The Main Sequence of Human Optokinetic Afternystagmus (OKAN)

Andre Kaminiarz, Kerstin Königs, and Frank Bremmer
Department of Neurophysics, Philipps-University Marburg, Marburg, Germany

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Kaminiarz A, Königs K, Bremmer F. The main sequence of human optokinetic afternystagmus (OKAN). J Neurophysiol 101: 2889–2897, 2009. First published March 18, 2009; doi:10.1152/jn.00114.2009. Different types of fast eye movements, including saccades and fast phases of optokinetic nystagmus (OKN) and optokinetic afternystagmus (OKAN), are coded by only partially overlapping neural networks. This is a likely cause for the differences that have been reported for the dynamic parameters of fast eye movements. The dependence of two of these parameters—peak velocity and duration—on saccadic amplitude has been termed “main sequence.” The main sequence of OKAN fast phases has not yet been analyzed. These eye movements are unique in that they are generated by purely subcortical control mechanisms and that they occur in complete darkness. In this study, we recorded fast phases of OKAN and OKN as well as visually guided and spontaneous saccades under identical background conditions because background characteristics have been reported to influence the main sequence of saccades. Our data clearly show that fast phases of OKAN and OKN differ with respect to their main sequence. OKAN fast phases were characterized by their lower peak velocities and longer durations compared with those of OKN fast phases. Furthermore, we found that the main sequence of spontaneous saccades depends heavily on background characteristics, with saccades in darkness being slower and lasting longer. On the contrary, the main sequence of visually guided saccades depended on background characteristics only very slightly. This implies that the existence of a visual saccade target largely cancels out the effect of background luminance. Our data underline the critical role of environmental conditions (light vs. darkness), behavioral tasks (e.g., spontaneous vs. visually guided), and the underlying neural networks for the exact spatiotemporal characteristics of fast eye movements.

INTRODUCTION

Saccades are fast eye movements that can be characterized by a tight relationship between several of their kinematic parameters. Saccade duration and peak velocity increase with saccade amplitude. This relationship has been termed “main sequence” (Bahill et al. 1975) and has been shown for different types of saccades, including visually guided saccades (Bahill et al. 1975; Baloh et al. 1975), memory-guided saccades (Becker and Fuchs 1969; Smit et al. 1987), antisaccades (Smit et al. 1987; Van Gelder et al. 1997), and catch-up saccades (Van Gelder et al. 1997). Although all these types of saccades adhere to a main sequence, the individual main sequences for different kinds of saccades show considerable variability. For example, memory-guided saccades and antisaccades have lower peak velocities (and longer durations) than those of visually guided saccades of identical amplitude (Smit et al. 1987). In addition, factors like fatigue (Bahill and Stark 1975; Riggs et al. 1974) and drug usage (Bittencourt et al. 1981) influence the main sequence. Concerning other factors like saccade direction and background luminance/structure the reports in the literature are less consistent (Bahill et al. 1975; Becker and Jurgens 1990; Boghen et al. 1974; Garbutt et al. 2003a; Hyde 1959; Pelisson and Prablanc 1988; Robinson 1964). Considering specific characteristics of the backgrounds across which saccades had to be made several studies reported faster saccades on illuminated (Henriksson et al. 1980; Riggs et al. 1974; Sharpe et al. 1975) compared with dark backgrounds, whereas others reported no such difference (Becker and Fuchs 1969; Ilg et al. 2006). Furthermore significant inter- and intraindividual differences have been reported (Bollen et al. 1993).

Aside from saccades a main sequence relationship has also been demonstrated for the fast phases of different kinds of nystagmus in several species (Garbutt et al. 2001, 2003a; Gavilan and Gavilan 1984; Henriksson et al. 1980; Mackensen and Schumacher 1960; Ron et al. 1972; Sharpe et al. 1975). Studies comparing saccades and fast phases of the vestibuloocular reflex (VOR) reported identical or very similar main sequences (Guittion and Mandl 1980; Ron et al. 1972; Sharpe et al. 1975), but lower velocities for the VOR have also been reported (Gavilan and Gavilan 1984). Fast phases during visually guided optokinetic nystagmus (OKN) have either been reported to follow the same main sequence as that of visually guided saccades (Mackensen and Schumacher 1960; Sharpe et al. 1975) or to be slower than saccades (Garbutt et al. 2001, 2003a; Gavilan and Gavilan 1984; Henriksson et al. 1980).

In primates the OKN is composed of two components: a direct/early/fast component and an indirect/late/slow component (Cohen et al. 1977). After an increase in stimulus velocity slow phase eye velocity first increases rapidly and, afterward, more gradually until a steady state is reached. The early component is supposed to reflect smooth pursuit (Pola and Wyatt 1985), whereas the late component charges the velocity storage mechanism located in the vestibular nucleus and is therefore essential for the execution of optokinetic afternystagmus (OKAN). OKAN can be observed in subjects who performed OKN for some time and are put in complete darkness thereafter. Like OKN, it consists of slow and fast phases, but amplitude of the fast phases is reduced in the dark.

It is widely accepted that the differences between OKN and OKAN slow phases are the origin of (partially) different neural structures underlying the execution of both types of eye movements. In this study we asked whether the different mechanisms controlling OKN and OKAN also influence their fast-phase characteristics.

Furthermore, we aimed at disentangling the relative influence of cortical control and stimulus characteristics on the main sequence by comparing main sequences for OKAN, OKN, spontaneous, and visually guided saccades.
METHODS

Subjects

In total, 10 healthy subjects (2 male and 8 female, 22–31 yr, mean age 25.7 yr (3.37 SD)) participated in the study. All had normal or corrected-to-normal visual acuity 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. Stimuli were projected onto a tangent screen (70 × 55°) via a CRT projector (Marquée 8000, Electrohome) running at 100 Hz and a resolution of 1,152 × 864 pixels. The screen was viewed binocularly at a distance of 114 cm, with the subject’s head stabilized by a chin rest. 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 using a 3 × 3 point calibration grid. The data were stored on hard disk for off-line analysis.

Experiment 1: OKAN

Eight subjects participated in this experiment [one male and seven female, 22–30 yr, mean age 24.5 yr (SD 2.5)]. Optokinetic eye movements were recorded while the subjects performed a visual localization task. A detailed description of the experimental paradigm can be found elsewhere (Kaminiarz et al. 2008). In brief, OKAN was induced by means of a random-dot pattern (RDP) consisting of black dots (size: 2.0°, luminance <0.1 cd/m², mean density: 0.065 dots/deg², unlimited lifetime) moving across a white background (22.1 cd/m²) at a speed of 80°/s for 15 s. Afterward the screen turned black for several seconds and the reflexive OKAN was recorded.

Experiment 2: OKN

The same eight subjects as in the first experiment and two of the authors participated in this experiment. OKN was recorded while the same RDP as in the OKAN experiment moved across a gray background (12.5 cd/m²) for 4,000 ms. The RDP velocity was adapted for each subject to match fast-phase amplitudes for OKN and OKAN. The average RDP velocity was 12.4 (SD 2.16) deg/s.

Experiment 3: spontaneous saccades

The same eight subjects as in the first experiment served as observers. Spontaneous saccades were recorded while subjects performed a localization task. In sessions with background illumination, subjects freely viewed a homogeneous gray (luminance 12.5 cd/m²) screen for 4,000 ms. After 3,500 ms a localization target was presented. At the end of the trial a ruler was presented and the trial ended automatically (all experiments), or a saccade not directed toward the target was executed in the analyzed time window (see following text; experiment on visually guided saccades only). The first 500 ms of eye movement data recorded on OKN, OKAN, and spontaneous saccade trials were discarded since we cannot exclude that the onset (OKN and spontaneous saccades with background illumination) or the change of the stimulus (OKAN and spontaneous saccades in darkness) influenced the eye movements. Additionally, all eye movements after presentation of the localization target were not considered for further analysis. For the experiment on visually guided saccades only the first saccade in a time window from 100 to 400 ms after the target step was analyzed.

Experiment 4: visually guided saccades

Seven subjects, five of whom also participated in the experiments described earlier, and two of the authors served as observers [one male and six female, 22–31 yr, mean age 26.1 yr (SD 4)]. Each trial started with subjects fixating a central green fixation target for 1,000 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°). Two different backgrounds were used in different sessions. For comparison with OKN fast phases a moving RDP with identical spatial properties as in the OKN experiment served as background (Fig. 1A). The RDP moved either left- or rightward at 10°/s throughout the trial. Saccades could be either in the same or in the opposite direction as the background motion. Accordingly subjects could not anticipate the direction of the upcoming saccade. A black background was used to control for a possible influence of background characteristics on the main sequence (Fig. 1B). Subjects were instructed to follow the target as fast and as 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 off-line. Trials were excluded from further analysis if 1) fast phases/saccades were contaminated by (partially suppressed) blinks that had not been detected automatically (all experiments), 2) subjects did not perform systematic OKN/OKAN (OKN/OKAN trials only), or 3) a saccade not directed toward the target was executed in the analyzed time window (see following text; experiment on visually guided saccades only). The first 500 ms of eye movement data recorded on OKN, OKAN, and spontaneous saccade trials were discarded since we cannot exclude that the onset (OKN and spontaneous saccades with background illumination) or the change of the stimulus (OKAN and spontaneous saccades in darkness) influenced the eye movements. Additionally, all eye movements after presentation of the localization target were not considered for further analysis. For the experiment on visually guided saccades only the first saccade in a time window from 100 to 400 ms after the target step was analyzed.

FIG. 1. Illustration of the reflexive saccade paradigm. Each trial started with subjects fixating a central target for 1,000 ms. Then the target jumped either to the left or to the right (± 1.5, 3, 4.5, 6, and 7.5°) and remained at the new position for another 1,000 ms. Two different types of background were used on different sessions. During background motion sessions (A) a random-dot pattern (RDP) consisting of black dots on a gray background was moving at 10°/s, either in the same or the opposite direction as the target step. On sessions without background motion (B) a uniform black background was used.
Saccade detection

Eye velocity was derived from unfiltered eye position data by differentiation. Saccades were detected using a flexible velocity criterion. Mean eye velocity was calculated in a 40-ms time window ($v_{\text{mean}}$). Whenever the eye moved faster than $v_{\text{mean}} + 24^{\circ}/s$ for three consecutive samples a saccade onset was detected. Saccade offset was detected when eye velocity dropped below the threshold for three consecutive samples.

Correction for slow eye movement components

Whereas earlier work suggested that fast and slow eye movement components do not add up when saccades are executed during pursuit (Carpenter 1988) some newer studies proposed that slow and fast eye movement components could be added during saccades to moving targets (Blohm et al. 2003; de Brouwer et al. 2002). Since during steady state OKN/OKAN fast phases are always temporally surrounded by slow eye movements we removed slow eye movement components from the eye-velocity traces. To do so we first determined the mean eye velocity in time windows before ($-50$ to $-10$ ms) and after ($10$ to $50$ ms) the saccade. Then we performed a linear interpolation for the time in between and subtracted this slow component from the velocity trace. Corrected saccadic/fast-phase peak velocity was calculated from the corrected velocity traces. Corrected saccadic/fast-phase amplitude was calculated by adding the additional change in eye position, which would have resulted from the slow-phase movement during this temporal interval.

Main sequence analysis

Peak velocity and duration of the fast phases/saccades were plotted as a function of their amplitude. The range of fast-phase/saccade amplitudes recorded varied for the different conditions. Lebedev and colleagues (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 as the maximum amplitude for the comparison. Afterward we fitted power functions to the data using least-squares procedures according to: $y = ax^p$. 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 bootstrap analyses and fitted a power function to each of the 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 10 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

In the following we will show main sequence plots (raw data) for only one single subject (the same subject for all plots). For comparison of the effects across subjects we will show the parameters of the power functions fitted to the data.

OKAN versus OKN main sequence

Figure 2 shows duration ($A$) and peak velocity ($B$) for fast phases as a function of fast-phase amplitude during OKAN (black) and OKN (blue) for a single subject. For this subject, OKAN fast phases last longer and reach a lower peak velocity than OKN fast phases of the same amplitude. For the duration versus amplitude relationship this was also the case for the remaining seven subjects. Statistical analysis showed the difference in the scaling factor ($a$) but not the exponent ($b$) of the power function to be significant ($a$: $P = 0.008$; $b$: $P = 0.742$; Wilcoxon signed-rank test) at the population level. Fit parameters for all eight subjects under both conditions are displayed in Fig. 3. The differences between OKAN and OKN concerning the relationship of the peak velocity and amplitude were less consistent (data not shown). Only two subjects exhibited higher peak velocities for OKN fast phases than those for OKAN fast phases; for one subject the opposite was true, whereas the remaining five subjects exhibited no clear difference. Statistics revealed no significant differences in the parameters of the power functions ($a$: $P = 0.148$; $b$: $P = 0.945$; Wilcoxon signed-rank test).

![Figure 2](image-url)
In a next step we compared the mean velocity traces for OKAN and OKN fast phases. In Fig. 4 the mean velocity traces are depicted for the same subject as before. As described in METHODS, these velocity traces were corrected for the velocity of the preceding and the following slow phases by linear interpolation. Solid lines represent data from OKAN fast phases, whereas dashed lines represent data from OKN fast phases. Fast phases of similar amplitudes are color-coded. As already shown in the main sequence plots, OKAN fast phases of a given amplitude are slower and last longer than OKN fast phases of the same amplitude. In addition, Fig. 4 indicates that for small-amplitude OKAN fast phases the peak velocity is reached later than that for OKN fast phases. That means that during OKAN fast phases the eyes accelerate less rapidly compared with OKN fast phases. Seven of the eight subjects showed longer acceleration intervals for small OKAN fast phases compared with OKN fast phases. Next we calculated the skewness (duration of the acceleration period/total duration of the fast phase) of the velocity traces and compared the skewness for OKAN and OKN fast phases. For both OKAN and OKN skewness increased with amplitude. The ratio OKAN_{skew}/OKN_{skew} was 0.93 (0.15 SD), indicating that velocity traces were skewed more strongly for OKAN fast phases.

In the first experiment we demonstrated that OKAN fast phases have a longer duration than that of OKN fast phases. OKAN is performed in total darkness, whereas during OKN a moving, structured background is permanently visible. Since saccade main sequence has been reported to depend on background illumination we asked whether the longer duration of the OKAN fast phases could simply originate from the different lighting conditions in the two experiments. In the literature OKN fast phases have mainly been compared with saccades to visual targets. In contrast, fast phases of OKAN and (stare-) OKN are not directed to a visual target. Therefore we recorded both spontaneous and reflexive saccades in darkness and across a gray background for comparison with OKAN and OKN fast phases.

Spontaneous saccades under different lighting conditions

Figure 5 shows the main sequence plots for the same subject as before. For this subject spontaneous saccades in darkness lasted longer and reached a lower peak velocity than those across a gray background for the considered range of amplitudes. Six of the eight subjects exhibited longer durations during saccades in darkness, whereas the remaining two subjects showed no such difference. Fit parameters for all eight subjects are depicted in Fig. 6. At the population level the difference for the scaling factor just failed to reach significance (a: \( P = 0.055 \); b: \( P = 0.641 \); Wilcoxon signed-rank test). Five of the eight subjects showed higher peak velocities for saccades in darkness. Statistical analysis revealed no significant difference at the population level (a: \( P = 0.25 \); b: \( P = 0.461 \); Wilcoxon signed-rank test).
Analysis of the velocity traces for OKAN and OKN showed faster acceleration of the eyes during OKN. Given the similarity of the results for spontaneous saccades and OKN/OKAN fast phases so far, we next analyzed the velocity traces for spontaneous saccades. Figure 7 shows the data for the same subject as before. Clearly the acceleration intervals are of similar length under both conditions. The duration of the acceleration intervals differed by <1% for the whole population (n = 8), indicating no differences in eye acceleration for spontaneous saccades in different environments. The ratio dark-sac_skew/gray-sac_skew was 0.94 (0.14 SD), indicating that velocity traces tended to be skewed more strongly for saccades in darkness. This result is analogous to our results for OKAN and OKN fast phases.

Visually guided saccades under different lighting conditions

Four of the seven subjects performing visually guided saccades did not show any significant influence of environmental luminance on the main sequence. For two subjects saccades in darkness had longer durations than saccades across a moving structured background, whereas for the last subject the opposite was the case. At the population level (n = 7) fit parameters (Fig. 8) were not significantly different for the duration versus amplitude relationship (a: P = 0.688; b: P = 0.938; Wilcoxon signed-rank test) and the peak velocity versus amplitude relationship (a: P = 0.938; b: P = 0.938; Wilcoxon signed-rank test). Analysis of velocity traces revealed that on average the acceleration interval lasted 3.2% longer for saccades in darkness. The ratio dark-sac_skew/gray-sac_skew was 1.02 (0.08 SD), indicating similarly skewed velocity traces for visually guided saccades under different lighting conditions.

OKN/OKAN versus spontaneous saccades

After having shown that spontaneous saccades are influenced by the background characteristics similarly to OKN/OKAN fast phases we directly compared the two types of eye movements. Comparison of the main sequences for OKN fast phases and spontaneous saccades across a gray background revealed longer durations for spontaneous saccades in all eight subjects (see Fig. 9, A and B for fit parameters). For seven subjects spontaneous saccades had lower peak velocities. Group analysis revealed significant differences for both duration versus amplitude and peak velocity versus amplitude relationships (duration vs. amplitude: a: P = 0.008; b: P = 0.195; peak velocity vs. amplitude: a: P = 0.008; b: P = 0.039; Wilcoxon signed-rank test).

Comparison of OKAN fast phases and spontaneous saccades in darkness revealed longer durations for spontaneous saccades in four of the eight subjects. Another three subjects did not show any difference and for the remaining subject fit quality...
was insufficient (Fig. 9, C and D). The signed-rank test performed on the seven subjects whose data allowed a curve fit of sufficient quality showed a significant difference for the exponent and a tendency for the scaling factor \( (a: P = 0.078; b: P = 0.039; \text{Wilcoxon signed-rank test}) \). Three of the eight subjects had lower peak velocities for spontaneous saccades than for fast phases. In the remaining four subjects we observed no significant difference. At the population level fit parameters were not significantly different \( (a: P = 0.148; b: P = 0.742; \text{Wilcoxon signed-rank test}) \).

Taken together spontaneous saccades and fast phases performed in lumiance-matched environments are not on the same main sequence. Rather, spontaneous saccades typically last longer and have lower peak velocities.

**OKN/OKAN versus visually guided saccades**

For three of the seven subjects OKN fast phases had longer durations and lower peak velocities than those of visually guided saccades. One subject showed no difference, either for duration or for peak velocity. For the remaining two subjects OKN fast phases lasted slightly shorter than visually guided saccades (Fig. 10, A and B), whereas the peak velocities were similar. Population analysis \( (n = 7) \) revealed no significant difference for the scaling factor. The exponent was different for both conditions in the duration versus amplitude relationship \( (a: P = 0.813; b: P = 0.031; \text{Wilcoxon signed-rank test}) \) and showed a tendency for the peak velocity versus amplitude relationship \( (a: P = 0.297; b: P = 0.078; \text{Wilcoxon signed-rank test}) \).

Fast phases of OKAN had longer durations than those of visually guided saccades on a black background in all five subjects (Fig. 10, C and D). In two subjects we also observed higher peak velocities for saccades. Both effects were not significant at the population level (duration–amplitude relationship: \( a: P = 0.125; b: P = 0.625 \); peak velocity–amplitude relationship: \( a: P = 0.438; b: P = 0.188; \text{Wilcoxon signed-rank tests}) \).

**Effects of correction for slow-phase velocity**

Since we do not know for certain whether eye velocity during fast phases of OKN is modified by the slow-phase eye velocity we finally tested to what extent the correction for the slow-phase eye velocity influences the data and whether the observed effect can still be observed without correction. For OKAN and OKN correction for slow-phase eye velocity on average resulted in higher peak velocities and shorter durations. At the population level statistical analysis revealed significant differences between parameters of the power functions fitted to the data for corrected and uncorrected data for fast phases of OKN (duration vs. amplitude: \( a: P = 0.008; b: P = 0.008; \text{peak velocity vs. amplitude: } a: P = 0.016; b: P = 0.008 \)). For OKAN this difference did not reach significance (duration vs. amplitude: \( a: P = 0.25; b: P = 0.74; \text{peak velocity vs. amplitude: } a: P = 0.95; b: P = 0.55 \)). The reason that we observed no significant effect for OKAN is probably that slow-phase velocities were about twice as high during OKN compared with that during OKAN. Since the effect of slow-phase correction differs between conditions we next tested whether the observed difference between OKAN and OKN can be observed in the uncorrected data set.

Statistical analysis showed the difference in the scaling factor but not the exponent of the power function to be significant for the duration versus amplitude relationship \( (a: P = 0.039; b: P = 0.688; \text{Wilcoxon signed-rank test}) \) at the population level. For the peak velocity versus amplitude relationship statistics revealed no significant differences in the parameters of the power functions \( (a: P = 0.313; b: P = 0.945; \text{Wilcoxon signed-rank test}) \). This is the same result as observed for the corrected data; therefore the observed difference between the main sequences of OKAN and OKN is not an artifact of correction for slow-phase eye velocity. Similarly we analyzed the data without correction for all other experiments. Although for single subjects results were sometimes different for corrected and uncorrected data sets, the results were the same at the population level for all experiments (data not shown).

**Discussion**

We have tested and compared various types of saccades and fast phases in the same human subjects. Our data clearly show that fast phases of OKAN and OKN are not on the same main sequence. Instead, OKAN fast phases lasted longer and had lower peak velocities compared with those of OKN fast phases. Similarly, spontaneous saccades on a black background lasted longer and had lower peak velocities than did spontaneous saccades in darkness. Although for spontaneous saccades this effect was very robust, it was absent in most subjects for saccades toward a visual target and, if present, it was much weaker.

**Visually guided saccades**

The main sequence of visually guided saccades has been the topic of various studies. In some studies power functions have been used to describe the main sequence. Comparing our

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**Fig. 10.** Comparison of fit parameters for reflexive saccades and fast phases. **Top row** comparison of OKN fast phases and reflexive saccades across a gray background. **Bottom row** comparison of OKAN fast phases and reflexive saccades in darkness. Circles represent individual data points. Other conventions as in Fig. 3.
results to those of Lebedev et al. (1996) and Garbutt et al. (2003b) we see that the exponents of the power functions are similar in all three studies. However, the factors denoting the duration/peak velocity of a 1° saccade indicate higher peak velocities and shorter durations in our study. One likely reason could be the different techniques used for measuring eye position. Lebedev et al. (1996) used electrooculography, whereas Garbutt et al. (2003b) used the scleral search coil technique, both of which were reported to underestimate peak velocity (Boghen et al. 1974; Byford 1962; Frens and van der Geest 2002). Two other likely reasons are that we 1) did not filter our eye data prior to analysis and 2) used a different algorithm to detect saccades. Since we are mainly interested in main sequence differences between experimental conditions measured in the same setup and analyzed with identical techniques in the same human subjects these differences are negligible. The main sequence of visually guided saccades was weakly influenced by the environmental luminance in one third of our subjects. This reflects the heterogeneous results reported in the literature. Although some authors reported faster saccades in the light (Henriksson et al. 1980; Riggs et al. 1974; Sharpe et al. 1975), others found no influence of background luminance (Becker and Fuchs 1969; Ilg et al. 2006).

**Spontaneous saccades**

We found spontaneous saccades to be slower than visually guided saccades under (nearly) identical luminance conditions. The main sequence of spontaneous saccades depended heavily on background illumination. We observed lower peak velocities and longer durations for spontaneous saccades in darkness. This is in accordance with studies demonstrating lower peak velocities and longer durations for voluntary saccades in darkness (Barton and Sharpé 1997; Riggs et al. 1974; Sharpe et al. 1975). However, the results of some of the studies have to be handled with care because the authors did not compare voluntary saccades in light and darkness, but instead compared voluntary saccades directed toward a visual target, with memory-guided saccades in total darkness (Henriksson et al. 1980; Sharpé et al. 1975), which have been shown to be significantly slower (Smit et al. 1987).

**Comparison of OKN and OKAN fast phases**

OKAN fast phases have a longer duration compared with that of OKN fast phases, lower peak velocities, slower acceleration, and stronger skewness. For both eye movements skewness increased with amplitude, which has also been shown for reflexive saccades (Smit et al. 1987). During OKN a moving RDP is constantly visible, whereas OKAN is performed in the absence of visual stimulation. Although it seems likely that the RDP causes the difference it is not possible to determine which aspect of the stimulus causes the difference. Two likely candidates are the difference in environmental luminance and the motion per se. We showed that spontaneous saccades are heavily influenced by the background luminance. Spontaneous saccades and fast phases of OKAN and (stare-) nystagmus are not deliberately directed to a visual target and are similarly influenced by cortical lesions (Tusa et al. 1986). Therefore the main sequence difference could be simply caused by the luminance difference.

**Comparison of OKN and visually guided saccades**

We observed higher peak velocities for saccades in half of our subjects. In the literature OKN fast phases have been compared with several types of saccadic eye movements. Garbutt and colleagues (2001) found OKN fast phases to be of slightly longer duration and to have lower peak velocity than those of reflexive saccades. Voluntary saccades have been reported to be faster than OKN with respect to peak velocity (Garbutt et al. 2003a; Henriksson et al. 1980) and average velocity (Gavilan and Gavilan 1984). Other authors reported similar peak velocities for OKN fast phases and voluntary saccades (Mackensen and Schumacher 1960; Sharpé et al. 1975). Therefore our data are in accordance with the literature.

As previously discussed by Garbutt (2001) one likely reason for the discrepancies in the literature is that various types of saccades were used for comparison, which have been shown to differ with respect to their main sequence. Another likely cause is the different background characteristics during OKN and saccades in some of the studies. For example, Henriksson and colleagues (1980) compared OKN fast phases with voluntary saccades performed in darkness. In our study we kept background properties identical and still observed significantly longer durations for fast phases in some subjects. As mentioned earlier, fast phases of stare-nystagmus are not deliberately directed toward a visual target, whereas visually guided saccades are. We did not use limited lifetime RDPs in our study. Therefore subjects presumably performed a mixture of look- and stare-nystagmus, adding a voluntary component to the fast phase. Under the assumption that the main sequence depends on the intentionality of the performed eye movement we expect (nearly) identical main sequences for look-nystagmus and visually guided saccades, whereas fast phases of pure stare-nystagmus, evoked by limited lifetime dots, should be slower and last longer than visually guided saccades.

**Comparison of OKN and spontaneous saccades**

Spontaneous saccades had longer duration and lower peak velocity compared with those of OKN fast phases. We compared spontaneous saccades across a uniform gray background and OKN fast phases. During OKN the background was obviously not uniform but instead an RDP moved across the screen. Since we showed that the main sequence of spontaneous saccades depends on background illumination the two conditions are therefore not completely identical. We nevertheless decided to use a uniform background because using the same structured background as that during OKN would have caused subjects to perform visually guided saccades between the elements of the RDP.

**Neuronal basis of the observed effects**

Saccades and fast phases are both generated by the same premotor network located in the brain stem (Leigh and Zee 2006). Burst neurons in the paramedian pontine reticular formation show identical firing characteristics before saccades and fast phases of OKN and VOR (Cohen and Henn 1972; Henn and Cohen 1976). Omnipause neurons stop firing previous to fast phases and saccades (Cohen and Henn 1972), whereas electrical stimulation inhibits the execution of saccades and VOR fast phases (Westheimer and 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 and Henn 1977a) and OKAN (Waespe and Henn 1977b). Boyle et al. (1985) demonstrated that neuronal activity reflects the late component of OKN but not the early component. According to these results the VN is assumed to be the neural substrate of the velocity storage mechanism. Interestingly, saccade-related activity has also been reported for VN neurons (Boyle et al. 1985; Waespe et al. 1992). Studies using single-cell recordings reported neurons in monkey nucleus of the optic tract (NOT) being activated during OKN slow phases. Activity returned to the spontaneous level during OKAN and shortly after fast phases (Ilg and Hoffmann 1996; Mustari and Fuchs 1990).

After extensive unilateral cerebral cortical lesions OKN, OKAN, and spontaneous saccades could still be elicited, whereas reflexive and voluntary saccades directed to the contralateral hemisphere were abolished (Tusa et al. 1986). Interestingly, peak velocity of OKN fast phases, OKAN fast phases, and spontaneous saccades was reduced similarly after the lesion. Single-cell recordings revealed OKN- but not OKAN-related activity in the medial temporal area (Bremmer et al. 2002; Ilg 1997). For both areas 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 et al. 1997; Dieterich et al. 1998, 2003; Galati et al. 1999; Konen et al. 2005). The activated network is reminiscent of the networks activated during smooth-pursuit eye movement (SPEM) and saccades (Dieterich and Brandt 2000; Petit and 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 activated only in subjects performing a combination of look- and stare-nystagmus. In subjects performing pure stare-nystagmus no activation in frontal eye field (FEF), supplementary eye field, and the ventral intraparietal area 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. Although FEF is strongly activated during voluntary saccades (antisaccades), it is less active during visually guided saccades (Gaymard et al. 1998; Mort et al. 2003; Pierrot-Deseilligny et al. 2004). We therefore hypothesize that FEF is part of the neural network causing higher peak velocities and shorter durations for voluntary fast eye movements compared with those of unintentional fast eye movements. FEF is also active during pursuit. Due to its low temporal resolution, functional magnetic resonance imaging (fMRI) 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.

**Phylogenetic/ontogenetic aspects of OKN**

Our results emphasize the importance of the cortical influence on OKN in humans. In adult cats, nonhuman primates, and probably humans input to the NOT is dominated by the cortex. In all three species OKN is symmetrical—i.e., if only one eye is stimulated, OKN is equally strong for nasal and temporal stimulation. In contrast, OKN is asymmetrical in species like rabbits and rats, where cortical input is less dominant or absent (Carpenter 1988). Furthermore, directional asymmetries can be observed in newborn humans, monkeys, and kittens. It has been hypothesized that after birth the NOT receives retinal input only and that, while cortical input increases, OKN becomes more symmetrical (Hoffmann 1989). Taking into account our results one could hypothesize that in humans, monkeys, and cats the dynamics of OKN fast phases should change with increasing cortical influence in the first months after birth.

**Conclusions**

We showed that OKAN and OKN differ with respect to their main sequence. This could be caused by the different environmental conditions or by (partially) different neural networks underlying the execution of both types of eye movements, which have already been proposed to be the origin of the differences between OKN and OKAN slow phases (Cohen et al. 1977). Knowledge about the cortical network underlying the execution of OKN/OKAN is still rather limited. This is particularly problematic since OKN fast phases are routinely used as a diagnostic tool (Garbutt et al. 2001, 2003a; Leigh and Zee 2006). Since fMRI cannot differentiate between activity related to slow and fast phases, electrophysiological studies in cortical areas revealed to be active during OKN should be performed to provide the required information.

**REFERENCES**


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