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SCIENCE

Visual Receptive Fields Sensitive to Absolute and Relative Motion during Tracking

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Visual Receptive Fields Sensitive to Absolute and Relative Motion during Tracking

Abstract. *Some neurons in the visual cortex of awake monkeys visually tracking a moving target showed receptive fields that were excited only by stimulus motion relative to a background, while other neurons responded to any kind of stimulus motion. This result was found with two methods, one in which tracking eye movements were identical in both relative-motion and absolute-motion conditions, and another in which stimulus motions on the retina were identical in both conditions. This response pattern can differentiate translation of the retinal image during eye movement from motion of objects in the world.*

Image motion across the retina does not necessarily provide information about object motion in the world; information about object motion is generated only when one pattern in the optic array moves with respect to another. To detect motion of objects in the world, some cells in the visual system must respond to motion relative to a background (which indicates object motion) rather than to displacement of the entire visual image across the retina (which indicates eye movement). The two conditions were separated by exploring the visual receptive fields (RF's) of single cells in the monkey's visual cortex (*1*, *2*) while the monkey tracked a slowly moving target. In one condition a stimulus was fixed to a screen so that its image scanned the retina during the monkey's slow eye movement; the stimulus moved with respect to the retina but not with respect to the background. In the other condition the stimulus moved with respect to both the retina and the background during identical slow eye movements.

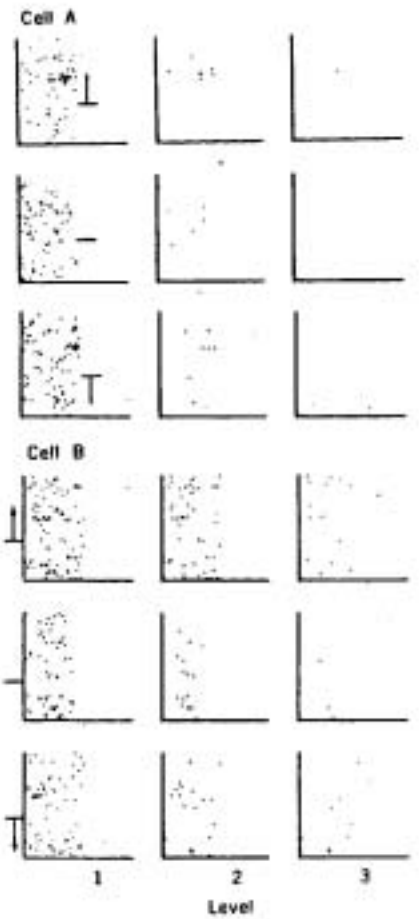

Fig. 1. Two cells with receptive fields responsive only to motion relative to a background. Each row shows a separate map made under visual tracking, and each pair of axes represents the 25° by 25° region of the stimulus screen over which the fixation target could be moved. A map consists of vertical scans separated by 0.5°, beginning at the left. Each scan is divided into 50 segments, each 0.5° (50 msec) long, and a spot is darkened in the display if the cell fired while the fixation target (a 1° disk) crossed the corresponding region of visual space. At levels 2 and 3 a spot is darkened only if the cell fired at least two or three times, respectively. The bar stimuli and their locations in relation to the scanned area are shown in the left column, with the stimuli moving through a 2° by 4° aperture in the directions indicated by the arrows attached to them. Moving bars are depicted in the centers of their apertures. About half of the 25° by 25° stimulus space was mapped in each condition. Receptive fields are apparent when the stimuli are moving but not when they are fixed on the screen. The two cells are from opposite hemispheres of the same monkey. Cell A shows one of the strongest fields found, and cell B one of the weakest. Control maps, with the fixation target moving upward but not tracked, showed only background activity (not illustrated).

Three immature rhesus monkeys were trained to sit in a primate chair and optically track a 1° target moving on a tangent screen. Eye movements were monitored with standard clinical electrooculogram electrodes fixed above and below the orbits, while the eyes were observed with a system based on the Mackworth eye camera (*3*). Because tracking accuracy improves with practice (*4*), each monkey was overtrained for at least 2000 trials before RF exploration began.

For RF determination a 25° by 25° region of the screen was divided conceptually into 2500 blocks, each 0.5° by 0.5° in extent. The fixation target passed through each block in succession, and a point was produced in the display when an action potential occurred. The displays of Fig. 1 are therefore maps of cell firing for corresponding positions of the fixation target on the screen. The target jumped to the edge of the scanned area, moved up and down (or right and left) at 10° sec^{-1}, and jumped back to a hidden origin point. If the monkey followed the downward movement of the target without saccadic eye movements, he was rewarded with apple juice. At any time the experimenter could initiate a new trial 0.5° to the right of the previous one; unsuccessful trials were repeated.

Each RF map was made with two stimuli on the screen, a fixation target and a mapping stimulus. To provide a mapping stimulus that moved relative to the screen, a horizontal bar 0.5° high was moved vertically through a fixed aperture 2° high and 4° wide. As the bar disappeared from one edge of the aperture it was replaced by another on the opposite edge, resulting in a moving display with a contant speed and direction. Light flux at the monkey's eye varied less than 1 percent as one bar replaced another. The aperture was always mounted contralateral to the hemisphere in which the cells investigated were located. With this apparatus, responses were mapped under three conditions of stimulus motion; the bars moved down the screen at 5° sec^{-1}, remained fixed, or moved up at 5° sec^{-1}. When the monkey's eye

scanned down the screen during tracking, the upward velocity of the bars across the retina was increased by 10° sec^{-1}, resulting in retinal stimulus speeds of 5°, 10°, and 15° sec^{-1}, respectively. Thus, absolute motion across the retina was present in all three conditions; but at the second, intermediate, speed there was no stimulus motion relative to the background. The hypothesis that relative motion is necessary for RF excitation predicts that some neurons will respond only under the first and third conditions, while a pure retinal-motion hypothesis predicts responses under all three conditions.

Brightness of the fixation target and the mapping stimulus was 60 lu/m^2 on a screen of 4 lu/m^2, yielding 1.2 log units of contrast. The screen was a finely textured black poster board 57 cm from the monkey's eyes (*2*).

A simple system was developed to record from single cells in awake monkeys (*5*). A tungsten microelectrode was advanced slowly into the lateral striate cortex (area 17), 5° to 10° from the foveal projection. When an action potential of a cell was isolated, the RF was first explored with large hand-held stimuli and was then mapped with the tracking method.

In the first experiment, data were obtained from 34 neurons. Of the 18 that were investigated under both relative-motion and absolute-motion conditions, 39 percent responded only to relative motion (Fig. 1), another 39 percent responded to both absolute and relative motion (Fig. 2), and the remaining 22 percent were unresponsive to any of the stimuli used. The lack of response when the mapping bar was fixed on the background (Fig. 1) was not caused by a threshold of stimulus speed across the retina, because retinal motions both faster and slower than the 10° sec^{-1} of the fixed-stimulus condition elicited clear RF's. [Wurtz (*6*), using a similar recording procedure, found no qualitative difference in response to absolute movements varying from 10° to 40° sec^{-1} during steady fixation.] Responses were not caused by abrupt appearance or disappearance of a stimulus, because this occurred only once every 0.4 second and was not synchronized with scanning. Responses to unsynchronized events would not appear consistently at the same height in the maps.

These results were tested statistically against a null hypothesis of identical responses to the moving bars and to the fixed bar. A chi-square test was significant ($P < .001$), showing that the results were not due to some uncontrolled factor.

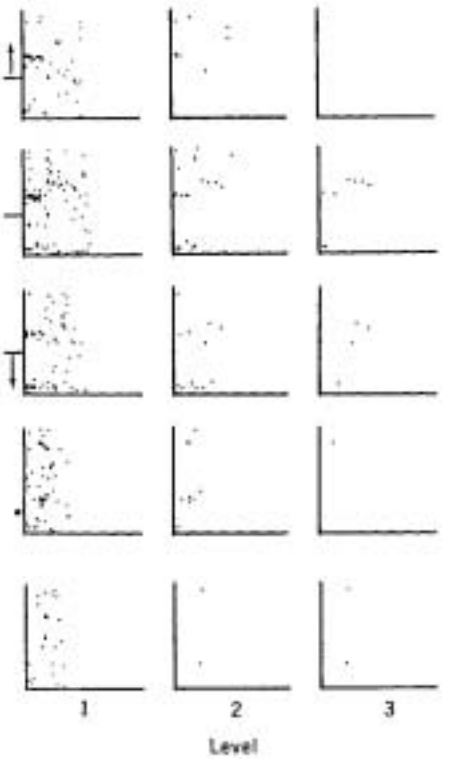

Fig. 2. A cell that responds to any movement of a bar stimulus across the retina. Mapping was done as in Fig. 1. The fourth map from the top (made with a fixed disk 1° in diameter) shows that some of the cells mapped in this experiment had small disk-shaped receptive fields; the bar-shaped response areas result from convolution of the mapping stimulus with the receptive field. The bottom map, a control with a fixation target but no other stimulus, shows no receptive field.

To test the relative-motion hypothesis further, another experiment was performed in which maps made with a fixed stimulus and slow tracking were compared with maps made during anesthesia with the eyes nearly immobile. In the latter condition, the moving spot, instead of being a fixation target, scanned the retina itself. Thus, relative motion was present, but the speed and direction of image motion on the retina was equal to that of the fixed stimulus during tracking. A cell was first examined under the tracking condition, with a peripheral stimulus (a 1° disk) fixed on the screen. The animal was then anesthetized with ketamine hydrochloride, the cell was remapped, and the optic disks were projected onto the screen with an ophthalmoscope to determine retinal position. Some cells showed responses only under anesthesia, when relative motion was present, even when the same mapping stimulus (a 1° disk) scanned the retina in both conditions.

Cells that could not be excited by any stimuli were found in the present experiments with about the same frequency as in a previous study with similar mapping methods (*2*); possible reasons for the inexcitability of these cells was discussed in that report. Inaccuracy of tracking eye movements did not obscure responses, because the presence of small RF's (Fig. 2) showed that the resolution of the mapping technique rather than tracking error was the limiting factor. Inactive cells may have had highly specific trigger properties (*6, 7*); thus, the results may represent a biased sample of motion sensitivities.

The contrast between these results and those of Wurtz (*6*) underscores the differences between slow and rapid eye movements. Wurtz found no differences between responses to stimuli moving at 900° sec^{-1} during steady fixation and responses to fixed stimuli during rapid eye movements. The Wurtz experiment, designed to search for a corollary discharge at the cortical level, is complicated (in a perceptual context) by retinal blur and saccadic suppression. More than two-thirds of the neurons in Wurtz's sample dramatically changed their responses with a transition from slow to rapid stimulus movement, a result suggesting fundamental changes in response properties.

Cells responding preferentially to relative motion have been found before, both in insect visual systems (*8*) and in direction-selective cells of the superior colliculus (*9*). In the latter system, response to movement in the RF center is reduced when a second stimulus in the inhibitory surround moves along with the first; and directional selectivity is lost with the removal of cortical input. Further work is required to define the relations between the cortical and collicular cells.

The presence of two types of cells in about equal numbers, one responding to any stimulus motion and the other only to motion relative to a background, means that information is available at the cortical level for a comparison mechanism that distinguishes eye movement from object movement. Both types of cells are activated by object movement, whereas only the absolute-motion cells respond to eye movement. This response pattern is consistent with Gibson's theory (*10*) that the visual world is stabilized by defining the optic array as a stable world, leaving motion to be perceived as a result of motion of one part of the array with respect to another.

Gibson (*10, 11*) pointed out that the features to which physiologists have found responses in mammalian visual systems—such as disks, lines, and edges moving on homogeneous screens—are highly ambiguous for perception. An edge in the optic array can specify the edge of an object in the environment, but it can also signal a shadow, a change in contour, or many other things. Useful structure in the ambient optic array comes not from differences in brightness, but from stabilities in optical patterns over time and the lawful transformations of these patterns.

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TECHNICAL CONTRIBUTION

A SIMPLE SYSTEM FOR EXTRACELLULAR MICRO-ELECTRODE RECORDING FROM AWAKE ANIMALS

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The increasing importance of experiments investigating single cells in conscious animals calls for a micro-electrode system for semi-restrained animals which permits precise electrode movement yet is inexpensive, reliable and easy to operate. The hydraulic-drive method of Evarts (1966), though precise, is somewhat cumbersome and expensive, requiring three fluid chambers and many specially machined parts. Humphrey's (1970) system, while using a direct drive, similarly requires dozens of small parts, and its screwdriver-controlled electrodes might prove clumsy to operate among recording wires, feeders, etc. The system of Thomas *et al.* (1968) is simpler than the others but shares with them the disadvantages that the electrodes cannot be seen when in place, it does not allow electrodes to be withdrawn under stereotaxic control, and requires a large and heavy implanted head plug on the animal.

To avoid these difficulties a new micro-electrode mounting system was developed. The heart of the system is a micro-drive made from a disposable hospital syringe. A micro-electrode is raised and lowered by the syringe's original piston, driven by a standard machine screw threaded in the end of the syringe. During recording the micro-drive is fixed on a cylinder which has been implanted over the desired brain area (Fig. 1).

The micro-drive connects with a removable plug of dental acrylic, which plugs into the animal's permanent implant and contains connectors for ground and indifferent leads as well as the field-effect transistor (FET) of a source-follower head stage. Wires go to the amplifiers from this plug rather than directly from the micro-manipulator so that the plug rather than the electrode-holding apparatus absorbs mechanical stresses. Location of the FET in the plug makes artifact-free recording easier and minimizes movement artifact: the high-impedance leads are kept short, and when the animal moves the high-impedance part of the circuit moves with him as a unit.

The pitch of the micro-manipulator screw thread determines the sensitivity with which the micro-electrode can be advanced, and is a compromise between fine manipulation at the recording site and quick descent to the site. Standard 40 turn/inch (16 turn/cm) threads advance the electrode 633 μ/turn, allowing easy descent to the recording area while still permitting fine movements of 10–20 μ (6–12°).

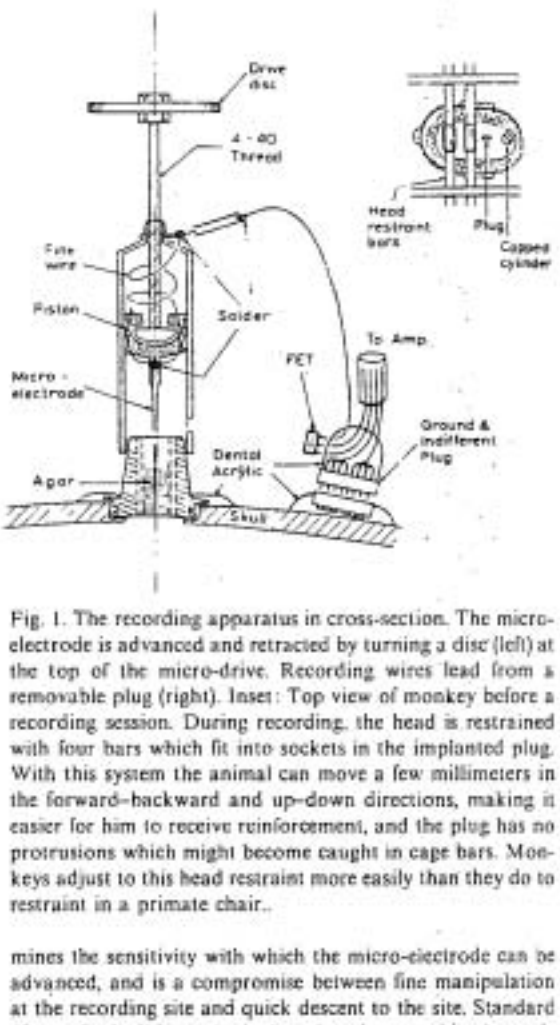

Fig. 1. The recording apparatus in cross-section. The micro-electrode is advanced and retracted by turning a disc (left) at the top of the micro-drive. Recording wires lead from a removable plug (right). Inset: Top view of monkey before a recording session. During recording, the head is restrained with four bars which fit into sockets in the implanted plug. With this system the animal can move a few millimeters in the forward–backward and up–down directions, making it easier for him to receive reinforcement, and the plug has no protrusions which might become caught in cage bars. Monkeys adjust to this head restraint more easily than they do to restraint in a primate chair.

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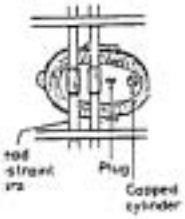
RODE



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The electrode is advanced by turning a small disc mounted at the end of the drive screw.

The micro-drive is easily manufactured from inexpensive parts. The body of a 3 ml "Tomac" polyethylene hospital syringe is cut to 33 mm and its tip to 2 mm in length, and small holes are drilled in the top and near the bottom as air pressure relief ports (Fig. 1, left). A 1.5 inch (3.8 cm) 4–40 thread machine screw is inserted in the syringe tip from the inside, threading itself. When it protrudes from the syringe it is heated by a soldering iron and turned further to form threads. The rubber piston is removed from its plunger and a fine wire (28-gauge tinned copper) is passed through it by piercing it along one side with a 23-gauge hypodermic needle and threading the wire through the needle, which is then removed, leaving the wire secured in place. The wire loops across the end of the piston and is threaded back through its opposite side, about 1 mm being bent parallel to the side where it emerges to prevent it from pulling out. A 2–3 mm length of thin tubing (the female segment of a single "Microdot" "pin-strip" connector) is soldered to the wire beneath the piston to hold the electrode. The other end of the fine wire goes through the upper air relief port and is soldered to a gold-plated wire which has been twisted tightly around the neck of the syringe with 1 cm extending as a connecting pin. The piston is then inserted into the micro-drive and forced over the screw head so that it can move the electrode in either direction. The connector is bent slightly to assure a tight contact. The micro-drive is completed by fastening a small plastic disc on the end of the drive screw.

The micro-drive plugs into a length of 23-gauge hypodermic needle extending on a short wire from the removable part of the head plug (Fig. 1, right). Though only two (ground and indifferent) leads are needed in the plug, a length of eight "pin-strip" connectors is used for greater mechanical strength and electrical reliability. The ground and indifferent leads go through shielded Microdot cable (202–3812) to the amplifiers. An identical parallel cable carries shielded leads from the source and drain of the FET (Motorola 2N3796) whose gate connects to the micro-manipulator jack. The electronic system is identical to that of Spinelli *et al.* (1970), and micro-electrode manufacturing is similar except that after the tip of the tungsten shaft has been etched to about 100 μ in diameter it is sharpened by immersing and etching until bubbling stops, leaving a more steeply tapered tip (Hubel 1957). This electrode combines the toughness of the Hubel electrode with the narrow shaft of the Spinelli method, minimizing tissue disturbance. Though the tip tapers too steeply to record fibers well, it records well from cell bodies and is easy to produce because the final etching step is self-terminating.

After insulating and testing, electrodes of 2–4 MΩ are marked at a length of 24 mm and stripped of insulation for 4 mm below that point. They are cut, inserted in a micro-drive, and fixed in place by tightly crimping the socket about the electrode. An electrode can be adjusted to make a penetration anywhere within the implanted cylinder by moving the socket laterally; the flexible wire holds it in the desired place. After mounting, the electrode tip is extended to the length of the implanted cylinder and the location of the piston marked on the micro-drive wall. Depth calibrations can be made from this mark. Friction between the piston and the syringe wall prevents the piston from rotating as it is raised and lowered. To prevent rotation, a drop of light silicon oil can be applied inside the piston to lubricate its junction with the drive screw.

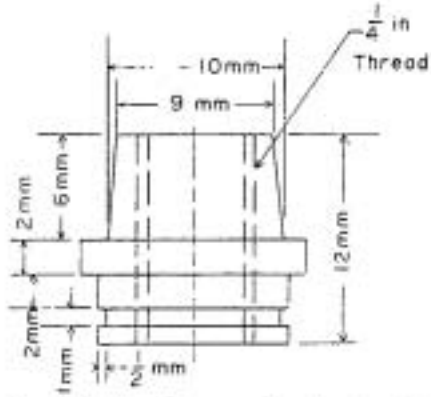

Fig. 2. Details of the mount for the micro-drive. Because of their small size, several cylinders can be implanted simultaneously. The cylinder's tapering sides are roughened to assure a tight fit for the micro-drive.

The micro-drive fits onto an implanted plexiglas cylinder, the only part of the system (except for the micro-electrodes themselves) requiring special machining (Fig. 2). Plexiglas tube is threaded with standard 0.25 inch (6 mm) threads on the inside, then lathe-turned to make a group of cylinders which can be sawed apart. The micro-drive is fixed on the cylinder for recording by its own elasticity, gripping the roughened, tapering sides. The cylinder's taper and its top diameter are the only critical dimensions in the system.

The cylinder and grounding electrodes are implanted surgically under aseptic conditions. Under anesthesia the skull is exposed and all membranes scraped away until the surface is dry. To anchor the implant three small stainless-steel screws are fixed to the skull by making keyhole-shaped openings in the skull, inserting the head of a screw in the large part of an opening and moving the screw until its shaft protrudes from the narrow slot with the screwhead firmly anchored between skull and dura. This method yields a stronger reinforcement than does simple reliance on screw threads in the skull. Ground and indifferent electrodes, soldered to a Microdot connector in advance, are fixed to the implant with the ground lead between the skull and scalp on one side and the indifferent lead in an edge of the hole made for implantation of the plexiglas cylinder. The dura under this hole is cut away so that electrodes can penetrate without damaging either them or the brain tissue. Experiments in cats showed that the dura would grow back to make the preparation unusable in 3–4 weeks, the same interval which Wurtz (1969) obtained without cutting the dura. The cylinder, plug and head restraints (Fig. 1) are fixed in place with dental acrylic. Before the final seal is made around the cylinder, agar is poured into it and allowed to harden, preventing cerebrospinal fluid accumulation after sealing.

The cylinder is protected with a cap made from a nylon screw cut to one turn in length. A notch cut in the threads on one side of the screw lets air escape as the screw is turned into

place; the screwhead forms an airtight seal with the top of the cylinder when firmly secured. A Microdot connector caps the electrode plug.

The agar, which protects the brain and stabilizes the micro-electrode, is replaced every few days to assure clean conditions and stable mechanical properties. Sterile forceps are inserted on the sides of the agar in the cylinder until they nearly reach the bottom of the well, then are rotated gently to bring the old agar out as a block. Sterile agar at 41° C is drawn into a "Tomac" 3 ml syringe, the same type as used for making micro-drives, whose tip is slightly shorter than the cylinder. The tip is inserted in the cylinder and an excess of agar slowly extruded to rinse the well. When the flow stops the syringe is withdrawn, leaving the agar at the proper height in the well for capping. The procedure can be performed in conscious animals without discomfort.

After several months of daily use a micro-drive becomes worn, but it is so inexpensive that it can be discarded and replaced by another. Several micro-drives are fitted with electrodes before each recording session so that a damaged electrode can be quickly replaced. Several cylinders can be implanted successively or simultaneously for maximum experimental flexibility.

With these techniques single cells have been held for more than an hour, and dozens of cells can be recorded over several months without use of drugs.

SUMMARY

An extracellular micro-electrode recording system is described for use in unanesthetized cats or monkeys. The system is simpler than previous ones, can be built from readily available components without specialized tools or any machining of metal, and is so inexpensive that the micro-drive itself is disposable.

The heart of the system is a micro-drive made from a 3 ml disposable hospital syringe, a standard machine screw and a length of fine wire. For recording it plugs onto an agar-filled plexiglas cylinder which is implanted in the experimental animal along with ground and indifferent electrodes and head restraints. Recording wires lead not directly from the micro-drive but from a removable plug which contains sockets for ground and indifferent leads as well as a field-effect transistor head stage for conversion from high to low impedance. The high-impedance leads are kept short, minimizing electrical noise. Ground, indifferent, and transistor leads go together from this plug to the amplifiers.

For maximum experimental flexibility several micro-drive mounting cylinders can be implanted successively or simultaneously. The system has been tested in cats and rhesus monkeys, where single cells can be held for over an hour and several dozen cells can be recorded over several months from a single animal.

RESUME

UN SYSTEME SIMPLE D'ENREGISTREMENTS PAR MICRO-ELECTRODE EXTRA-CELLULAIRE CHEZ L'ANIMAL EVEILLE

L'auteur décrit un système d'enregistrement par micro-électrode extra-cellulaire utilisable chez le chat ou le singe non-anesthésié. Ce système, plus simple que les précédents, peut être fabriqué à partir d'éléments disponibles dans tout laboratoire, sans outils spéciaux ni usinage mécanique. Il est si bon marché que même le microdescendeur est accessible.

La base du système est constituée par une seringue d'hôpital de 3 cc, une simple machine à fileter et un morceau de câble fin. Pour l'enregistrement, cette pièce est fixée à un cylindre de plexiglass rempli d'agar, implanté dans l'animal en même temps que l'électrode de terre, les électrodes indifférentes et les pièces de contention de la tête. Les fils d'enregistrement ne descendent pas directement du microdescendeur mais sont reliés à un connecteur amovible avec contacts pour la terre, les électrodes indifférentes et un étage d'entrée à transistor à effet de champ qui opère la conversion de haute à basse impédance. Les connexions à haute impédance sont ainsi très courtes ce qui réduit le bruit de fond. Les fils de terre, des électrodes indifférentes et du transistor sortent ensemble de ce connecteur vers les amplificateurs.

Pour permettre une grande souplesse expérimentale, plusieurs supports de microdescendeurs peuvent être implantés successivement ou simultanément. Ce système a été éprouvé sur des chats et des singes rhésus chez qui des unités ont pu être conservées pendant plus d'une heure et plusieurs douzaines de cellules peuvent être enregistrées pendant plusieurs mois chez le même animal.

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