]. Statistical analysis revealed no significant differences between saccades and fast phases of look nystagmus (duration vs. amplitude relationship: (a) $p = 0.641$; (b) $p = 0.148$; peak velocity vs. amplitude relationship: (a) $p = 0.383$; (b) $p = 0.297$; Wilcoxon Signed Rank Test).

Taken together our results demonstrate that saccades and fast phases of look nystagmus are on the same main sequence, while fast phases of stare nystagmus are clearly different from saccades.

Discussion

We have tested and compared fast phases of look and stare nystagmus and visually guided saccades in the same human subjects. Our data show clearly that fast phases of look and stare nystagmus are not on the same main sequence. Instead, fast phases of stare nystagmus lasted longer and had lower peak velocities as compared to fast phases of look nystagmus. The main sequence of stare nystagmus was largely independent of the lifetime of the dots used to induce nystagmus. We observed no differences between the main sequences of visually guided saccades and fast phases of look nystagmus while clear differences exist for saccades and fast phases of stare nystagmus.

Saccades

The main sequence of visually guided saccades has been the key topic of various studies. In some studies power functions have been used to describe the main sequence. Comparing our results to those of Garbutt, Harwood, Kumar, Han, and Leigh (2003) and Lebedev et al. (1996) we see that the exponents of the power functions are similar in all three studies. However, the scaling factor indicates higher peak velocities and shorter durations in our study. One likely reason could be the different techniques used for measuring eye position. Garbutt, Harwood et al. (2003) used the scleral search coil technique while Lebedev et al. (1996) used electro-oculography, which both have been reported to underestimate peak velocity (Boghen et al., 1974; Byford, 1962; Frens & van der Geest, 2002). In addition we (1) did not filter our eye data prior to analysis and (2) used a different algorithm to detect saccades. However, since we are mainly interested in main sequence differences between experimental conditions measured in the same setup and since we analyzed our data with identical techniques in the same human subjects these differences are negligible.

Comparison of fast phases of look and stare nystagmus

Fast phases of stare nystagmus had a longer duration, lower peak velocity, and stronger skewness as compared to fast phases of look nystagmus. Since the visual stimulus was identical (using unlimited dot lifetime) under both conditions these differences are likely caused by the different neural networks underlying the execution of the eye movements. While fast phases of stare nystagmus are not deliberately directed to a visual target, subjects actively choose a single dot during look nystagmus. Therefore areas active during the execution of voluntary goal-directed eye movements are probably more strongly involved during look as compared to stare nystagmus. This interpretation would be in line with findings from previous imaging studies (Konen, Kleiser, Seitz, & Bremmer, 2005; Schraa-Tam et al., 2008).

Effects of limited dot lifetime

Main sequences for stare nystagmus evoked with unlimited and limited (80 ms) dot lifetimes were almost identical for our sample of subjects. Therefore the dynamics of OKN fast phases are not or only slightly influenced by the different stimulus characteristics, while the slow-phase gain (averaged across subjects) was reduced from 0.9 for stare nystagmus evoked with unlimited lifetime dots to 0.6 for stare nystagmus evoked with limited lifetime dots. Mackensen and Schumacher (1960) reported that the main sequence of OKN fast phases is independent of the stimulus velocity. Slow-phase gain, on the other hand, depends on stimulus velocity with lower gains for higher velocities (Abadi, Howard, Ohmi, & Lee, 2005). In our view the fact that fast- and slow-phase characteristics are differentially influenced by stimulus characteristics demonstrates that both eye movements are controlled by largely independent neural networks. An interesting question arising is how the two systems interact, e.g., how and when a fast phase is initiated during the execution of a slow phase.

Fast phases versus saccades

Visually guided saccades and fast phases of look nystagmus turned out to be on the same main sequence while the main sequences of saccades and fast phases of stare nystagmus were quite different. Similarly the skewness of fast phases of stare nystagmus was much more pronounced than that of saccades and fast phases of look nystagmus. These differences are one likely reason for the discrepant results in previous studies comparing the main sequence of saccades and nystagmus. Saccades have either been reported to be faster with respect to peak velocity (Garbutt, Han et al., 2003; Garbutt et al., 2001; Henriksson

et al., 1980) or average velocity (Gavilan & Gavilan, 1984) or to be on a similar main sequence (Mackensen & Schumacher, 1960; Sharpe et al., 1975). Since none of these studies had used limited lifetime dots to induce OKN it seems likely that in studies reporting no differences subjects had performed a mixture of look and stare nystagmus or pure look nystagmus. On the other hand, in the studies reporting differences subjects had probably performed pure stare nystagmus. Other reasons are different types of saccades that have been used for comparison with fast phases and that have been reported to differ with respect to their main sequence (visually guided, memory guided, and so on). Furthermore in some studies the background characteristics during OKN and saccades had been quite different. Our results highlight the relevance of an explicit visual target and/or the behavioral task of the subject for the dynamics of fast eye movements.

Interaction of fast- and slow-phase eye movements

While earlier work suggested that fast and slow eye movement components do not add up when saccades are executed during pursuit (Carpenter, 1988) some more recent studies proposed that slow and fast eye movement components might add during saccades toward moving targets (Blohm, Missal, & Lefevre, 2003; de Brouwer, Missal, Barnes, & Lefevre, 2002). During steady-state OKN fast phases alternate with slow eye movements. Since look nystagmus is closely linked to smooth pursuit slow- and fast-phase eye velocities might add up during OKN. We did not observe a significant influence of slow-phase eye velocity on the main sequence neither for look nystagmus nor for stare nystagmus. For look nystagmus peak velocity increased slightly but not significantly with stimulus velocity. Such an increase could in principle be caused by a linear addition of the slow and fast phases (de Brouwer et al., 2002).

Neuronal basis of the observed effects

While for a long time the neural networks underlying the execution of voluntary saccades and smooth pursuit eye movements have been assumed to be anatomically separated more recent findings show that both eye movements are controlled by largely overlapping neural networks (for reviews, see Krauzlis, 2004, 2005; Orban de & Lefevre, 2007). Our knowledge about the neural networks underlying the execution of slow and fast phases during OKN is more limited, especially when different forms, i.e., look and stare nystagmus, are considered.

Saccades and fast phases are both generated by the same premotor network located in the brainstem (Leigh & Zee, 2006). Burst neurons in the paramedian pontine reticular formation (PPRF) show identical firing characteristics

before horizontal saccades and fast phases of OKN and VOR (Cohen & Henn, 1972; Henn & Cohen, 1976). Omnipause neurons stop firing previous to fast phases and saccades (Cohen & Henn, 1972) while electrical stimulation of these neurons inhibits the execution of saccades and VOR fast phases (Westheimer & Blair, 1973).

Recordings from single units in the vestibular nucleus (VN) of the rhesus monkey demonstrated that neural activity and slow-phase activity are correlated during OKN (Waespe & Henn, 1977). Interestingly, saccade-related activity has also been reported for VN neurons (Boyle, Buttner, & Markert, 1985; Waespe, Schwarz, & Wolfensberger, 1992). Studies employing single-cell recordings reported neurons in the nucleus of the optic tract (NOT) of the monkey to be activated during OKN slow phases (Ilg & Hoffmann, 1996; Mustari & Fuchs, 1990).

Lesions of the oculomotor vermis influence the dynamics of saccades in the monkey (Takagi, Zee, & Tamargo, 1998). Similar lesions of the fastigial nucleus influence the main sequence in the cat (Goffart, Pelisson, & Guillaume, 1998) and in the monkey (Robinson, Straube, & Fuchs, 1993). Helmchen, Straube, and Buttner (1994) recording from the fastigial nucleus and in the vermis (Helmchen & Buttner, 1995) of the monkey reported similar activity related to spontaneous saccades and fast phases of OKN. Functional imaging studies in humans also reported cerebellar activation during OKN (Bense et al., 2006; Dieterich, Bucher, Seelos, & Brandt, 2000; Konen et al., 2005).

After extensive unilateral cerebral cortical lesions OKN, OKAN, and spontaneous saccades could still be elicited, while reflexive and voluntary saccades directed to the contralateral hemifield were abolished (Tusa, Zee, & Herdman, 1986). Interestingly, peak velocity of OKN fast phases, OKAN fast phases, and spontaneous saccades was reduced similarly after the lesion. Single cell recordings revealed activity during OKN in the medial temporal area (MT; Ilg, 1997). The activity was not related to the execution of fast phases.

The cortical network underlying the execution of OKN in humans has been investigated using functional imaging (Bucher, Dieterich, Seelos, & Brandt, 1997; Dieterich, Bense, Stephan, Yousry, & Brandt, 2003; Dieterich, Bucher, Seelos, & Brandt, 1998; Galati et al., 1999; Konen et al., 2005; Schraa-Tam et al., 2008). The activated network is reminiscent of the networks activated during SPEM and saccades (Dieterich & Brandt, 2000; Petit & Haxby, 1999). One study directly comparing OKN and SPEM found largely overlapping patterns of activation especially with respect to the oculomotor regions (Konen et al., 2005). Interestingly these regions were only activated in subjects performing a combination of look and stare nystagmus. In subjects performing pure stare nystagmus no activation in the frontal eye field (FEF), the supplementary eye field (SEF), and the ventral intraparietal area (VIP) could be observed. This finding was

confirmed in a recent study comparing activation patterns during stare nystagmus and combined look and stare nystagmus (Schraa-Tam et al., 2008). Saccadic activity within FEF has also been reported to depend on the intentionality of the executed saccade. While FEF is strongly activated during voluntary saccades (antisaccades) it is less active during visually guided saccades (Gaymard, Ploner, Rivaud, Vermersch, & Pierrot-Deseilligny, 1998; Mort et al., 2003; Pierrot-Deseilligny, Milea, & Muri, 2004). In addition neurons in FEF of the monkey show no build-up activity before spontaneous saccades that is typical for voluntary saccades (Bruce & Goldberg, 1985). We therefore hypothesize that FEF is part of the neural network causing higher peak velocities/shorter durations for voluntary fast eye movements, including fast phases of look nystagmus, as compared to unintentional fast eye movements. FEF is also active during pursuit. fMRI, due to its low temporal resolution, cannot differentiate between activity related to slow and fast phases. Therefore differences could also be related to the execution of the slow phase of the eye movement.

Conclusions

We showed that fast phases of look and stare nystagmus differ with respect to their main sequence. Furthermore, saccades and fast phases of look nystagmus are on the same main sequence while fast phases of stare nystagmus show different spatiotemporal characteristics. Our results highlight the relevance of an explicit visual target and/or the behavioral task of the subject for the dynamics of fast eye movements. The observed differences could be caused by (partially) different neural networks underlying the execution of the eye movements. Knowledge about how the cortical networks underlying saccades and fast phases differ is still rather limited. This is particular problematic since OKN fast phases are routinely used as a diagnostic tool (Garbutt, Han et al., 2003; Garbutt et al., 2001; Leigh & Zee, 2006). Since fMRI cannot differentiate between activity related to slow and fast phases, electrophysiological studies in cortical and subcortical areas (i.e., the FEF and cerebellum) of non-human primates are needed in order to provide the required information.

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