

tively, on the deep side; $z = .86$ and $z = 1.42$, for hooded and albino rats, respectively, for initial placement on the shallow side). Moreover, there was no species difference in response behavior between albino and hooded rats ($\chi^2 = .04$ for deep placement; $\chi^2 = .01$ for shallow placement). Though there appears to be a tendency for rats to move "on" or "toward" the deep side, depending on initial placement, the locomotion responses, summing over species, did not depart from chance expectancy ($z = .73$ and $z = 1.74$, for rats placed on the deep and shallow sides, respectively). The results indicate that a lack of optical support is of little concern to the rat, as long as tactual stimulation is available.

It is clear from the data that chicks and two species of rats differ in their reactions to the presence or absence of optical texture surrounding their feet. The chick avoids an optical void even though physical support is provided; the rat, on the other hand, is indifferent to a lack of optical information for support when physical support is provided. This helps explain why rats ever descend from a centerboard of a visual-cliff to the deep side; there is evidence that this presumably maladaptive response increases with a decrease in the height of the centerboard (4). This, coupled with the present findings, indicates the intrusion of tactual stimulation in a presumably visual task. Only when tactual information from the surface is eliminated, as in the case of a relatively high centerboard, can the choice of descent for a rat on the visual-cliff be attributed to the utilization of visual information.

Results concurring with those presented here have been obtained by employing a different procedure and examining a different response measure. Walk and Gibson (3), and Walk (5) report incidental and quantitative data, respectively. Indirectly, these investigators have observed that chicks, but not rats, exhibit fear reactions to placement on the deep side of a standard visual-cliff apparatus. Walk placed 90-day-old hooded rats and 3- to 4-day-old chicks on the glass of either the deep or shallow side and measured the latency of a forward locomotion. His results indicate greater "fear of high places" for the chick than for the hooded rat; that is, only in the case of the chick did the median latency for a forward locomotion on the deep side

significantly exceed the median latency when it was placed on the shallow side.

The technique described here is a comparative one, useful for studying reactions to apparent depth in a wide range of animals and for quantifying species differences on the basis of visual or haptic dominance. To what extent and under what conditions such sensory dominance exists for these and other testable species are questions for further study.

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Cells Related to Fighting Behavior Recorded from Midbrain Central Gray Neuropil of Cat

Abstract. *Cells were recorded in the midbrain central gray neuropil of the cat that responded with action potentials only during fighting behavior and not while the cat was resting or while control manipulations were performed. Some other cells in the same region responded maximally during fighting, and all cells responded to at least one manipulation. Brain stimulation at sites of cells related to fighting caused the animals to hiss.*

The central gray neuropil surrounding the aqueduct of Sylvius in the midbrain is related to fighting behavior in the cat. Electrical stimulation of this region elicits hissing, dilation of the pupils, piloerection, and a well-directed striking or biting attack (1, 2). Lesions confined to this region can abolish, at least for several weeks, similar behavior elicited by a barking dog (2, 3). I have attempted to locate, and to record from, the cells responsible for these phenomena.

The responses of single cells were recorded during fighting behavior elicited by confrontation of the cat with a second attacking cat. Until an attack the attacking cat remained on the other side of a partition from that from which records were being taken; then the partition was opened, the brain of the attacking cat was stimulated to produce hissing and striking, and the animal was moved toward the second cat until this cat responded with hissing, or striking, or both. The response of each cell was also recorded during control manipulations of the cat including presentation of clicks and flashes, lifting and dropping of the cat, pinching of its tail, and retraction of cat's foreleg after it had been extended by the experimenter.

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Most cells encountered in and around the midbrain central gray neuropil were highly active when the cat was fighting. The firing rates of 32 cells recorded in 11 cats increased from a median baseline rate of 0.2 action potentials (spikes) per second to a median rate during fighting of 12.0 spikes per second. Most of these cells also responded to a variety of control manipulations of the cat and were not maximally active during fighting. A few were particularly responsive to perception of visual movement (cells in the superior colliculus or near the oculomotor nucleus), to auditory stimuli, or to head movement. Four cells, however, responded only during fighting, and five others responded maximally during fighting. No cells which were primarily inhibited or which were unresponsive to any manipulation of the cat were recorded in this region. Cells which fired only or maximally during fighting were found in five cats, whereas cells which fired only during fighting were found in three.

Three of the four cells which fired only during fighting were found within the central gray neuropil immediately dorsal or lateral to the aqueduct of Sylvius. These cells never fired while the cat was resting, and they did not

begin to fire until the cat in which they were recorded began to hiss or strike at the attacking cat (Fig. 1). They fired during fighting at median rates of 6, 11, and 15 spikes per second, respectively, and stopped firing when the display ended. They responded in the same manner trial after trial—seven trials for one cell, five trials for another, and two for another. They responded on trials when the cat was striking but not hissing, as well as on trials when the cat was both hissing and striking. With three slight exceptions, these cells never fired during any of the control manipulations of the cat. One cell fired one spike when the cat was dropped. Another cell fired one spike when the partition was opened and the cats faced each other but no attack was launched. The third cell fired when the tail was pinched and the cat hissed and struck at the experimenter, but it did not fire when the tail was pinched and the cat did not attack. Otherwise, these cells fired only during fighting.

One other cell fired only during fighting, but never during control manipulations. It was located immediately lateral to the central gray neuropil and was recorded during only two attack trials. This cell fired two spikes exactly coincidental to one fighting display and three spikes coincidental with the other.

The response of the cells which fired only during fighting were not electrical artifacts since the waveforms of these and all other cells recorded had relatively constant amplitude and shape and the same spike duration (about 0.5 msec). They did not seem to be caused by mechanical irritation of the cell since they began to fire prior to movement artifacts and they were not influenced by dropping of the cat. They did not seem to be an artifact of increased blood pressure; current work on the same behavioral situation suggests that transient increases in blood pressure are sometimes, but not consistently, associated with fighting and they occur only during or after the first movement artifact (4). The responses did not seem to be caused by the skeletal response of striking since they did not fire during other movements such as being dropped and retracting the leg. They were not specific to hissing since they fired on trials with striking but no hissing. Of course, there always remain some components of behavior which have not been factored out (for example, in this case

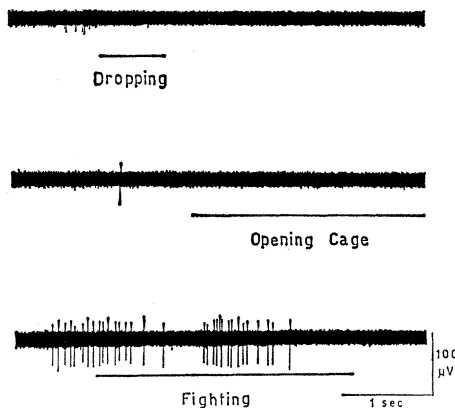


Fig. 1. Extracellular potentials recorded from a cell in midbrain central gray neuropil which fired only during fighting. In the first trace the cell is silent when the cat is lifted from the floor and dropped. In the second trace the cell fires once when the partition is opened between the two cats, but no fighting occurs. In the third trace it fires repeatedly during fighting behavior (hissing and striking). The event marker lags a fraction of a second behind the actual event because of the reaction time of the experimenter. Potentials were recorded on magnetic tape, played back into an oscilloscope and photographed on 35-mm film.

piloerection) but it seems reasonable to hypothesize that the responses of these cells were related to the integrated behavior itself.

Five other cells, including three from the central gray neuropil lateral to the aqueduct of Sylvius, responded maximally during fighting. The central gray cells increased from baseline firing rates of 0.1, 0.2, and 0.4 spikes per second to median rates during fighting of 26,

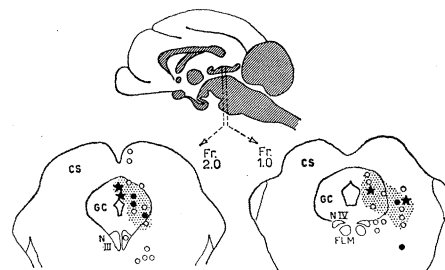


Fig. 2. Location of cells recorded in and around midbrain central gray neuropil at frontal levels 2.0 and 1.0. Cells which fired only during fighting are shown as stars. Other cells which fired maximally during fighting are shown as closed circles. Other cells are shown as open circles. Area from which hissing was obtained during electrical stimulation is stippled. GC, central gray; CS, superior colliculus; N III and N IV, nuclei of third and fourth cranial nerves; FLM, media longitudinal fasciculus.

19, and 10 spikes per second, respectively. All five cells were also responsive to many or all of the control manipulations of the cat. Several were particularly responsive to the noise made by tapping the partition between the two cats, more than to other auditory stimuli of equal intensity; this fact suggests that the auditory response might have been conditioned to the fighting behavior.

After all recording from a particular cell was finished, the region around that cell was electrically stimulated through the barrel of the electrode, and the intensity of stimulation was increased until a behavioral response was obtained. Hissing was obtained at the sites of all but one of the cells which fired only during fighting or maximally during fighting; the one exceptional site was located in the reticular formation relatively distant from the central gray neuropil. Attack as well as hissing was generally produced by electrical stimulation at these sites, but it was not always well directed, and it was sometimes dominated by a competing response of contralateral turning.

Most of the cells particularly related to fighting are located along a line through the center of that region which elicits hissing when electrically stimulated (Fig. 2). I determined the location of cells by passing an anodal dc current through the barrel of the electrode at certain points along the penetration and later detecting, on serial brain sections, the deposited iron by its reaction with Prussian blue.

Maintaining contact with a single brain cell during violent movement by the cat was particularly difficult. It required the development of a special microelectrode and drive system which could be securely fixed in position with respect to the braincase and which could anchor the tissue surrounding a cell. The electrode was stainless steel, bipolar, and concentric. The diameter of the insulated shaft was 0.8 mm; that of the inner recording tip was 30 to 50 μ m. Responses were amplified differentially from between the tip and barrel of the electrode and permanently recorded on magnetic tape. On the day of the experiment, the electrode was introduced into the brain through a guide which had previously been mounted on the cat's skull with dental cement. The guide consisted of a stainless-steel machine screw drilled longitudinally and lined with polyethylene tubing into which the electrode shaft

fit tightly. The butt of the electrode was permanently secured in a nylon sleeve threaded to fit the guide. The electrode could be advanced by turning the sleeve so that it screwed down the threads of the guide, and it could be fixed in position by tightening a set screw on the side of the sleeve. This system permitted recording from the same cell during repeated trials involving violent movement for periods of up to several hours. Two-thirds of the cells encountered were recorded before, during, and after at least one fighting trial, without signs of injury, pronounced changes in spike amplitude, or loss of electrical contact with the cell. After the electrode had been in place for several hours, however, cells could no longer be held; their spikes would diminish in amplitude or disappear whenever the cat moved and reappear again after it came to rest.

Because the technique of recording from single brain cells during free-moving, violent behavior is relatively unprecedented, particularly strict criteria were used for the acceptance of a response as being that of a single uninjured brain cell. All recordings were played back into an oscilloscope, and only responses with a waveform of constant shape, duration, and amplitude were accepted as coming from a single cell. Records of multiple units were discarded unless a single cell had a spike amplitude consistently greater than the highest background activity. Most spikes, including those of all cells which fired only or maximally during fighting, were initially negative; purely positive spikes were also accepted although the literature suggests that they may be axon recordings. Cells which changed irreversibly in baseline firing rate, which had spontaneous and sudden high-frequency discharges, or which had notches or changes in waveform were discarded as probably injured.

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Straight Lines on Semilog Paper

In his report concerning distribution of capillary blood flow through a homogeneous tissue (1), Hills proves that washout data which give a straight line on semilog paper can come from a system made up of two or more compartments in parallel only if the time constants of all the compartments are the same. My objection is that Hills wrongly attributes to me his straw-man premise that the time constants could vary and still yield a straight line. My work (2) has been devoted to cases where experimental results do *not* yield a straight line; I point out that although a curve on semilog paper can easily be "peeled" into two or three straight lines (each supposedly representing a compartment with its own time constant), the underlying system may actually be a large number of compartments with a whole frequency distribution of time constants.

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The objection raised is incidental to the main theme of my report (1) which shows that the overall response for the elimination of a tracer from a single tissue type cannot be linear if heterogeneous blood perfusion is the rate-limiting process.

My comment that "Van Liew . . . has indicated the need to consider whether any linear response obtained from a biological system is contributed by a continuum of exponential processes" was included to acknowledge his presumed recognition that there could be a continuous spectrum of responses within one or more compartments. The comment was carefully phrased to avoid discussion of a gross assumption in his report (2), which is essentially repeated in the above objection, and would appear to form the basis of this issue.

Van Liew's technique of "peeling" components from a semilog plot is feasible *only* if the overall response can be expressed as the sum of a number of exponential terms. However, this overall form can be obtained only from a system whose compartments give responses of such form when isolated. This can be seen from

analysis by Laplace transforms, such as used by Segre (3) for a general biological system covering all feasible arrangements of compartments. Deviation from linearity cannot be accommodated in parallel models, and in compartments in series only if their isolated responses have imaginary components—not a practical case.

The vital issue therefore is whether there can be any frequent distribution of linear responses within one compartment, or of simple compartments in parallel, which can give an overall response that can be expressed as two or more exponential terms.

If we repeat the analysis given in my paper for Van Liew's suggestion of a two-component curve, then the frequency distribution would need to be

$$\int_0^\infty \exp(-kt) dR \equiv A_1 \exp(-K_1 t) + A_2 \exp(-K_2 t) \quad (1)$$

where R is the fraction of the maximum possible change responding linearly with a time constant less than or equal to k ; t represents time. K_1 and K_2 are the time constants of the two components postulated, and A_1 and A_2 are their respective amplitudes.

Taking successive derivatives with respect to time and putting $t = 0$

$$\int_0^\infty dR = A_1 + A_2 = 1 \quad (2)$$

$$\int_0^\infty k dR = A_1 K_1 + A_2 K_2 \quad (3)$$

$$\int_0^\infty k^2 dR = A_1 K_1^2 + A_2 K_2^2 \quad (4)$$

Now

$$\begin{aligned} \int_0^\infty (k - K_1)(k - K_2) dR = \\ \int_0^\infty k^2 dR - (K_1 + K_2) \int_0^\infty k dR + \\ K_1 K_2 \int_0^\infty dR = 0 \end{aligned} \quad (5)$$

after substituting for the integrals according to Eqs. 2-4.

Since K_1 and K_2 must be real, k is real only if $(k - K_1)(k - K_2) \geq 0$. This is compatible with Eq. 5 only if $(k - K_1)(k - K_2) = 0$, for which the only real solutions are $k = K_1$ or $k = K_2$ (but not both simultaneously nor any distribution); that is, all elements must have the same response time.

Thus there would appear to be no frequency distribution of linear proc-