ON THE OPTOKINETIC RESPONSE DURING STEP-WISE CHANGES IN STIMULUS VELOCITY IN SQUIRREL MONKEYS

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Abstract — In two awake untrained squirrel monkeys the horizontal optokinetic nystagmus (OKN) was studied. The goal was to quantify the buildup of the slow-phase eye movement velocity during the first two seconds and the eye movements after OKN interruption by a stationary surround. We intended to uncover possible effects of a 'charged' velocity storage on eye movements at a stationary surround. Using an optokinetic drum, a paradigm was designed to create sudden changes of the pattern (within 5 ms) between appearing to be stationary or rotating. Velocity steps from zero to 14 to 73°/s and back to zero could be achieved. OKN onset: 201 velocity trajectories were analyzed. The mean latency between the onset of pattern movement and the onset of slow-phase eye movements was 82.8 ± 16.5 ms. Over a limited period the initial increase in slow-phase velocity could be approximated by a straight line. The slope was on average 103 ± 67°/s² and did not show a significant dependency on pattern movement velocity. Eye movement velocity at the end of the linear part increased linearly with drum velocity; the slope was 0.59. After the linear range, the slow-phase velocity increased further but at slower accelerations and usually reached the final gain within the two seconds. The initial linear acceleration component is an open-loop reflex response and we conclude that closing the loop happens when about 60% of the stimulus velocity is reached.

OKN-offset: The influence of a fully charged OKN velocity storage mechanism on eye movements after a sudden exposure of a stationary surround was studied in 23 trials. After OKN interruption the velocity decay commenced after an interval of 83.5 ± 16.6 ms. On average the slope of the consecutive linear velocity decay was −195.4 ± 83.66°/s². During 5.8 ± 0.98 s the OKN still had some impact on the fixating eye movements. We conclude that this time represents the time for velocity storage discharging. An active process seems to control the impact of velocity storage on eye movements.

Keywords — optokinetic nystagmus; OKN; onset; fixation suppression; stimulus velocity; monkey

Introduction

Most investigations of optokinetic nystagmus (OKN) have focussed on steady state conditions (1). In many of them, eye movements during the onset of optokinetic stimulation were also studied (2-9). Fewer reports presented a quantitative analysis of the OKN time course during the very onset of optokinetic stimulation: Collewijn (10) reported a minimum transport time of 75 ms between illumination of a moving stimulus and the beginning of eye movements in the rabbit. He also reported an initial constant acceleration of the OKN slow-phase. In a report on rhesus monkeys (11) the linearly approximated acceleration during the first 100 ms of the OKN was measured. Also in experiments with monkeys, Miles and colleagues (12) and Kawano and Miles (13) found a very early, brief and transient velocity increase of 50 ms after the stimulus onset, followed by a second larger one. In the studies of OKN ter-
mination, the afternystagmus (OKAN) was usually investigated (1,2,5,6,14,15,16) whereas eye movements after OKN in the presence of a stationary visible pattern (15,17,18) have been of less interest.

One goal of the present work was to study the OKN onset to a true stepwise increase in pattern velocity. As opposed to earlier reports (11,12), we left the moving stimulus on continuously and studied the slow-phase velocity buildup over 2s. To achieve fast stimulus velocity jumps, we designed a paradigm to switch between the drum appearing stationary or rotating and a physically stationary or rotating one. Secondly, we compared the velocity increase with the velocity decay after optokinetic stimulation. As OKAN represents a long-lasting open-loop condition, it was of greater interest to compare OKN onset to OKN termination at stepwise velocity reduction of a moving pattern to zero velocity. Therefore the return to holding phases after OKN (comparable to fixation suppression) was quantitatively analyzed. The comparison of the velocity increase and the offset response revealed strong similarities in the time courses of the slow phase eye velocity.

**Methods**

Experiments were conducted in two adult squirrel monkeys; in one animal with horizontal OKN to the right (M86) and in the other to the left (M103). The recordings were obtained during the initial experiments of a single-neuron study in which the animals were also confronted with a variety of visual stimuli other than the purely horizontal drum rotation to the side of penetrations. The animals were placed in a primate chair; the head was fixed in the upright position by means of an acrylic support screwed to the skull. They were not deprived of water and not rewarded or trained for any movement or behavior. About 20 min prior to the recording session d-amphetamine sulfate was administered orally (mixed with some juice) at dosages between 0.25 and 0.75 mg/kg to keep the monkeys awake. A horizontally rotating drum (diameter 60 cm) with vertical black and white stripes was used to elicit OKN. The pattern periodicity was 2.37°; drum velocities were between 14 and 73°/s. Eye movements were recorded by means of the scleral search-coil technique (19). Technical details and the calibration procedures were described earlier (20,21). The sampling interval was 4 ms. Eye velocity was obtained by computing the slope of regression lines for each sampling point of the eye position trajectory. The linear approximation was computed over \(2n+1\) data points; \(n\) points at each side of the respective sampling point. \(n\) was selected between 5 and 10; it was 8 in the trajectory samples of Figure 1. Before doing the analysis, we tested the influence of \(n\)-values up to 30. In doing so, we ensured that the amount of smoothing finally accepted in the analysis was clearly not critical to create distortions of the slow phase velocity component. The shape of the quick phases was slightly changed (reduced peak velocity and increased duration), which, however, could be neglected when focusing solely on the slow phase velocity.

OKN onset: Velocity steps in drum rotation started at zero and jumped to a given constant-speed drum rotation in the following way: Before recording, the drum was set into motion and simultaneously illuminated stroboscopically (flash duration 50 μs). Flash frequency and rotation speed were adjusted so that a flash appeared after the drum had rotated the distance of one black and white stripe. Therefore, the pattern appeared stationary and the monkeys performed not nystagmus but spontaneous eye movements, as they usually do when perceiving a stationary drum. When, in addition, constant illumination of the drum was switched on (shutter opening time 5 ms), the drum motion became visible and the monkey immediately began optokinetic eye movements. Thus, a true step response from zero velocity to a given value could be obtained. During the constant light illumination, the flashes were practically not visible and normal steady-state OKN responses were observed when comparing gain and stability of slow phases to pure constant light illumination. The periods of visible pattern movements were longer than 20 seconds and presented at random intertrial intervals between 5 and 30 seconds. OKN interruption: In some
experiments OKN under flash illumination in the presence of a stationary drum could be elicited (22–24). Then sudden constant illumination let the monkeys change from OKN to fixation periods.

Time and amplitude measurements in the eye velocity trajectories were done graphically [25]. The plots could be enlarged to any desired amplification to achieve sufficient preciseness (the samples in Figure 1 were scaled at low magnitude to give an overview of the velocity time courses). For each trial of OKN onset, we tried to determine four parameters: (1) Latency between the onset of the constant light and the first clearly detectable increase or decrease in eye movement velocity. By inspection we determined the moment when the eye velocity clearly escaped from the random fluctuations of the holding phases. Faced with noisy velocity trajectories, not always monotonic velocity increases, a wide scatter of slopes of increase and superimpositions of rapid phases, we found this simple decision-based procedure superior to any automatic onset detection. (2) Slope, with the initial part of the velocity increase linearly approximated. (3) The slow-phase velocity at the end of the linear portion (end velocity). (4) The latency from the stimulus onset to the end of this linear range (onset-termination interval).

Results

**OKN Onset**

Typical samples of optokinetic onset responses from both monkeys are shown in Figure 1. Left of the vertical line, the rotating drum appeared stationary. At the line, the constant light went on and the OKN commenced. Figure 1 shows responses in three trials during drum rotation to the right (M86) and in three with drum rotation to the left (M103). In total, 201 trials of onset responses were inspected, showing that after the drum rotation became visible, eye-movement velocity jumped to a given value. Eye movements during lower drum velocities could not be analyzed, because it was difficult to create the impression of a stationary drum when the flash frequency was too low. Only the trials in which no saccade/quick-phase was present at least half a second before the moving stimulus onset were analyzed quantitatively. In most of the recordings, the initial velocity increase could be well approximated by a...
straight line (begin and end of the linear portion indicated by vertical arrows in Figure 1). After the linear increase, the velocity trajectory was quite variable among the different recordings. Usually the velocity increased in a curved manner until the stationary velocity was reached. No further attempts were made to describe this portion quantitatively. The data for the two monkeys did not deviate significantly, therefore in Figures 2–5 their results were pooled; the statistical analysis was done for the pooled and the separated data.

Because the monkeys were untrained and sometimes showed reduced attention or restlessness, some trials had to be left out of further analysis, showing no clearly measurable parameters at all. In other trials, not all parameters could be determined with certainty, for example, when a rapid eye movement spontaneously occurred shortly after constant light onset. In other cases, the termination of the linear part could be clearly discerned, and then the end velocity and the duration of the linear part were not accessible. Therefore, the number of data points in the statistical analysis of the four parameters is different, reflecting subpopulations of the total number of 201 trials.

Latencies. The distribution of latencies from both monkeys is shown in Figure 2. The average was 82.8 ± 16.5 ms for the pooled data of both monkeys; it was 85.3 ± 16.6 ms for the data from the animal M103 (n = 45) and 81.7 ± 16.5 for the other monkey M86 (n = 106). In the trials from one experiment, we found three clearly longer latencies within others of the usual length. The nature of these long values is unclear; blinks may have played a role. These long intervals were not used when determining mean and standard deviation. A linear regression analysis verified a slight increase of 0.08 ms/s between latency and drum velocity; the correlation coefficient, however was insignificantly small (0.084). The latency was also not correlated to the slope of the velocity increase. In the monkey M86, we also recorded a few responses to alternations from full darkness to the visible drum moving at velocities in the order of 30°/s. The latencies obtained were 79.0 ± 16.0 ms (n = 7).

Linear velocity increase. The mean acceleration of the linear portion was 136.4 ± 64.4°/s² (n = 51) for M103 and 87.8 ± 62.3°/s² (n = 117) in M86; pooling the results from both monkeys provided 102.5 ± 66.5°/s². Thus, the velocity increase showed a wide scatter including a significant difference between the two animals (alpha < 0.001). Linear regression analysis did not reveal any correlation between drum velocity and lin-
ear eye acceleration. Similarly, the interval between pattern movement onset and termination of the linear range was widely scattered, however, this ‘onset-termination interval’ seemed to increase with drum velocity. The linear regression analysis yielded (pooled data): interval (ms) = 6.4 × drum velocity (degrees/second) + 109.7 ms and a weak correlation (r=0.46). On average, the onset-termination interval was 300 ms. The slow-phase eye velocity at the end of the linear range, the ‘end velocity’, was more closely related to the stimulus velocity (Figure 3, r=0.80). The slope of 0.59 (0.68 in M103 and 0.55 in M86) indicates that, irrespective of the stimulus velocity, the slow-phase eye velocity increases linearly until 59% of the stimulus velocity is reached. When forcing the regression line through the coordinate system’s origin, the slope of the regression line is 0.55. In the few trials with change from darkness to a visible moving pattern, the slope of the linear velocity increase was 145.1 ± 29.5°/s² (n=8).

OKN Offset

In the experiments mentioned so far, drum rotation velocity and flash frequency were adjusted to create the impression of a stationary pattern. This was verified when the monkeys performed only spontaneous irregular eye movements as they did in the presence of a stationary, constantly illuminated drum. Under a different condition, the monkey’s perception of the same stimulus combination, however, can be different: When presenting an appropriate combination of rotation speed and flash frequency in the presence of ongoing optokinetic eye movements, the moving stroboscopically illuminated pattern could be perceived as moving and the nystagmus is continued. This phenomenon has described as sigma-OKN (22-24). It was further shown that one can even let the monkey perform OKN when the stroboscopic illuminated drum is stationary. We will call these eye movements ‘apparent movement OKN’ and simply use them as a tool to produce abrupt OKN terminations. The speed of the corresponding apparent drum motion can be calculated by multiplying pattern periodicity by flash frequency. In some experiments, we could elicit such an apparent movement OKN on a stationary drum. The OKN gain was similar to the gain during real pattern movement. When we could
achieve 2 to 3 minutes of stable apparent OKN, we switched on the constant light and then created a true step to zero velocity.

Figure 4A gives an example of the velocity trajectory after termination of an apparent movement OKN. The eye movement deceleration could be well described by two parameters. The first was the interval between the moment of constant illumination and the beginning of the decay; the second was the slope of decay. In two recordings, the edge between constant slow-phase velocity and deceleration was not sharp, and in four cases quick phases appeared at this moment. The mean of the remaining 17 latencies was $83.5 \pm 16.6$ ms (Figure 4B). The data from the two monkeys did not vary significantly: M103 82.4 ± 17.0 ms ($n = 8$); M86 84.6 ± 17.1 ms ($n = 9$). In 22 of 23 trajectories, the velocity decrease could be well approximated by a straight line (Figure 4A). In some cases the linear decay did not immediately reach zero velocity. But in these cases the major part of decay was also linear. The slopes of linear decay (Figure 5) are only weakly dependent on drum velocity during OKN ($r = 0.34$). Averaged over all drum velocities, the slope of velocity decay was $-195.4 \pm 83.6^\circ/s^2$ ($n = 22$). Separated for the two monkeys, the respective values were M103 $183.0 \pm 68.1$ ($n = 10$), M86 $205.8 \pm 96.8$ ($n = 12$). The lower dashed line shows that the slopes of decay were on average slightly higher than the slope of increasing velocity at OKN initiation. The upper dashed line was redrawn from Lisberger and colleagues, report (11) on early OKN initiation slopes after steps from darkness to a moving pattern.

Figure 6 shows that stored OKN-related neural activity is not totally erased by movement suppression during fixation. In all recordings, we found that after the sharp drop in slow-phase velocity, the eye movements during the fixation period were not stable as they usually were in the presence of an unmoved pattern. There was always a slow but constant drift in the direction of the previous OKN slow phase. The slow drift velocity never exceeded 10% of the OKN slow-phase velocity. The drift was always interrupted by some saccades or quick phases. We interpreted this drift as indicating remaining activity of the velocity-storage mechanism. In 18 cases, from position or velocity trajectories the end of this slow component could be detected quite precisely as shown in Figure 6, although the amplitudes were low. The duration of the slow drift was $5.82 \pm 0.98$ seconds (M103 $5.78 \pm 0.93$, $n = 6$; M86 $5.84 \pm 1.04$, $n = 12$); it was not related significantly to the stimulus velocities applied.

Discussion

The aim of the present work was to describe the time course of the horizontal optokinetic
nystagmus during the first 2 s and after steps from a given pattern movement velocity to zero in untrained monkeys.

**Latencies**

The mean delay of 83 ms that we found did not depend on stimulus velocity or properties of the consecutive eye movement. In experiments with stimulation-onset after darkness, Collewijn (10) found a comparable value in rabbits of 75 ms. Both latency values fit the latency of 60 ms for the activation of NOT neurons [15] after onset of oculomotor stimulation in the rabbit. A fast velocity rise requires an intact flocculus (26), and according to Waespe and colleagues (17), the initiation of flocculus neural activity in monkeys occurred after 70 ms. Therefore, our data support the idea that the direct OKN loop involving the flocculus could play a role in controlling the initial OKN onset. The latency from movement onset to movement initiation was very close to the latency from OKN interruption to the drop in eye movement velocity. This finding shows that the latency is also independent of the preexisting eye movement and the state of the velocity storage mechanism. Probably the same pathway in the brain controlled OKN onset and stable gaze holding phases after OKN. In the experiments of Waespe and colleagues (17), the OKN onset latency was longer (132 ms) than in the present results. Waespe and Schwarz (18) reported a latency of about 110 ms between OKAN interruption and onset of velocity decay in rhesus monkeys. This also is clearly longer than what we found.

In monkeys, Miles and colleagues (12) applied brief velocity steps (100 ms holding phase) of a large-field stimulus. They found clearly shorter latencies (50 ms) from the movement onset to a very early velocity peak, and a dependence of the amplitude of this peak and of the following eye acceleration on the pattern movement velocity. These findings are not in agreement with our data. An explanation for the different results can be that we did not couple the stimulus onset to preceding saccades as Miles and colleagues had done, since the early velocity peak depended on a postsaccadic enhancement (13). In our data, saccades or quick phases were always more than 0.5 s prior to the onset of the pattern movement. Nevertheless, this is not a completely satisfactory explanation for the deviating results, since we recorded some trials in which the onset moment was less than 300 ms after a quick-phase. In none of these trials did we see latencies shorter than those shown in the data in Figure 2. In Robinson's early report on smooth pursuit in man (27), a comparable value for the initiation of eye movements was 130 ms. More recently, shorter latencies of 91 to 112 ms (28) and 93 ms (29) were found for smooth pursuit. These results are closer to the latencies we found in monkeys.

**Linear Acceleration During OKN Onset**

Applying a stimulus change from darkness to movement in monkeys, Kurzan and colleagues (30) reported initial eye movement acceleration values below $100^\circ/s^2$, while Lisberger and colleagues (11) found accelerations between 200 and $300^\circ/s^2$ for drum velocities from 30 to 90°/s. We found values in between (mean $103^\circ/s^2$). The monotonic increase of the linear slope with drum velocity in the data of Lisberger and colleagues does not correspond to our findings. The reason for the deviating results can be that we alternated from a visible stationary pattern to a moving one, while Lisberger and colleagues changed from darkness to a moving stimulus. In such a paradigm the change in stimulation can probably increase alertness.

Similar to the effect of body vibration in rabbits (31), a variable attention level in our experiments can explain the wide scatter of the slope of the velocity increase. The wide scatter we found is in disagreement with the results of Miles and colleagues (12). They showed for both latency and time course of velocity increase an amount of intertrial variability that was an order of magnitude smaller than in our experiments. In their experiments, the animals were trained to fixate and were rewarded for saccades; the intertrial interval was 3 s at most, and the beginning of pattern movement was
triggered by saccades. In contrast, in our experiments the monkey's cooperation was not facilitated, which could explain the deviating results. A further comparison with Miles and colleagues' data is difficult because they finished the analysis 140 ms after pattern movement onset, whereas none of the linear acceleration we determined ended at or before 140 ms.

Studying smooth pursuit in monkey experiment, Lisberger and Westbrook (32) measured eye movements during steps to different velocities while starting from zero and found much larger values for the acceleration under foveal onset of stimulus movement than we found for the OKN. A separation of the acceleration into a portion before 20 ms and a longer one, as was possible in their data, does not correspond to our data. In their data, the second acceleration component (60 to 80 ms) depended on both the speed of the fixation point and the starting position of a step-ramp paradigm. The early acceleration component at 20 ms after movement onset vanished when the step amplitude became zero, indicating similarities between foveal onset of smooth pursuit and the present OKN data. Smooth pursuit in humans provided some lower values for the average acceleration (time window below 100 ms (28)). From Figure 4 of Behrens and colleagues (29), we evaluated the acceleration during smooth pursuit in the order of 4°/s².

Taken together, two velocity peaks have been described in related experiments that do not exist under the present stimulation conditions: (a) the early postsaccadic enhancement in a large-field stimulation commencing 50 ms after optokinetic stimulus onset, and (b) the velocity peak 20 ms after movement onset in a smooth pursuit task. Interestingly, the early velocity peak during smooth pursuit (28) and the linear acceleration phase in our data have a similarity in that neither depends on stimulus velocity. This finding provides evidence that the initial OKN velocity increase stems from the smooth pursuit system.

In our experiments, at least the first 83 ms of the eye movement have to be under open loop conditions. Using continuous open loop conditions (stabilized retinal image on the stimulated eye (33,34), Dubois and Collewijn (35) showed an eye movement recording during optokinetic stimulation that displayed a slow-phase velocity increase interrupted by three quick phases within the first 2 seconds after stimulus onset. However, the slow-phase velocity increase was much slower than the linear slope that we found. From a recording of Behrens and Grüsser (36), one can estimate an acceleration on the order of 4°/s² under open loop obtained by retinal image stabilization. Thus, there is a clear discrepancy in velocity increase between the data from stabilized retinal images and the transient open loop at OKN onset.

In our results the slope of the linear portion seems to be an independent variable, probably influenced by attention, but not stimulus velocities between 14 and 73°/s. The transition from the initial linear to the following curved and slower increase takes place when about 50% to 60% of the required eye movement velocity is obtained by the reflective component (assuming a final gain of about 0.9). Since the uniform initial velocity rise can continue unchanged up to several hundred milliseconds, the movement remains under open loop, in all likelihood, until the linear velocity increase ends. Thus, the velocity increase of the direct OKN component can be divided into two portions: a fast reflexive acceleration, followed by a slower one that is probably feedback controlled. With the stimulation velocities of the present report, the final eye velocity was always reached within 2 seconds and afterwards remained constant. The even slower velocity increase from the indirect OKN component at higher drum velocities is not considered in this report.

Gaze-Holding Phase after OKN

With the present work, we intended also to observe the influence of velocity storage on eye movements after the change from a moving to a stationary stimulus (corresponding to fixation suppression). The velocity changes of the present decay were between the results for the increasing velocities and clearly not lower than the increase in velocity in the data from our laboratory (Figure 5). As a necessary prerequisite for any statement on velocity storage impact on
non-nystagmic eye movements, we found that after a long lasting apparent movement OKN, the afternystagmus in darkness was well developed. This is in accordance with earlier reports (22,24,37). Therefore, we could be sure that the velocity storage mechanism was maximally 'loaded' when the animals were suddenly faced with the stationary pattern. The 'loaded' storage mechanism should be able to continue moving the eyes in the direction of the previous OKN. However, other mechanisms had to be considered: (1) Frictional forces could facilitate the velocity decay compared to acceleration. (2) After the stationary pattern became visible and before the eye velocity reached zero, the retinal slip changed to the opposite direction. Its velocity activated the contralateral pathways from retina and nucleus of the optic tract [38-40] and could actively decelerate the eye until zero velocity was reached.

Thus, during OKN termination, two neuronal mechanisms, velocity storage and retinal slip velocity, seem to counteract. The onset-velocity increase stems from the direct OKN component and retinal slip velocity, but is not influenced by the velocity-storage mechanism. Thus, from similar slopes of OKN onset and offset in our results, it is clear that there is no impact of the fully loaded velocity storage on the slope of the velocity decay. One might consider 'discharging' of the loaded storage mechanisms to explain the missing effect on the velocity decay. However, this disfacilitation seems not fast enough (18) to explain the missing impact that occurs at the shortest latency after OKN interruption. Instead, this fast interruption of any storage impact on eye movements could indicate that, in squirrel monkeys, a third mechanism controls the velocity storage impact on eye movements. Because of corresponding latencies, the pursuit system and the ipsilateral flocculus (Waespe and colleagues [17,41]) could serve this purpose. Only supplying the storage mechanism with a stationary visual pattern over about 6 seconds was sufficient to set its activity to zero. The interval agrees with earlier time measurements of Waespe and Schwarz (18), who determined the duration of OKN effects from the amount of 'dumping' of the OKAN slow phase velocity in EOG recordings. The persisting slow nystagmus beats during the fixation phase after OKN show that the velocity-storage activity is turned down only by about 90%. In the current study, the coil technique enabled us to determine the small nystagmus beats during the fixation period fairly precisely (Figure 6) without relying on the afternystagmus.

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