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Short Communications

Dynamic characteristics of saccadic eye movements in the albino rat

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SUMMARY

Using the magnetic search coil technique it was shown that the rat made saccadic eye movements spontaneously. Most saccades were horizontal. Although their amplitude was usually less than 10 degrees (deg.), the peak velocity could reach 400 deg/s. The peak velocity increased as a linear function of the amplitude at a rate comparable to that in the monkey and higher than in other species. Only a weak correlation between saccade and neck electromyogram (EMG) activity was observed.

The rat is one of the most popular laboratory animals. However, there has been only one report to our knowledge that described voluntary eye movements of the rat in a quantitative manner[10]. This contrasts with a wealth of eye movement studies in the cat[5,7,15], monkey[2,8] and human[1,3,12,17]. Studies using the rat have been concentrated on vestibularly or optokinetically induced eye movements (see ref. 11): the rat makes fast eye movements (quick phase) which reset ocular deviations induced by reflex mechanisms. It is unclear whether and how efficiently the rat makes such fast, saccadic eye movements in a non-reflexive manner to scan its visual environment. In this study we investigated saccadic eye movements of the rat using the magnetic search coil technique[9,11]. This technique allowed us to analyse the rat's eye movements quantitatively.

Six adult male albino rats (Wistar) were used. Under sodium pentobarbital (Nembutal) anesthesia two brass tubes (diameter 3 mm), used for restraining the head, were fixed to the skull by means of dental cement which was anchored by 4 stainless steel screws implanted into the bone. One of the brass tubes was placed in parallel with the interaural line with both its ends open, and the other was directed in the antero-

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posterior direction with its anterior end open; the rest of the tubes were embedded in dental cement. A pair of electrodes for bipolar recording of the electromyogram (EMG) were inserted into the lateral neck muscles on each side. The electrodes were made of teflon-coated multi-stranded stainless steel wires, their tips being exposed by 2 mm. Electrical stimulation through the pair of electrodes evoked horizontal turning of the head to the ipsilateral side. The proper placement of the electrodes was further confirmed anatomically after a series of experiments.

During experiments the rat's head was tightly fixed using 3 metal rods which connected the brass tubes via their open ends to a stereotaxic holding device. The rat's body was suspended using a jacket made of elastic material. Eye position was measured with the magnetic search coil technique[9]. A sensing coil was made of teflon-coated platinum–iridium wire (diameter 25 μm) and had a diameter of 1.4 mm (80 turns). After administration of a local anesthetic (oxybuprocaine) to the eye, the sensing coil was glued directly to the cornea of one eye by means of a drop of adhesive cyanoacrylate, following the method of Hess et al.[11]. At the end of the experiment the coil together with the adhesive was removed after administration of local anesthetic. The animal showed no sign of distress during or after experiments. Calibration of eye position was done before and after each experiment by placing the sensing coil in the same position inside the magnetic field and by rotating it.

Horizontal and vertical eye positions and the right and left neck EMG activities were recorded on a pen-recorder and at the same time stored in an analog data recorder. Eye positions were digitized at a rate of 500 Hz and then differentiated to yield instantaneous eye velocities, using a computer system (PDP11/73). Saccadic peak velocity was defined as the maximum of instantaneous eye velocities in the course of a saccade. Saccade duration was defined as the time during which instantaneous eye velocities exceeded 10% of the saccadic peak velocity.

As shown in Fig. 1, the rat was seen to move its eyes once a second or more if it was aroused. Two types of eye movement were observed: fast, saccadic movements and

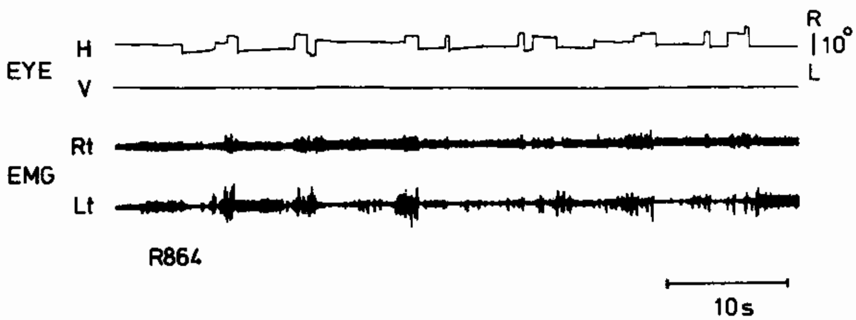

Fig. 1. Eye movements and neck EMGs of a rat (R864). H and V indicate horizontal eye position (up: rightward; down: leftward) and vertical eye position (up: downward; down: upward), respectively. Rt and Lt indicate EMGs of the neck muscles on the right and left sides, respectively. These records were obtained when the rat was moving its eyes actively and voluntarily.

inter-saccadic slow drifts. The inter-saccadic drift was usually directed to a central position in the orbit (primary position). The rate of the drift varied between different animals; the example in Fig. 1 shows one of the slowest drifts. These eye movements were observed either in the light or in the total darkness; however, no attempt was made to eliminate auditory cues.

Direction of saccadic eye movements was largely horizontal; no obvious vertical saccades were seen in rat R864 throughout the recording session. Amplitudes of saccades rarely exceeded 10 degrees (see also Fig. 2). Visual inspection of the optic disc of the other eye indicated that these saccades were conjugate, although the presence of disjunctive or monocular saccades cannot be excluded. In many cases the eye was unstable at the end of saccade; it sometimes swung back and, after a transient slow drift, assumed a steady position. Although neck EMGs showed phasic and tonic changes, they were not necessarily coupled with saccadic eye movements.

Fig. 2 shows the relationships between saccade parameters obtained from 2 rats. Rat R864 was the one which made large saccades most frequently among 6 rats studied;

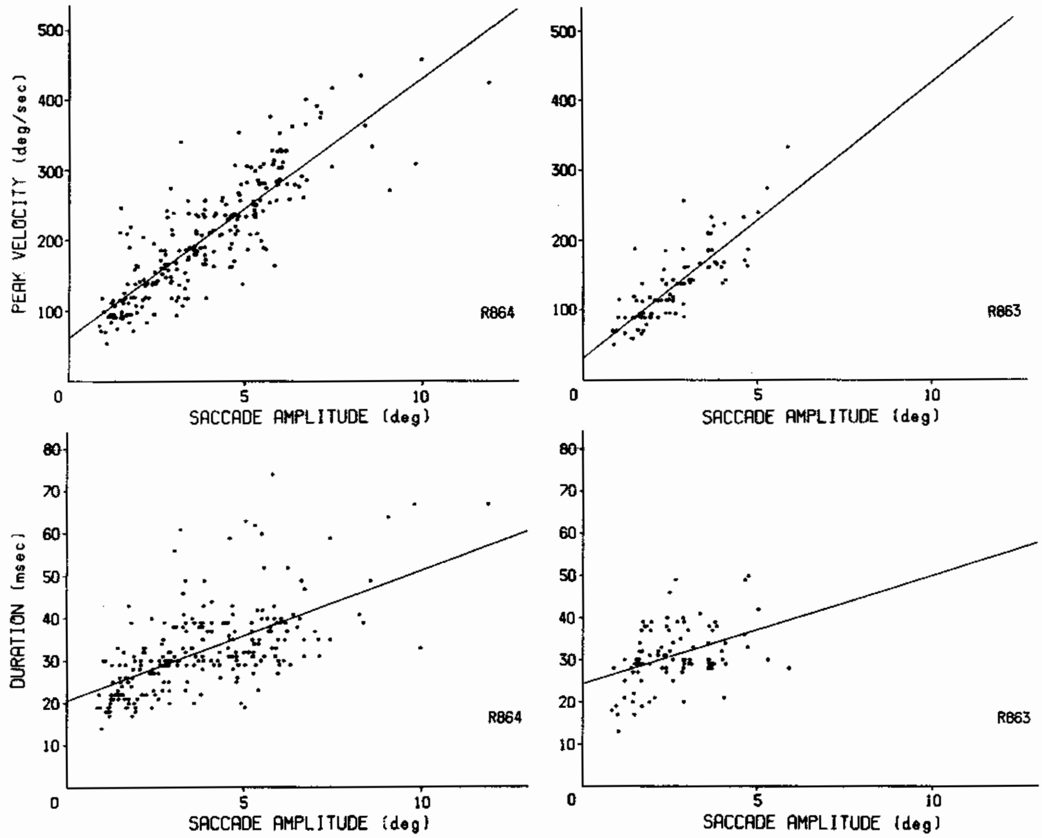

Fig. 2. Relationships between saccade parameters in two rats (R864, R863). Top: peak velocity vs amplitude. The straight line indicates the linear regression line for each rat. Correlation coefficients were 0.85 (R864) and 0.82 (R863). Bottom: duration vs amplitude. Correlation coefficients were 0.60 (R864) and 0.40 (R863).

however, only 2 saccades among 253 exceeded 10 degrees in amplitude. Mean saccade amplitudes for rats R864 and R863 were 3.8 and 2.6 degrees, respectively. In spite of individual differences in oculomotor working range, the relationships between saccade parameters were similar. Saccadic peak velocity increased almost linearly with saccade amplitude (Fig. 2, top). Linear regression lines were similar: $y = 37.2x + 61.9$ (R864); $y = 39.6x + 31.1$ (R863). Saccade duration also increased with amplitude (Fig. 2, bottom). The relationship was apparently non-linear; duration tended to be saturated for larger saccades, although a number of exceptions were seen. The relationship between peak velocity and duration (not illustrated) showed less significant correlation.

The amplitude of rat saccades was mostly less than 10 degrees. This range was much more limited than seen in other species; man[1,3,12,14,17], monkey[2,8], cat[5,7,15], rabbit[4] or goldfish[6], although the rat might show larger saccades in different situations or if it is trained to do so. Unlike the striking correlation between eye position and neck EMG activity in the cat[16] and the monkey[13], only an inconsistent and weak correlation was seen in the rat. Only eccentric eye positions attained by larger saccades than observed in this study might be accompanied by clear modulation of the neck EMG activity.

In spite of the limited range of rat eye movements, the peak velocity of saccades was fairly high, reaching 400 degrees/s. The peak velocity of 5 degree saccades was 220 degrees/s on the average. This value was considerably higher than in cat (80 degrees/s[7]; 120 degrees/s[5]), was slightly higher than in man (180 degrees/s[1,3]) and goldfish (150 degrees/s[6]), but was lower than in monkey (330 degrees/s[8]).

Like other species the peak velocity of rat saccades increased as a function of their amplitude. The function was roughly linear. In the rat the slope of this function (37–40 degrees/s per degree) was similar to the monkey (40 degrees/s per degree[8]), but was higher than other species; cat (10 degrees/s per degree[7]), man (20 degrees/s per degree[3]), rabbit (13 degrees/s per degree[4]), or goldfish (21 degrees/s per degree[6]). The saturation of peak velocity for large saccades seen in monkey[8] and man[1,3] was not observed for rat saccades, possibly because of the limited range of saccade amplitude.

The increase in the duration of rat saccades with their amplitude was not linear: it showed an inflection around 2 degrees and the slope was lower for the larger amplitude range. A similar inflection has been noted for cat saccades[7].

These results were qualitatively similar but quantitatively dissimilar to those reported by Fuller[10]: the largest voluntary saccade was 17 degrees, its peak velocity being about 360 degrees/s; the slope of the velocity–amplitude relationship was 20 degrees/s per degree. The difference might be explained by the species difference: Fuller used pigmented rats while we used albino rats. Alternatively, it might be accounted for by methodological differences. Fuller used the electro-oculogram for eye movement measurements, which would have rendered the calibration only tentative. We attached a coil directly on the eye. This procedure was certainly artificial, but would not account for the difference in eye movement data because it would have decelerated, not accelerated, saccades.

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