Basic Neuroscience

A new, behaving, head restrained, eye movement-controlled feline model for chronic visual electrophysiological recordings

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HIGHLIGHTS

- A new model for chronic visual electrophysiological recordings in behaving cat.
- A novel body position for recording (suspension).
- Rigorous control to avoid the confounding effects of eye movements.
- Stable recording for over two years.

ARTICLE INFO

ABSTRACT

Background: Anesthetized, paralyzed domestic cats are often used as model organisms in visual neurophysiology. However, in the last few decades, behaving animal models have gathered ground in neurophysiology, due to their advantages over anesthetized, paralyzed models.
New Method: In the present study a new, behaving, awake feline model is described, which is suitable for chronic visual electrophysiological recordings. Two trained, head-fixed cats were suspended in a canvas harness in a specially designed stand. The animals had been trained to fixate the center of a monitor during static and dynamic visual stimulation. Eye movements were monitored with implanted scleral coil in a magnetic field. Cell-level activity was recorded with eight electrodes implanted in the caudate nucleus.
Results: Our two trained cats could maintain accurate fixation, even during optic flow stimulation, in an acceptance window of ±2.5° and ±1.5°, respectively. The model has yielded accurate recordings for over two years.
Comparison with Existing Method(s): To our knowledge, this is the first awake, behaving feline model with rigorous eye movement control for chronic, cell-level visual electrophysiological recordings, which has actually proven to work during a longer period.
Conclusions: The new model is optimal for chronic visual electrophysiological recordings in the awake, behaving domestic cat.

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1. Introduction

The domestic cat is a classical mammalian model organism in visual neurophysiology and neuroanatomy. Several high-impact discoveries have been based on the feline model, of which the most well-known may be those of the Nobel laureates Hubel and Wiesel (1961, 1962). In the last few decades, animal research has seen a clear tendency toward the use of awake, behaving animals, instead of the previously used anesthetized, paralyzed models.

In visual electrophysiology the anesthetized, paralyzed feline model was optimal for the analysis of visual receptive field properties of single neurons, as the confounding effect of eye movements was eliminated by the paralysis. However, the exclusion of the effects of the eye movements in awake, behaving experiments is not less necessary, as several visually active structures (e.g. the superior colliculus or the basal ganglia) show saccadic responses too (Hikosaka et al., 2000; Munoz and Fecteau, 2002). This necessitates

a continuous monitoring of eye movements. For this purpose, implantation of scleral magnetic search coils was introduced (Fuchs and Robinson, 1966; Judge et al., 1980; Robinson, 1963). The model was developed for primate models, but it was successfully adapted to cats too. Awake, behaving animal models have two major advantages over anaesthetized ones: first, significantly fewer animals are required. Second, this way, the modulatory effects of anesthetics can be excluded. Such a modulatory effect was clearly demonstrated in the superior colliculus, a multisensory midbrain structure of the mammalian brain, where the large enhanced multisensory responses, which were described in anesthetized animals (Stein, 1998), could never be recorded from awake, behaving cats (Populin and Yin, 2002). Furthermore, different anesthetics have different effects on the visual sensitivity of the brain, which undermines the comparability of the results (Villeneuve and Casanova, 2003). Behaving animal models are often used in primate experiments, but they have rarely been utilized in cats, due to technical difficulties. In visual electrophysiology, only a few research groups are known that have performed visual experiments on eye-movement controlled, behaving cats. Pigarev and his colleagues investigated the visual cortical areas (Pigarev and Levichkina, 2011; Pigarev and Rodionova, 1998). Populin and Yin performed mainly auditory and auditory-visual experiments on the superior and inferior colliculi (Populin and Yin, 1998, 2002; Tollin et al., 2005). Huxlin and Pasternak (2004) investigated the training-induced recovery of visual motion perception after extrastriate cortical damage in adult cats. In each case, the head of the animal was fixed and its body was put either in a box or on a trolley, which could move along a 3-m long railway or in a canvas bag on a platform.

In our laboratory we investigate the sensory properties of the basal ganglia and the connected ascending tectofugal visual system. We have hitherto performed our experiments on anaesthetized and paralyzed cats (Gombkoto et al., 2013; Nagy et al., 2006, 2008). Our main goal was to introduce a feline model, which would be suitable for chronic visual and multisensory electrophysiological recordings in the awake, behaving cat. Here we present the entire experimental setup and demonstrate how eye-movements were monitored and controlled for. The applicability of the new model is demonstrated through recordings of neuronal responses from the caudate nucleus.

2. Materials and methods

Experiments were performed on one male (3.5 kg) and one female (2.5 kg) adult domestic cats. All experimental procedures were carried out to minimize the number and the discomfort of the animals involved, and followed the European Communities Council Directive of 24 November 1986 (86 609 EEC) and the National Institutes of Health guidelines for the care and use of animals for experimental procedures. The experimental protocol was accepted and approved by the Ethics Committee for Animal Research of the University of Szeged.

### 2.1. Animal preparation and surgery

The animals were initially anesthetized with ketamine hydrochloride (Calypsol (Gedeon Richter®), 30 mg/kg i.m). To reduce salivation and bronchial secretion, a subcutaneous injection of 0.2 ml 0.1% atropine sulphate was administered preoperatively. A cannula was inserted in the femoral vein and after intubation of the trachea the animals were placed in a stereotaxic headholder. All wounds and pressure points were treated regularly with local anesthetic (1%, procaine hydrochloride). Throughout the surgery, the anesthesia was maintained with 1.5% halothane in a 2:1 mixture of N_2O and oxygen. The depth of anesthesia was monitored

by continuously checking the end-tidal halothane concentration and heart rate (electrocardiogram). The minimum alveolar anesthetic concentration (MAC) values calculated from the end-tidal halothane readings were kept in the range recommended by Villeneuve and Casanova (2003). The end-tidal halothane concentration, MAC values and the peak expired CO_2 concentrations were monitored with a capnometer (Capnomac Ultima, Datex-Ohmeda, ICN). The O_2 saturation of the capillary blood was monitored by pulse oxymetry. The peak expired CO_2 concentration was kept within the range 3.8–4.2% by adjustment of the respiratory rate or volume. The body temperature of the animal was maintained at 37 °C by a computer-controlled, warm-water heating blanket. Craniotomy was performed with a dental drill to allow a vertical approach to the target structures. The dura mater was preserved, and the skull hole was covered with a 4% solution of 38 °C agar dissolved in Ringer's solution. Then a reclosable plastic recording chamber (20 mm in diameter) was installed on the skull. Following this, the eight electrodes were implanted in the brain with the help of an adjustable microdrive system (a modified Harper-McGinty microdrive for the first animal, see McKown and Schadt (2006), and a modified Korshunov microdrive for the second animal, see Korshunov (1995)). The implanted chamber and microdriver system allowed a stable recording background for long-time (at least two years in the first cat). In order to monitor the eye movements of the animals, a scleral search coil was implanted into the eye. Although this method was originally developed for primates (Fuchs and Robinson, 1966; Judge et al., 1980; Robinson, 1963), **it was later adapted to cats, too** (Huxlin and Pasternak, 2004; Pigarev and Levichkina, 2011; Pigarev and Rodionova, 1998; Populin and Yin, 1998, 2002; Tollin et al., 2005). Additionally, a stainless steel headholder was cemented to the skull for head fixation purposes.

Surgical procedures were carried out under aseptic conditions. Before the surgical procedure, a preventive dose of antibiotic was given (1000 mg ceftriaxon, i.m., Rocephin 500 mg (Roche®)). The first five postoperative days 50 mg/kg antibiotic was provided intramuscularly. Nalbuphin and non-steroidal anti-inflammatory drugs were administered until the seventh postoperative day.

2.2. Behavioral training of the animals

The experimental animals were selected with distinguished care, in a one-year process, during which the animals were adapted to the laboratory environment and their temper was also observed. It was only after this selection and training process that the insertion of the recording electrodes took place. Water deprivation was not used. Cooperative behavior and adaptation to the laboratory environment was formed by a feeding routine. Independently of behavioral training or recording, the animals received food only in the laboratory (150–250 g/day). During the weekends, the animals had access to food in their cage ad libitum, without any weight control. Once the cat got accustomed to the laboratory environment, it was carefully clothed into the canvas harness. This harness leaves the head, tail and legs free. Initially, the cat spent only a few minutes in the harness, which was extended to two hours. It was also during this period that we gradually shifted to pulpy food provided trough a plastic tube. The next step in training, which is a novelty of our model, was the suspension of the animal. Cats, by nature, like to lie in a hammock; therefore, it is relatively easy to get them accustomed to the canvas harness in a suspended position. In this specific case, it was done as follows: First, we lifted the animal manually only a few centimeters from the floor in the canvas harness, while it was being fed. When the animal got used to being suspended this way, it was gradually introduced to the experimental stand (Fig. 1). The experimental stand is a cubical structure with each side open, in which the suspension harness is fastened at two points in by a rope pulley block. Before the implantation of the electrodes, it
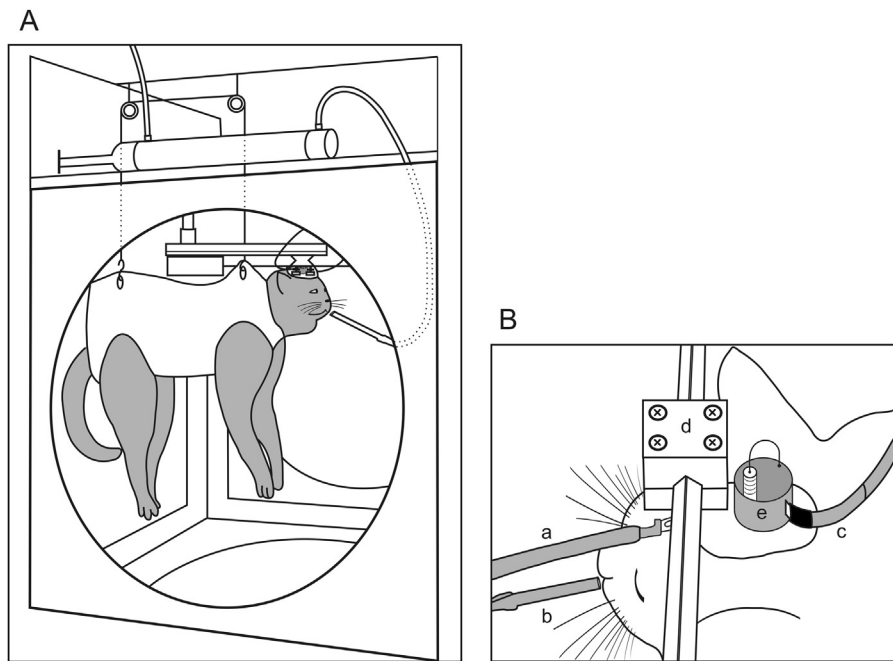
Fig. 1. Schematic drawing of the experimental setup. (A) the suspended cat in the canvas harness in the experimental stand. The head of the suspended cat is restrained in the stereotaxic frame. The cat is inside an electromagnetic field, generated by metal coils, installed in the four walls of the stand. Above (outside the magnetic field) is a hydraulic pump, which doses the food reward. (B) The schematic drawing of the head of the cat with the accessories for chronic recordings. The head of the cat is restrained via the implanted steel headholder (d) with two stainless steel bars, which are attached to the stereotaxic frame. The recording chamber with adjustable microdrive, which moves the eight recording wire-electrodes (e) and the recording cable with preamplifier (c) are placed behind the headholder. On the other side of the headholder, the adapter of the eye movements recording cable (a) can be seen. The cat receives the food reward through a plastic tube (b).

took approximately three months to adapt the cat to these circumstances. In the following step, the head of the suspended cat was fixed to the stereotaxic frame by the implanted steel headholder with two stainless steel bars (see Fig. 1B). In this paradigm, the stereotaxic device is placed within an electromagnetic field, which is generated by metal coils, installed into the wall of the stand. Once in the stereotaxic device, the animals were fed only with pulpy food (now as reward for successful trials, see below) through a plastic tube, dosed by a computer-driven hydraulic pump installed outside the magnetic field.

Having established the physical circumstances, the animals had to be taught the behavioral paradigm. A standard 17- inch CRT monitor (at 80 Hz refresh rate) was placed in front of the animal, at a distance of 57 cm. The initial part of behavioral training concentrates on fixation. The fixation point is projected on the center of the CRT monitor within an acceptance window of changeable size. The size of the fixation point is constant, 0.8° in diameter. If the cat holds fixation for a pre-set duration within the acceptance window, it receives food reward. During the fixation training, the fixation time was gradually increased from 100 ms to 1500 ms. Square fixation windows were used. The size of the initial fixation window was ±10° for both cats. During the training period, it was reduced to ±2.5° in ±2.5° steps, which took two months. This was the final size of the fixation window in the case of the first cat, but with the second animal we could further reduce the window to ±1.5° by three extra weeks of fixation training. After the fixation training, either random dot kinematogram (static) or optic flow (dynamic) stimuli were applied, while the animal maintained fixation. The size of the dots was 0.1° in diameter and their speed increased 0–7°/s toward the periphery. A trial consisted of the following stages: the cat first fixated on a central green fixation point ("Fixation"). During fixation, static random dots appeared in the visual field ("Random stationary dots") for 200 ms. After 200 ms, the static dots started moving radially as an optic flow for 1000 ms ("Optic flow"). A trial was considered successful if the cat managed

to fixate during all phases of the trial. After each successful trial, the animal received reward. To minimize the influence of eye movements on neuronal activity, the trial was aborted immediately if the animal broke fixation. In such cases, no reward was given either. The intertrial interval was between 5000 and 10000 ms. Recording sessions began when the cats reached a stable 80% efficiency at the task.

Both the aforementioned training phases and the recordings took place in a dark laboratory room. Sessions (either training or recording) lasted 1–2 h a day, four to five times a week. The weight of the animals was checked regularly and was kept at least 90% of the initial value. The survival time of the implanted and trained cat appears to be long. In the first cat, the recordings have been going on for 2.5 years, while in the second cat, recordings began 3 months ago.

2.3. Recording and data analysis

Extracellular multielectrode recordings were made with eight implanted nichrome or platinum-iridium wire-electrodes (25 μm and 20 μm respectively, in formal insulation) in the caudate nucleus (CN). The implantation of the electrodes was made according to the Horsley–Clarke system (anterior 12–14 mm, lateral 5–6.5 mm at stereotaxic depths between 9 and 13.5 mm). Amplified neuronal activities were recorded without online filtering, at 20 kHz sampling rate. The signals were band-pass filtered offline (300–3000 Hz) to analyze multiunit activity in detail. Multiunit activity recorded by each electrode was first processed by Neuro-Scope, NDManager, KlustaKwik and then broken down into single unit signals by the use of Klusters (Harris et al., 2000; Hazan et al., 2006) under manual control. All statistical analyses were performed in Matlab® (MathWorks Inc., Natick, MA). Low frequency activities under 300 Hz (local field potentials) were also investigated.
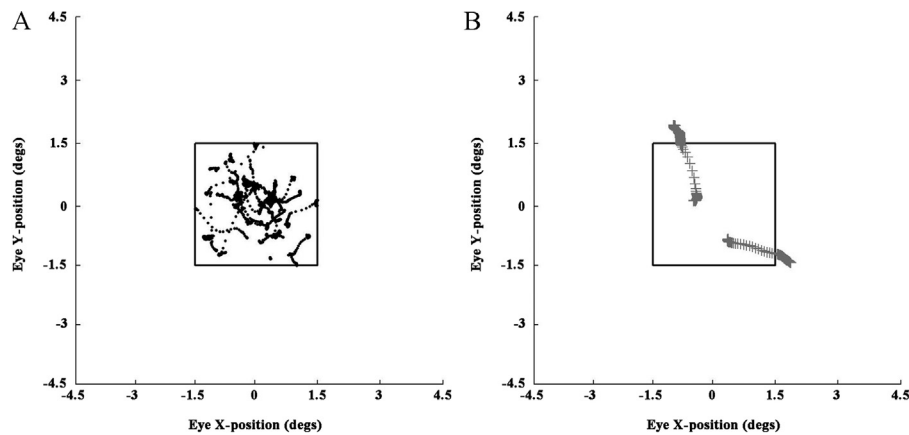
Fig. 2. Eye movement control during the experiments. (A) shows successful fixation as described in Section 2. (B) depicts failed fixation. During all phases of the task the cat was to maintain the fixation on a stationary fixation point, which was centered to the middle of the CRT monitor ($0°, 0°$). The black squares denote the fixation acceptance window ($\pm1.5°$). Each black dot and each gray cross shows a particular position of the eye during recording. Abscissa and ordinate denote the horizontal and vertical positions of the eye in degrees, respectively.

Eye movements were recorded via a search coil system (DNI Instruments, Newark, DE, USA) with a sampling rate of 1000 Hz, and these were also processed by Matlab®. The experiment was controlled by a custom-made software, including eye movement-recording, stimulus presentation, reward delivery and data collection via National Instruments DAQ®. The stimuli were generated by the Psychophysics Toolbox of Matlab®.

3. Results

In the present study we suggest a new chronic animal model, which is suitable for electrophysiological recordings from visual brain structures. The most straightforward points of the model are the daily at least two hours recording time, the several years recording period, the continuous eye control and the restrained head of the suspended animal during the experiments, which makes this model ideal for classic visual electrophysiological experiments.

3.1. Control of eye movements

In order to exclude the effect of eye movements on the recordings of neuronal activities the head restrained, cats had to be able to maintain their fixation. The final result of the training is that the head restrained, suspended animals can fixate quite accurately (within a $\pm2.5°$ fixation acceptance window for the first cat, and within a $\pm1.5°$ fixation acceptance window for the second cat), even during dynamic visual stimulation (Fig. 2).

A continuous control of eye movements was an essential part of our experiments. By the eye-tracker method (as described above), it became possible to follow and exactly reconstruct (visualize) the
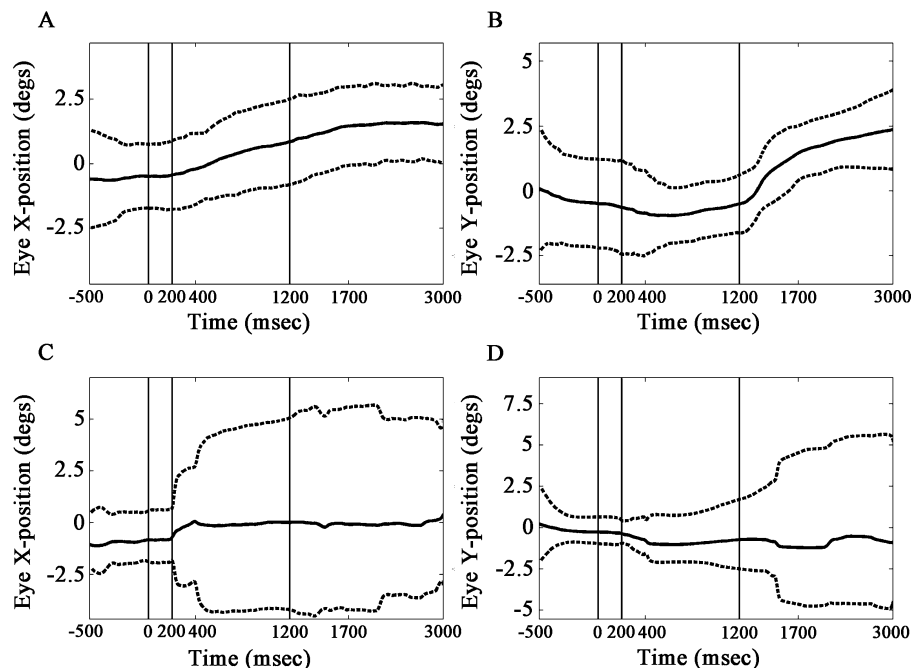
Fig. 3. Eye movements of the cat during the visual fixation paradigm. Top (A) and (B): successful fixation, bottom (C) and (D): failed fixation. (A) and (C) horizontal eye positions. (B) and (D) vertical eye positions (assuming a $\pm2.5°$ acceptance window). The bold black line shows the mean of eye movements, and the dotted lines denote standard deviations. Time is marked on the abscissa, and the ordinates show the horizontal (X) or the vertical (Y) positions of the eye. The vertical black lines separate the different epochs of the paradigm: fixation period (-500 to 0 ms), random static dot stimulation (0 to 200 ms), optic flow (200 to 1200 ms) and reward (1200 to 1700 ms). Fixation failure is demonstrated by the strong and suddenly increasing of the standard deviation in the horizontal plane (C) but not in the vertical one (D).
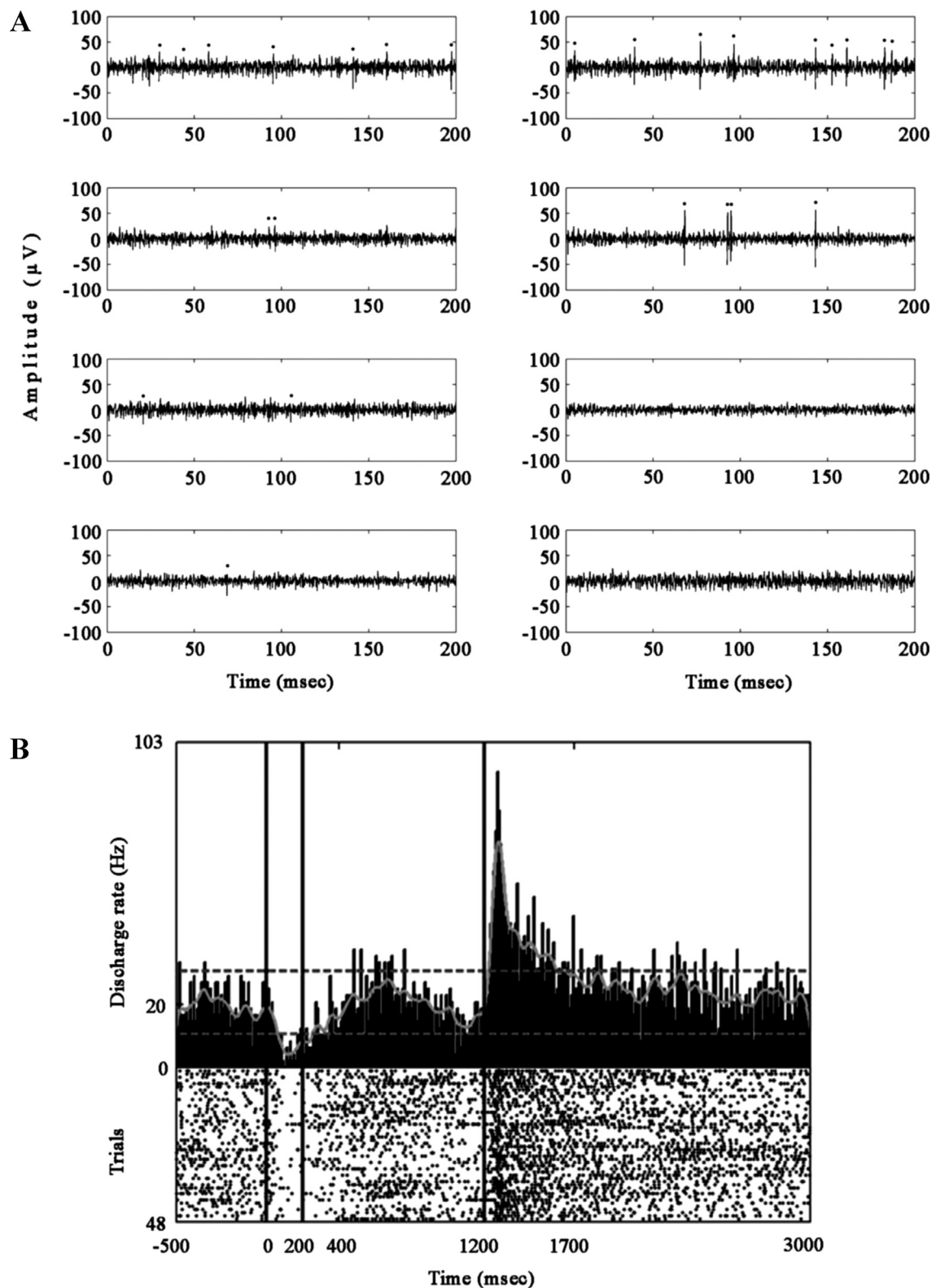
Fig. 4. Visual electrophysiological recordings. (A) shows the band pass filtered (from 300 Hz to 3000 Hz) neuronal activities from the eight electrodes implanted in the caudate nucleus. This recording was performed 433 days after the implantation of the wire-electrodes. The black points above the raw signals denote spikes (single cell activity). The abscissa denotes the time and the ordinate shows the amplitude of the electric signal. (B) depicts the peristimulus time histogram (top) and the raster plot (bottom) of the activity of a particular neuron, the spikes of which are marked on the right uppermost plot of (A). The vertical black lines separate the different epochs of the paradigm. Fixation period (−500 to 0 ms), random static dot stimulation (0 to 200 ms), optic flow (200 to 1200 ms) and reward (1200 to 1700 ms). The cat had to maintain fixation from the appearance of the fixation point (−500 ms) until the disappearance of the optic flow stimulation (1200 ms). Note the decreased activity during random static dots visual stimulation, and then the increased activity upon successful task completion (reward activity). The abscissa denotes time in milliseconds. The ordinate beside the raster plot denotes the number of the successful trials, while the ordinate beside the peristimulus time histogram shows the activity of the neuron (spikes/s, Hz). The continuous gray line is a smoothed curve of the activity, and the dashed gray lines show the ±2 SD of the average discharge rate.

eye movements of the animals. This also enabled us to detect failed fixation, in which cases the trial was rejected (Fig. 3).

3.2. Chronic visual electrophysiological recordings

Local field potentials and band pass filtered (300 Hz to 3000 Hz) neuronal activities from the CN to static as well as to dynamic visual stimulation were recorded and analyzed (Fig. 4).

4. Discussion

In the last few decades, behaving animal models have gradually gathered ground in neurophysiology, due to their advantages over anesthetized, paralyzed models. Behaving animals can be relatively easily used after brief behavioral training for several experimental purposes, but this is unfortunately not the case in visual and multisensory electrophysiological research. In sensory visual electrophysiology, the investigated structures often exhibit also visuomotor activity (e.g. saccades). This makes a continuous monitoring of eye movements indispensable. Furthermore, to minimize the visuomotor modulation of the recordings, teaching of the animal to fixate accurately is also essential. This is a relatively easy task for primates but requires a lengthy training in non-primate mammals.

Behaving feline models have gone through several stages of development. Since the beginning of the second half of the 20th century, mostly anesthetized, paralyzed cats were used in the investigation of the primary visual (striate) cortex, but in the first years some experiments were performed with behaving, unrestrained cats, too (Griffith and Horn, 1963; Hubel, 1959). In the next experiments, behaving cats were placed in a restraining box and they could put out their head through a small hole. The cats were in this position during the experiments. The head- and eye-movements were not controlled (Berkley, 1970; Blake et al., 1974; Franklin et al., 1975). Strecker et al. (1985) used freely moving cats, which were placed in a sound-attenuated behavioral chamber, however, also without eye control. Stryker and Blakemore (1972) took a step further, fixated the body and head of the cat with a canvas bag on a platform, and the eye movements were put under video surveillance. For some time, the scleral magnetic search coils developed for primates were utilized (Fuchs and Robinson, 1966; Judge et al., 1980; Robinson, 1963), but later they were adapted to cats (Huxlin and Pasternak, 2004; Pigarev and Levichkina, 2011; Pigarev and Rodionova, 1998; Populin and Yin, 1998, 2002; Tollin et al., 2005).

In the present study we give a detailed description a new feline model for chronic visual electrophysiology recordings. Our model apparently yields at least two hours recording time per day throughout several years from the same animal, with continuous eye movement control and stable head position. The head was restrained in some earlier used feline models, too (Hubel, 1959; Huxlin and Pasternak, 2004; Pigarev and Levichkina, 2011; Pigarev and Rodionova, 1998; Populin and Yin, 1998, 2002; Tollin et al., 2005), and some form of eye movement control was also present in other studies (e.g. Stryker and Blakemore, 1972), but to our knowledge we have been the first to utilize this whole range of methods at the same time. That is, in our model, the cats have to tolerate a canvas bag around their body, being in a suspended position, head restraint and also a scleral search coil. The suspended position is a further novelty as compared to earlier feline models where the cat was placed either in a box/on a trolley (Pigarev and Levichkina, 2011; Pigarev and Rodionova, 1998) or in a canvas bag on a platform (Huxlin and Pasternak, 2004; Populin and Yin, 1998, 2002; Tollin et al., 2005). It must be added that we experimented with the lying position too, but the animals either tolerated this poorly

for longer periods, or simply fell asleep. We found the suspended position superior both in terms of its tolerability for the animals and handling.

Our fixation training method also proved to be successful. At the end of the training sessions, our first cat was able to keep fixation in a ±2.5°, square acceptance window, while the second one performed even better (±1.5°). This means a more rigorous control of eye movements, and possibly more accurate recordings than in some previous studies. Populin and Yin (1998, 2002) ±7.5° and ±5° square fixation acceptance windows for auditory, and for visual stimulation, respectively. Pigarev and Rodionova (1998) and Pigarev and Levichkina (2011) used a comparable, ±2° square acceptance window. It is true that Huxlin and Pasternak (2004) used a smaller, round fixation acceptance window of a diameter of 1.5°, but gave mainly the summarized and subjective account of the neuronal activities and not recorded the activity of the single cells from trial to trial. Our acceptance window was ±2.5° in the case of the first cat and ±1.5° in the case of the second cat. During these rigorous conditions the cats were able to hold the fixation in these small windows even during the optic flow dynamic visual stimulation. Optimal fixation, laborious behavioral training and the eight implanted wire-electrodes therefore made it possible to record visually evoked signals from the awake feline brain. Recordings in the two cats have been going on for over two years now, and stable signals of good quality are recorded. Thus we propose that the demonstrated model is an optimal behaving model for chronic, cell-level visual electrophysiological recordings.

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