Rabbit and monkey visual cortex: more than a year of recording with up to 64 microelectrodes

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Abstract

In the visual cortex of rabbits and a marmoset monkey, 32 and 64 microwires, respectively, were chronically implanted by an indirect insertion method so that the cortex was penetrated from the white matter. Recording stability was judged by spike shape, spike train autocorrelograms, and spike rates: within recording sessions, stability was essentially perfect. Periods in which the signals of several electrodes were stable could last for several days. A method of in vivo reconstruction of the electrode locations by micro-X-rays and subsequent stereophotogrammetry is presented. The aspect of animal welfare is considered. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Multielectrodes have been applied in a great variety of studies. Their essential benefits (for further details see e.g. Krüger, 1983) are the simultaneity of the recorded signals, the greater recording stability and the economy of animals and time. Our concern is the chronic implantation of multiple microelectrodes, to record from many neurones over prolonged time spans. We have developed this technique to investigate the visual cortex of monkeys by a 'reverse' method (see e.g. Eggermont (1990), 'neuronal recognition': Krüger and Becker (1991)) in which the neuronal excitations are the primary variables from which one attempts to conclude the events in the outer world. Most frequently, this technique is used for recording or stimulation in freely moving animals, or, in special cases, in humans (Adelson et al., 1995; Schmidt et al., 1996; Maynard et al., 1997).

Moveable multielectrodes have been constructed to record in each experimental session from the largest possible number of neurones, or from neurones along a track of the electrode. Most of these types of multielectrodes have been used to study deeper brain structures as, for instance, the hippocampus (McNaughton et al., 1983; Buzsaki et al., 1989).

To observe rarely repeating events like specific neural correlates of behaviour, or complex states of neuronal activity, stable recordings are required. In these cases, mainly fixed multielectrodes have been used. Their implantation into loci at the brain surface were typically performed under direct visual control (Burns et al., 1974; Salcman and Bak, 1976; Schmidt et al., 1976, 1993, 1996; Legendy et al., 1984; Mioche and Singer, 1988, 1989; Palmer, 1990; Adelson et al., 1995; Maynard et al., 1997). Deeper cortical sulci have been approached stereotactically (Chorover and Deluca, 1972; Gassanov and Galashina, 1975; Palmer, 1978; Merzhanova, 1979; Fontani, 1981; Merzhanova and Porada, 1991; Nicolelis et al., 1997). From these studies it is apparent that recordings from electrodes deeply submerged in the brain are generally more stable than those in the surface (recording times up to 30 days versus a few days, respectively). An exception
is the time intensive and costs expensive technique of Schmidt et al. (1976, 1993, 1996), for which each electrode has to be attached individually to the pia mater. Stable recording periods of up to 29 days were reported with these electrodes.

2. Methods

2.1. Animals

Rabbits with body weights of 3–4 kg were obtained from Charles River, Kifstr (Germany). The marmoset was taken from our own colony. Housing and experimentation were authorized by local government license.

2.2. Electrode construction

2.2.1. Rabbit

The technique was developed in eight rabbits. Microelectrodes consisted of 60 mm pieces of Ni-Cr-Al wire (12.5 μm diameter, polyimide insulated; ‘Isalam’, Isabellenhütte Dillenburg, Germany) soldered (silver-tin solder; Number 157, Castolin, Lausanne, Switzerland) to a block (8 × 7 mm) of four rows of eight-pin microconnectors (F. Binder, Neckarsulm, Germany). The 32 wires were then glued together over a length of 40 mm by photographic film carrier material dissolved in dichlorethylene (Merzhanova and Porada, 1991). The ends of the wires were cut 5 mm behind the glued part at an angle so that they formed a primitive kind of tip. Thus, an electrode brush was formed in which the lengths of individual electrodes differed within a range of about 1 mm. The bundle was then inserted into a guiding tube which was a syringe cannula with a 0.5 mm outer diameter.

Electrode impedances measured in saline at 1000 Hz (sine wave) ranged between 2 and 4 MΩ. The same range of values was found in vivo, while a good recording quality was observed. In two rabbits, degradation of the recording quality were observed to be accompanied by increases of the impedances above these limits.

2.2.2. Marmoset (Callithrix jacchus)

The technique was similar except that a 64-fold microelectrode was implanted and a curved instead of a straight cannula was used.

2.3. Implantation technique

2.3.1. Rabbit

In the first operation a headholder, containing a 3 mm thread, was mounted near the spina nasalis un-
2.3.2. Marmoset
The procedure differed insofar as instead of the microdrive for guiding tube and electrode bundle (Fig. 1) a device rotating around an axis was used and the curved cannula was adjusted so that it advanced exactly on a circular path. To fix the microplug, the extremely thin skull bone required the use of finer bone screws (0.9 × 3 mm; Elekta, Umkirch Germany). No headholder was used for this animal. Fig. 2 shows an overview microradiograph at low magnification (Feinfocus GmbH Garbsen Germany). From the known retinotopy we conclude that the electrodes capture signals about 3° horizontally off the fovea. Since the accuracy requirement of the procedure is only to bring the electrode tips to a site that is 1 mm distant from the ‘skull pointer’ touching the skull bone occipitally, there cannot be any doubt on whether the electrodes are located in V1 since there is no other neuronal tissue near that locus.

2.4. Recording

2.4.1. Rabbits
After about 10 days of recovery following implantation, the first recordings were taken. The animals were restrained in a box where the head movements were reduced by a plexiglas collar. Head movements were further restricted by a magnet attaching the head via the headholder to a frame. In cases of excessive movements the magnet detached from its counterpart to avoid the implanted headholder from breaking off. A small 32-channel preamplifier was directly mounted on the microplug on the animal’s head. Signals were further amplified and filtered between 500 and 10,000 Hz. Spikes were hand-triggered under oscilloscopic inspection and the resulting impulses were sampled by a computer. A window-discriminating system allowed us to segregate spikes of different amplitudes. On a separate storage oscilloscope the triggered spikes of each channel were superimposed and then printed or photographed. Their positive and negative peak coordinates were measured by hand-movable pointers. The rabbits were visually stimulated by moving bars and gratings in four orientations (visual angle of the stimulated field: 100°).

2.4.2. Marmoset
The animal was not trained to maintain a stable gaze direction, so receptive field locations could not be determined. A restraining box was used, and the head was fixed by a pair of padded clamps gently pressing the head from both sides. The 64-channels were recorded sequentially in two sets of 32. The unfiltered raw data were recorded and stored via an analog-digital converter at 12 kHz/channel (National Instruments, Austin, TX). Although for high-quality spike sorting a higher sampling frequency would be desirable, the results presented here are not affected by this limitation.
Fig. 2. In vivo low-power radiomicrograph of a marmoset head with 64 implanted microelectrodes. The black mass at top is acrylic cement containing the microplug. Below is the curved cannula and at its end the brush of electrode wires. The wire ends are located in the occipital cortex in V1. The corresponding visual field representation is about 3° horizontally off the projection of the foveal centre. The 64 electrode tips fan out into a cortical surface of 1 mm.

Spikes were extracted after digital filtering above 300 Hz, by a simple flexible spike-template match which, however, was not able to sort the spikes. The marmoset was stimulated by moving gratings in four orientations within a visual angle of about 60°, but we also relied on image shifts induced by saccadic eye movements. The latter were measured by a video-based eyetracking system (M. Fahle, M. Repnow, Tübingen).

2.5. Histology

The brains of three successfully implanted rabbits were histologically examined. The rabbits were killed with an overdose of nembutal and transcardially perfused with phosphate-buffered saline and thereafter with 5% formaline. After extraction of the electrodes and the carrier cannula the brain was removed, soaked in 30% sucrose in phosphate-buffered saline and sectioned sagittally at 30 µm thickness on a cryotome. Sections were stained with cresyl violet or immunohistochemical for glial fibrillary acid protein (GFAP), a marker for astrocytes.

2.6. In vivo reconstruction of electrode positions

Since we intend to evaluate the data recorded while the implanted electrodes are still functional the positions of the electrodes in the brain are determined by X-ray microradiography (Fa. Medixtec, Wendelstein, Germany). Two such micrographs taken in different directions are analysed by stereophotogrammetry (Zeiss P3; Section of landscape information systems, University of Freiburg). So far, a complete reconstruction of an electrode brush has been achieved post mortem in a rabbit brain. To identify each electrode individually a number of 50–400 µm pieces of Pt-wire (10 µm diameter) were glued by epoxy at variable distances from the tip of each electrode. Before implantation for each electrode the characteristic distribution of Pt pieces was determined under a microscope, and the correspondence to the individual microplug in the connector matrix was established. Fig. 3a shows one of the two microradiographs used for that purpose. The outcome is a computerized 3D picture which in Fig. 3b has been rotated relative to Fig. 3a. Radiographic markers on the skull together with the knowledge of the quality of the neuronal signal are necessary to determine the cortical layers. For example, if flat oscilloscope traces are observed for an ensemble of electrodes whose tips are located beyond a certain plane parallel to the bone this indicates that the corresponding electrodes are in the white matter.
3. Results

The implantation technique was developed in eight rabbits. In three of the animals and later in one marmoset we obtained satisfactory long-term recordings. A loosening of the acrylic cement construction on the skull was never observed. The surrounding skin was dry and there were no signs of irritation.

3.1. Recording performance

In the rabbits the amplitudes of the recorded spikes ranged from 50 to 400 μV, with the noise level being around 25 μV. On average, one to four out of 32 electrodes were not functional for technical reasons. On 14–22 of the remaining electrodes we obtained spikes discriminable from noise. Usually spikes from several units were superimposed (multi-unit activity). We de-
duced from the absence of spike counts in the first two bins of the autocorrelation function (bin width 0.5 ms) that the fraction of recorded single units was about 20% in all three rabbits.

In the marmoset there were 60 technically intact electrodes. We had noted in all animals that the recording quality generally increased during the first few weeks after implantation, which we interpret to result from a waning of edema elicited by the implantation. In the marmoset this improvement lasted for half a year. At the time of this report, one and a half years after implantation, 54 electrodes yielded discriminable spikes. The overall recording performance, and the range of spike sizes (Fig. 4) was about the same as in the rabbits.

We found that in the untrained marmoset responses to large field (on-off or moving texture) stimuli were unreliable. Much clearer responses, obtained in nearly all neurones, were evoked by saccadic eye movements while the animal freely inspected the laboratory environment. Fig. 5 shows the post-saccade time histograms for 32 of the electrodes.
3.2. Stability of the recorded signals

3.2.1. Rabbits

Fig. 6 yields a general impression of the stability of the neuronal activity recorded on all microelectrodes. The parameter depicted is what we term the ‘quality’ of the recorded signal (for details see the figure legend for Fig. 6). Each column of rectangles stands for a recording day. The darkest symbols signify the highest quality. Longer recording pauses occurred at the white vertical columns.

Our device does not correspond to the idea of the ‘floating electrode’: the electrodes and the cannula are firmly linked to the skull bone. With such a system one should expect that in cases of a larger displacement of the brain tissue all the electrode signals should change at the same time. It is noteworthy that this was not generally observed, although there were instances where the recording quality changed at the majority but not at all of the electrodes (Fig. 6; arrow). As a whole, the time courses of quality changes of any kind did not correlate in a conspicuous way between different electrodes.
However, quality changes were somewhat more frequent during the first 100–150 days. Later, over time spans of 50–100 days no changes were observed on some electrodes. This does not mean that the recorded signals were stable because the spike quality specified here is not a very sensitive parameter. Our tentative interpretations are that movements of individual microelectrodes might be caused by changes of the microcirculation in nearby blood vessels.

To gain more insight into long-term stability, for each electrode we considered the following two spike shape and two spike train parameters. These were:

1. The range of peak amplitudes of the first phase of the spikes. We determined the largest and the smallest amplitudes of the recorded spikes occurring during a session lasting 5 min. This measurement gives a rough estimation to which extent large and small spikes are mixed. The overlap between these ranges from one recording session is a measure of recording stability.

2. The spike shape. We characterized it by a vector whose components were three empirically weighed and normalized parameters: 0.05 times the amplitude of the first phase of the spike in micro-volts...
Fig. 5. Post-saccadic time histograms of spikes recorded by 32 of the 64 electrodes from the marmoset. The depicted durations are 500 ms. The columns of numbers are the electrode labels. Electrode number 28 was defect. Ordinate scales (from baseline to next baseline): electrode numbers 1, 2, 6, 8, 9, 17, 18, 20, 22, 27: 11 spikes/s, remaining electrodes: 22 spikes/s. The animal freely viewed the laboratory environment with its right eye. The left eye was occluded. Responses through the other eye (not shown) were very similar.

Fig. 6. Temporal evolution of recording quality in a rabbit. A black rectangle indicates that a single spike was properly isolated. Dark cross-hatched rectangles stand for multi-unit activity containing large spikes and light-hatched rectangles for multi-unit activity where background noise was included. Light stippling indicates absence of spike activity. The white column across all rows indicates a longer interruption of recording. The time scale is somewhat irregular because recording sessions were not equally spaced in time.
thereby ranging from about 2.5 to 20, the ratio of the amplitudes of the first to the second phase (ranging from about 1 to 2) and ten times the inter-peak-interval in milliseconds (ranging from about 2 to 6). The similarity of the spike shapes from one recording session to the next was assessed by calculating the euclidean distance between the averaged vectors of the largest spike taken from each session.

3. The range from maximal to minimal spike frequency occurring within one session. The frequencies were determined in windows 2 s wide.

4. The spike train autocorrelation histogram. It was calculated for bin widths of 5.5 ms and was normalized by the spike rate. The first 20 bins of each histogram were taken as components of a vector, and euclidean distances between such vectors were used to compare firing characteristics of spike trains.

In principle, these variables might be partially interdependent since particular combinations of variables might be linked to types of neurones. We have examined part of our rabbit data, and did not find significant evidence for this. Although thereby we do not pretend that these interdependencies are absent, at least they are not very pronounced, so that the use of several such variables can be expected to increase the likelihood of detecting recording instabilities.

We first consider individual electrodes. In one third of the cases in which the stability obviously broke down (e.g. Fig. 7A, days 165/172; arrows) all four parameters abruptly changed: the minimal and maximal spike amplitudes (a), rose as well as the spike rate (b), and the similarities of both the spike shapes and the autocorrelograms showed a low value (c). The break can directly be recognized in (d): the autocorrelogram shapes as well as the spike shapes and sizes change abruptly between days 165 and 172 while they are fairly constant before (days 159 and 165) and after this point (days 172, 173 and 207).

If the activity recorded was a multiunit mixture the spike amplitudes often tended to remain within the one-session variance range over periods of a 100 days. In half of all abrupt alterations there was a change in only one or two of the remaining parameters, usually the spike shape or spike frequency. Sometimes also the autocorrelation histogram was affected. An example of rather subtle changes is shown at (*) in Fig. 7A(c); there was a change of the spike shape or, more precisely, the peak-to-peak interval (see Fig. 7A(d); days 207/213). All other parameters, even the autocorrelogram shape, remained unaltered. Yet, it would be difficult to accept that the cells of days 207 and 213 are the same. Otherwise the recordings of this electrode were quite stable, e.g. from days 129 to 144, and from days 172 to 194, corresponding to 15 and 22 days of stable recordings, respectively.

The case of large, well-isolated spikes recorded over very long time intervals is shown in Fig. 7B. The absence of further spikes manifests itself by the shorter bars in Fig. 7B(a) as compared to those in Fig. 7A(a). We observed an abrupt change of the spike amplitude (arrow) but the other parameters remained largely unaltered for 4 months. At the instant of change, either the electrode had suddenly moved to another neurone with similar properties, or the same cell was recorded all the time, and there was a slight motion of the electrode relative to the cell soma. Generally a large spike recorded over an exceptionally long time is likely to originate from a large cell. In such a case indeed one would expect only variations of the spike amplitude if the instability is moderate. Thus, we possibly have recorded for 140 days from the same cell but, however convincing this may be there is no hard proof for our assertion.

The average stable recording period of an individual electrode was most frequently found to be 2–4 days. Out of all electrodes on which neuronal activity was recorded about 40% showed rather stable recording conditions: longer periods of 5–80 days occurred about 4–6 times during the whole recording duration of 500 days.

When multielectrodes are used the obvious question is how stable the entire multichannel stream of data is. For the time span from the beginning to the end of a single recording session the parameters mentioned so far yield convincing evidence that frequently there is excellent stability within a session. For example, autocorrelograms of spike trains are shown in Fig. 8a, for the beginning (a) and (b) for the end of a session lasting 45 min. For each of the 21 electrodes with spike activity the corresponding curves are very similar in (a) and (b). The range of possible dissimilarities between curves can be estimated by comparing the curves of different electrodes.

While multichannel stability within a single recording session is easily demonstrated with the aid of any relevant parameter, a corresponding demonstration across different recording days is not so obvious. To do this, all the above-mentioned parameters have to be taken into account. We have transformed them into similarities from one recording session to the next which was usually a few days later. In Fig. 9 each symbol depicts the four variables for six electrodes. The four rays of each symbol represent the similarity of spike shapes (up), the similarity of the autocorrelograms (right), the overlap of spike rate ranges (down) and of spike amplitude ranges (left). Large symbols signify stability of all variables, one short ray signifies instability of the corresponding variable. In Fig. 9a an early period after the implantation is shown (126 days from days 104 to 230). It can be seen that there is a rather stable period at least for the five upper electrodes between days 136 and 144. In a later period (Fig. 9b)
stability for 10 days at six electrodes (days 367–377) occurs.

3.2.2. Marmoset
We did not find marked differences of recording quality and its evolution in time between marmoset and rabbits. Again, recordings were rather stable within recording sessions lasting 20 min. An impression of the evolution from day to day is obtained by the inspection of printouts of superimposed spikes (Fig. 4): between recordings at successive days (a, b) there were only two electrodes (row/column 2/2 and 3/1) where it was sufficiently clear, by applying gross criteria, that the entire set of superimposed spikes had changed. For further

Fig. 7. Examples of temporal evolution of stability for several months for two electrodes (parts A and B of the figure, respectively; rabbit ik1). (a) Range between maximal and minimal spike amplitudes encountered in a recording session. A larger range indicates a mixture of spikes of different sizes. (b) Range between maximal and minimal spike rates (measured in windows lasting 2 s) encountered within a recording session. (c) In contrast to (a) and (b) similarities are shown here for pairs of successive recording days, namely between spike shape ‘vectors’ (white squares) and autocorrelogram ‘vectors’ (black diamonds). (d) Examples of autocorrelograms (bin width 5.5 ms; top) and printouts of superimposed spikes for selected days.
electrodes only a fraction of the spikes differed; e.g. first row sixth column: only the large spike had disappeared. Of course, upon a closer look some finer, yet significant changes can be seen on some additional channels. Comparing two printouts taken 36 days apart (b, c), again applying gross criteria, there are already six electrodes showing a complete change, and nine others with partial differences.

3.3. Histology

The staining for GFAP, one of the most sensitive indicators of CNS damage, showed an increased diffuse GFAP production in an area of 100–150 μm around microelectrode tracks. In GFAP-stained sections a single microelectrode track appeared as a hole of about 28 μm wide. The outer diameter of the wire insulation was 18
Fig. 8. Spike train autocorrelation histograms for the 21 electrodes showing spike activity in rabbit ik1 at day 293. Bin width: 5.5 ms. Tic-mark distance: 55 ms. (a) Early section of the recording session. (b) Section 30 min later than (a).
μm. In cresyl violet stained tissue the tracks of single electrodes were not detectable. Some tracks could only be identified by comparison of neighbouring sections, the one stained for GFAP and the other by cresyl violet. The neurones near the electrode tips appeared normal.

4. Discussion

In the present communication we have demonstrated that long-term recordings from many neurones in the central nervous system are feasible. We recorded signals for up to 711 days, during which time the recording quality did not degrade. Periods of stability of ensembles of electrodes lasted several days. This is sufficient to study neural processes requiring long-term observations. Topics of this type are plasticity and memory, diseases and drug action and investigation of ensemble coding by an approach like classification and recognition of excitation patterns, i.e. ‘reading in the brain’.

To estimate the stability of the recordings one has to rely on several parameters. If a large, well isolated spike is recorded the most sensitive parameter is the spike amplitude. When the amplitude fluctuations between recording sessions exceed those observed within a session it is likely that another unit is recorded. In contrast, the spike amplitude is an insensitive parameter when multi-unit activity is recorded: its changes may be inconspicuous, while those of the spike shape, the spike frequency and the shape of the autocorrelation histogram may indicate instability.

Stability is difficult to estimate, because, even when only one neurone is recorded, the statistical properties of spike trains, the relationships of the latter to stimuli, or the shapes and sizes of individual spikes may vary due to uncontrolled neural influences and due to minute displacements of the electrode, respectively. On the other hand, if all spike-related characteristics remain constant from one recording session to the next, this does not prove that the signals originate from the same cell: nearby cells may have similar properties. However, in our experience most neurones recorded at the same electrode showed different spike shapes and autocorrelations.

We believe that there were two major reasons for the stability and durability of the recording conditions obtained with our technique. The first is the stereotactic approach ‘from below’: the recording site is minimally disturbed. There is no mechanical stress due to dura and pia mater penetration, blood vessels are minimally destroyed, and no surgical manipulations take place at the recording site. Secondly, the large number of microwires,

![Fig. 9. Star symbol plot to monitor the temporal evolution of stability for six electrodes implanted into rabbit ik1. In this type of plot the four rays represent the described variables. Long rays signify large values. Each symbol refers to a pair of successive recording sessions. The four rays of each star symbol represent the similarities of: spike shape (up), autocorrelogram (right), spike rate (down), range of spike amplitudes (left). Large/small symbols stand for stability/instability of all variables, each short ray signifies instability of the corresponding variable. The variables are the same as those used in Fig. 7. (a) Section lasting 116 days from an early part of the total observation period. (b) Section lasting 180 days from a later part of the total observation period.](image)
each running for 5 mm through the tissue presumably provides a sufficient degree of friction so that locally the tissue is prevented from moving relative to the electrodes. In addition, the need did not arise, as proposed by Schmidt et al. (1993), to improve recording conditions by electrical microstimulation.

A further improvement of recording stability results from a more favourable geometry with respect to tissue destruction. In the marmoset, the 64 electrodes fan out within an area that is about 1 mm$^2$ near the tips. The summed electrode cross-sections occupy only 2% of that area. The value is not much larger 1 mm away from the tips.

In contrast, a single classical metal microelectrode at the same distance from its tip may have a cross-section corresponding to that of 30 of our wires. Thus, using a single electrode to record sequentially from 64 sites within a cubic millimeter would contain a high risk of hitting previously damaged sites, or to record from a neuronal network that is degraded at a short distance from the actual recording site. Also with regard to stability an implanted multielectrode is superior to the classical technique using one movable electrode: with the present technique we rarely observed signs of instability during a recording session lasting 20–45 min and often in the stored records one can select groups of electrodes from which stable signals have been obtained for many days.

Of course the guiding cannula produces a larger defect. However, no visual-field defect was apparent: presenting visual targets in various parts of the visual field we regularly could evoke corresponding turns of the gaze direction. Moreover, the cannula end is located 5 mm off the recording sites so that it is unlikely that the neurones at the defect are directly related to the cortical tissue investigated. The ‘defect per electrode penetration’ is certainly inferior to that caused by the shafts of single electrodes when multiple penetrations into deeper brain structures such as area MT or IT are done.

In comparison to individually movable electrodes the number of well-isolated spikes may be inferior to those obtained by our multielectrode. However, it must be borne in mind that biases may be created if the good isolation of a spike becomes a criterion for studying a neuronal signal: large spikes are more likely to stem from large neurones. Our electrodes are neutral in this respect: the locations of their tips could not be selected according to spike isolation.

Long-term implanted multielectrodes offer several advantages with respect to animal welfare: the time spent by the animals under the experimental conditions is much more efficiently used than in single electrode experiments. Moreover, once the electrodes are implanted the carrying out of the experiments resembles that in which no neuronal recordings at all are taken but only the animal behaviour is examined. To bring the animal to the recording position, and connecting it to the preamplifier takes a minimum of only 5 min. Thereafter, the recording can start. Immediately after the end of the recordings, lasting from 20 min to 1 h in our cases, the animal returns to the cage. While the animal is in the experimental set-up, there is no need for a time consuming search for cells, as is required in experiments with single electrodes or with moveable multielectrodes and there is no need to fixate the head. The extraction of single units can be done after the experiment. Due to the high data output in an 1 h recording session of more than 50 unsorted spike trains, several unrelated studies can be conducted without new damage on the same animal.

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