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# SINGLE UNIT RECORDING IN THE MIDBRAIN OF RATS DURING SHOCK-ELICITED FIGHTING BEHAVIOR

FRED J. POND, HARRY M. SINNAMON and DAVID B. ADAMS

*Department of Psychology, Wesleyan University, Middletown, Conn. 06457 (U.S.A.)*

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## SUMMARY

Single unit activity was recorded extracellularly from the midbrain of rats during fighting behavior and during non-fighting control manipulations. Fighting behavior was elicited by footshock or startle stimuli or occurred spontaneously as a result of prior footshock presentations.

Seven cells were found in the midbrain reticular formation and central gray which displayed maximum firing rates during fighting behavior. These cells also fired to a limited extent to some of the control manipulations, particularly contralateral vibrissae stimulation. These cells fired phasically during fighting behavior and their firing was correlated with either the approach or paw-strike of the opponent animal or to the response of the recording animal to a tactic of the opponent animal. However, no specific movement or sensory event reliably predicted the firing of these cells during fight sequences.

Cells located in other midbrain areas, such as the deep tectum or the area of the red nucleus, also responded during fighting behavior. However, the discharge of these cells was correlated with specific body movements or sensory events. The activity during fighting was similar in rate and pattern to activity during control manipulations whenever similar movements or sensory stimulation were produced. Cells were also found which did not discharge during fighting behavior although they fired under a variety of other conditions.

## INTRODUCTION

The aim of this study was to explore patterns of single unit activity in neural structures implicated in the control of certain forms of intraspecific fighting behavior in the rat. Of the several types of fighting behavior in the rat we studied shock-elicited fighting which has particular advantages for chronic unit recording techniques.

It is relatively stereotyped across subjects, requires little training, and can be elicited repeatedly in a several-hour recording session. Although the behavior is intense, it is not incompatible with successful single unit recording.

The region including the midbrain reticular formation and central gray was a particular focus of this study. In the cat this area contains cells which fire exclusively or maximally during defense against another attacking cat[1]. In the rat, lesions of the central gray and the adjacent reticular formation abolish or severely reduce shock-elicited fighting[5,9]. Stimulation of the same midbrain region in cats elicits defensive posturing and striking accompanied by hissing[3]; lesions of this region abolish affective defense behavior in cats[7,14].

In contrast with previous studies which have recorded the activity patterns of midbrain neurons of anesthetized or paralyzed or active rats in a specific conditioning paradigm[2,11,13], our strategy in this initial venture was to use an open-ended observational approach. Analysis of videotape records has uncovered relations between the stereotyped elements of the fighting pattern (e.g., upright posture, paw striking, gaping) and changes in unit activity.

## METHODS

### *Subjects and behavior*

Male rats at least 120 days old from the laboratory's colony of inbred DA agoutis served as subjects. The animals were housed individually with food and water always available. Pairs of animals were given pre-surgical experience with footshock-induced fighting behavior, two sessions of 25 trials with twenty 0.5-sec shocks per trial. Two such sessions normally resulted in a stable level of fighting behavior.

Pain-induced fighting in rats is characterized by the upright posture (rats standing on their hindlegs facing each other with vibrissae overlapping) and boxing (rats sparring at each other with their forepaws). The initial assumption of the upright posture is always preceded by mutual vibrissae contact. While in the upright posture, movements and mouth gaping by one animal generally are followed by compensatory postural shifts or boxing by the opponent animal.

The presentation of a painful stimulus (footshock) is necessary for the initial occurrence of the behavior. With repetition of fighting episodes, however, startle stimuli (handclaps) or presentation of the opponent animal are sufficient to induce fight sequences. Animals that did not show consistent fighting behavior to a minimum of footshock during pretraining were not prepared for recording.

### *Surgery*

Pretrained animals were anesthetized with sodium pentobarbital (50 mg/kg) and surgically prepared for chronic unit recording by stereotactically placing a nylon well (5 mm diameter) over a 5 mm hole drilled in the skull. The base of the well was sealed with Parafilm and the hole in the skull was filled with an antibiotic ointment (Bacimycin). The underlying dura was left intact. The well, a stainless steel ground screw and an Amphenol connecting plug were anchored to the skull with dental cement and screws. Animals were allowed 3–5 days to recover before testing.

*Recording procedures*

Unit activity was recorded extracellularly by means of glass-coated tungsten electrodes with tip diameters of 1–2 $\mu$m and tip exposure of 5–20 $\mu$m. The electrodes were lowered into the brain by means of a miniature microdrive which screwed into the nylon well on the animal's head. Initial amplification and impedance reduction were accomplished by means of a miniature DC preamplifier (Frederick Haer Model 40-20-2) mounted on a microdot cable which connected to the Amphenol strip on the animal's head. The preamplifier output was displayed on a Tektronix oscilloscope after bandpass filtering between 10,000 and 200 Hz. The signal was then fed into a spike amplitude and fall time discriminator.

Unit activity was recorded during aggressive behavior against another male rat in a plexiglass enclosure (20 mm $\times$ 15 mm $\times$ 45 mm) equipped with an opaque partition which separated the animals between fighting trials. A videotape system (Sanyo Model VTC 7100) was employed to record simultaneously: (1) the behavior of the animals; (2) the spike amplitude discriminator output (both on a counter for visual monitoring and on the videotape sound system for aural monitoring); and (3) a counter which enumerates each television frame (at 60/sec) for frame-by-frame reference. The amplified unit activity was also tape recorded along with a voice description of the animals' behavior on an additonal tape system. The latter recording was used to verify the accuracy of the spike discrimination and to identify any artifacts in the recording.

The animal was anesthetized with Fluothane to facilitate insertion of the microdrive into the well and connection of the microdot cable. While the animal remained anesthetized with Fluothane, the microelectrode was lowered into the brain until neural activity was encountered. The electrode was advanced until an isolated unit was encountered; if activity with a signal to noise ratio of at least 5:1 was encountered within the first 1.5 mm of the brain, the electrode was judged acceptable and the Fluothane was removed. If the electrode appeared unacceptable, a new electrode was placed in the microdrive and advanced into the brain in a different quadrant of the well. Following removal of the Fluothane, the animal was allowed to recover for at least half an hour before testing was begun.

As the microelectrode was moved through the brain, fighting trials were systematically presented every 100 $\mu$m and isolated cells were tested during fighting and appropriate sensory control procedures. These included a moving visual stimulus (plastic wand), handclaps, tactile stimulation of the vibrissae, back and lateral surfaces of the animal's body, passive movement of the animal's head and controls associated with fighting behavior, i.e., partition movements which did not expose the opponent animal, and footshock with the partition in place. Fight sequences and control procedures were generally repeated 3 times for each cell. Unit activity which fluctuated more than 25% in amplitude and spikes with distorted wave shapes (the presence of notches) were not analyzed further. Spike discrimination was monitored continuously during recording by one of the experimenters. Such monitoring, although requiring two experimenters for all testing, proved necessary for adequate maintenance of spike discrimination which was critical to later videotape analysis of the data.

*Histology*

Following completion of testing, a small electrolytic lesion was made at the deepest penetration of the microelectrode. With the microelectrode remaining in the brain, the animal was anesthetized with sodium pentobarbital (50 mg/kg) and perfused intracardially with isotonic saline and formalin. Brains were sectioned transversely at 50 $\mu$m using frozen tissue technique and the sections were stained with cresyl violet. The location of cells encountered during recording was plotted on line drawings of the midbrain based on extrapolation from the depth of the lesion and electrode depths for each encountered unit.

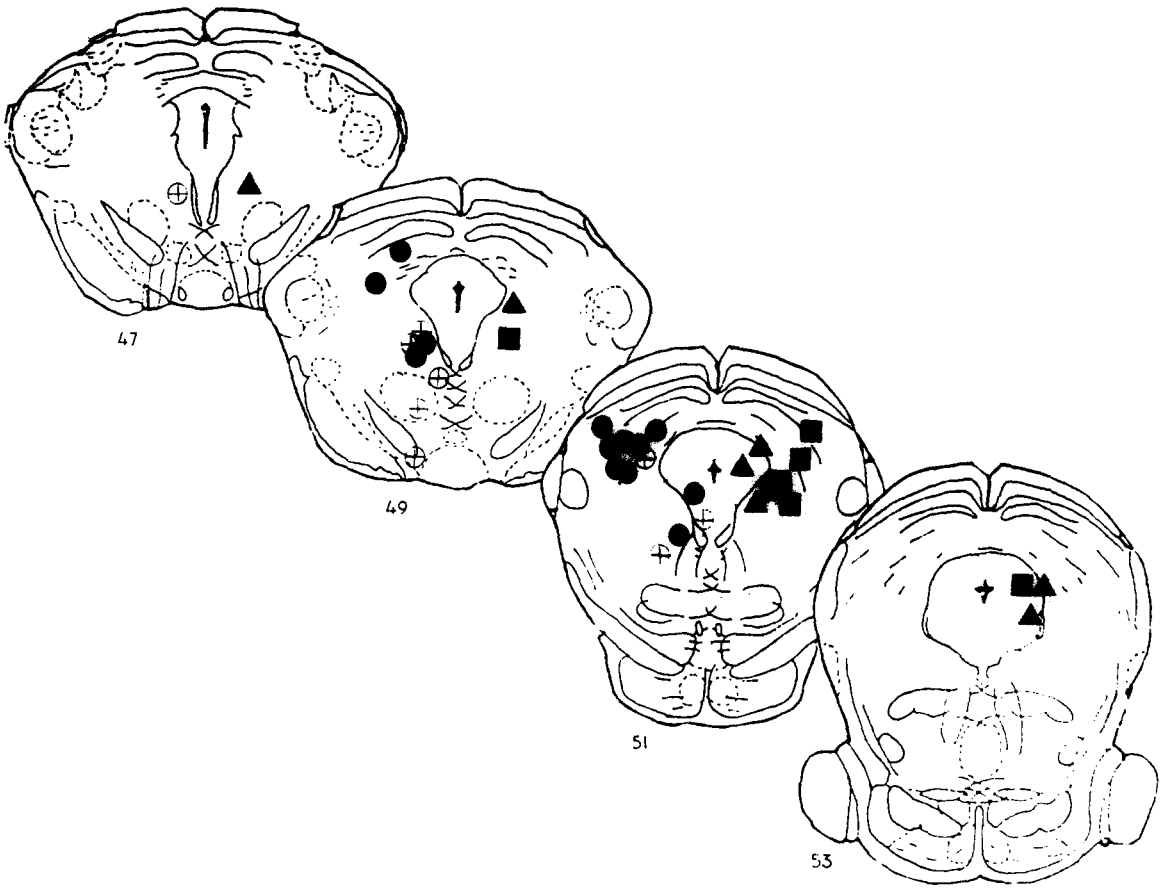


Fig. 1. Location of neurons in the 4 response categories projected onto diagrams of the midbrain adapted from the atlas of König and Klippel[10]. Closed triangles indicate category I units that fired maximally during fight sequences. Closed circles indicate category II units with increased firing during fighting due to sensory components of the behavior. Open circles indicate category III units with changes in firing during fighting due to motoric components of the behavior. Closed squares indicate category IV units that did not increase in firing during fighting behavior. Numbers below plates indicate related König and Klippel[10] figures.

## RESULTS

The activity of 60 midbrain neurons was recorded extracellularly in 24 animals. The recordings of 37 of these cells were sufficiently stable and free of artifacts during fight sequences and appropriate sensory and motor controls to allow analysis. An example of acceptable stability is shown in the oscilloscope tracings of Fig. 5. The remainder of the cells evidenced either instability during fighting (fluctuation of spike amplitude and/or wave shape) or were lost during a fight sequence; data from these cells are not included in this report.

The 37 cells with sufficiently complete records have been classified into 4 categories: (1) 7 cells with maximal firing rates during fight sequences and without sensory or motor explanations for the increased firing rates; (2) 13 cells with increased firing during fight sequences apparently due to sensory stimulation associated with the behavior; (3) 9 cells with changes in firing rate during fight sequences apparently due to motor acts associated with the behavior; and (4) 8 cells with no increase in firing during fight sequences, in most cases despite the fact that they increased firing during various sensory or motor control procedures.

A correspondence between the categories of cells in terms of their firing patterns during fight sequences and control procedures and their histological localization is evident in Fig. 1. Cells which fired maximally during fighting without sensory or motor explanations for the firing were clustered in and immediately lateral to the midbrain central gray. Cells whose firing during fight sequences could be explained in terms of sensory events were located for the most part in or near the tectum. Cells whose firing during fight sequences could be explained by correlations with specific motor acts were located for the most part ventral to the central gray, often in the region of the red nucleus or third nerve nuclei. Cells which did not fire during fight sequences were located throughout the midbrain, however.

### *Category I*

The 7 cells which fired maximally during fight sequences fired in response to contralateral vibrissae or tactile stimulation as well, although the firing rates were lower during these control procedures. As may be seen in Table I, the maximum firing rates during fighting ranged from 17 to 80/sec, with three of the cells firing maximally at approximately 60/sec. Maximum firing rates to control manipulations were usually seen in response to stroking of the contralateral vibrissae and they ranged from 3 to 33/sec, except in the case of cell 12-2 which will be described in greater detail below. Partition movement without exposing the opponent animal was also effective in eliciting responding in these cells. Partition movement is a complex stimulus with visual, auditory and tactile components; it is difficult to specify the effective modality. Responses to ipsilateral vibrissae or tactile stimuli were observed in only one of the cells and were much weaker than the response to contralateral stimulation. When the animal was "resting" quietly between fight sequences with the partition closed these cells fired at minimal rates, from zero to 1.5/sec.

TABLE I

*Response pattern of cells firing maximally during fight sequences*

| *Cell* | *Responses to all manipulations** | | | *Firing rates* | | |
|---|---|---|---|---|---|---|
| | *Increase* | *Decrease* | *No change* | *Initial quiet period*** | *Fighting behavior**** | *Other manipulations*§ |
| 8-1 | AD, P, OP VB-C | — | VS, PM, VB-I, T | 0.2/sec | 50/sec | 17/sec P |
| 11-1 | AD, PM VB-C | — | OP, VB-I | 0/sec | 17/sec | 3/sec VB-C |
| 12-2 | OP, P, VB-C VS | — | VB-I | 0.6/sec | 57/sec | 10/sec OP 100/sec VS§§ |
| 14-1 | AD, T-C VB-C | — | OP, PM, T-I, VB-I | 0/sec | 60/sec | 23/sec VB-C |
| 14-2 | AD, OP, P T-C, VB-C VB-I | — | VS, PM | 1.5/sec | 60/sec | 27/sec VB-C 27/sec P |
| 18-6 | T-S | — | OP, AD | 0/sec | 30/sec | 20/sec T-S |
| 41-1 | AD, OP, P, PM, T-C, VB-C | — | VB-I, T-I | 0.9/sec | 80/sec | 33/sec VB-C |

* Letters refer to following manipulations: AD, handclaps; O-A, approach by opponent; OP, open partition; P, move partition without exposing opponent; PM, passive movement of head; T, tactile stimuli to side or back; T-S, tactile stimulus to snout; VB, touch vibrissae; VS, moving visual stimulus. -C indicates contralateral manipulation; -I, ipsilateral.

** Mean firing rate per second for 10 sec epoch at the beginning of testing of the unit during which the partition was closed and the animal was not moving.

*** Average of maximum 1 sec firing rate from each fight sequence.

§ Highest 1 sec firing rate during any manipulation other than a fight sequence.

§§ Maximum 1 sec firing rate for visual stimulus presented after a fight sequence.

The firing patterns of cells which fired maximally during fighting were analyzed for overall trends by means of ratemeter writeouts with 1-sec epochs (Fig. 2) and for fine detail by means of writeouts of spike discharges (Figs. 3 and 4). The ratemeter writeouts shown in Fig. 2 show that these cells all fired phasically during fight sequences which suggests that they were related to specific aspects of the behavior rather than signaling a general tonic increase in arousal. A detailed analysis of the firing patterns was undertaken with the aid of the stop-frame and slow motion playback features of the videotape system. Detailed analyses of two cells are shown in Figs. 3 and 4. Increases in firing were correlated with the upright approach, mouth gape or paw-strike of the opponent animal or the resultant response of the recording animal, although it was not possible to specify any one movement which could account for all of the data. The activity of the cells appeared to increase in rate and duration when several components of fighting occurred simultaneously, e.g., upright approach, mouth gape and paw-strike by the opponent or some equivalent combination by the recording animal (see Figs. 3 and 4). Somewhat more subjectively, it appeared that the activity of the cells was related to the "intensity" of a sparring episode. Rate increases occurred both when the recording animal received paw-strikes passively and when it was the initiator of sparring episodes (see Fig. 2, cells 14-1 and 14-2).

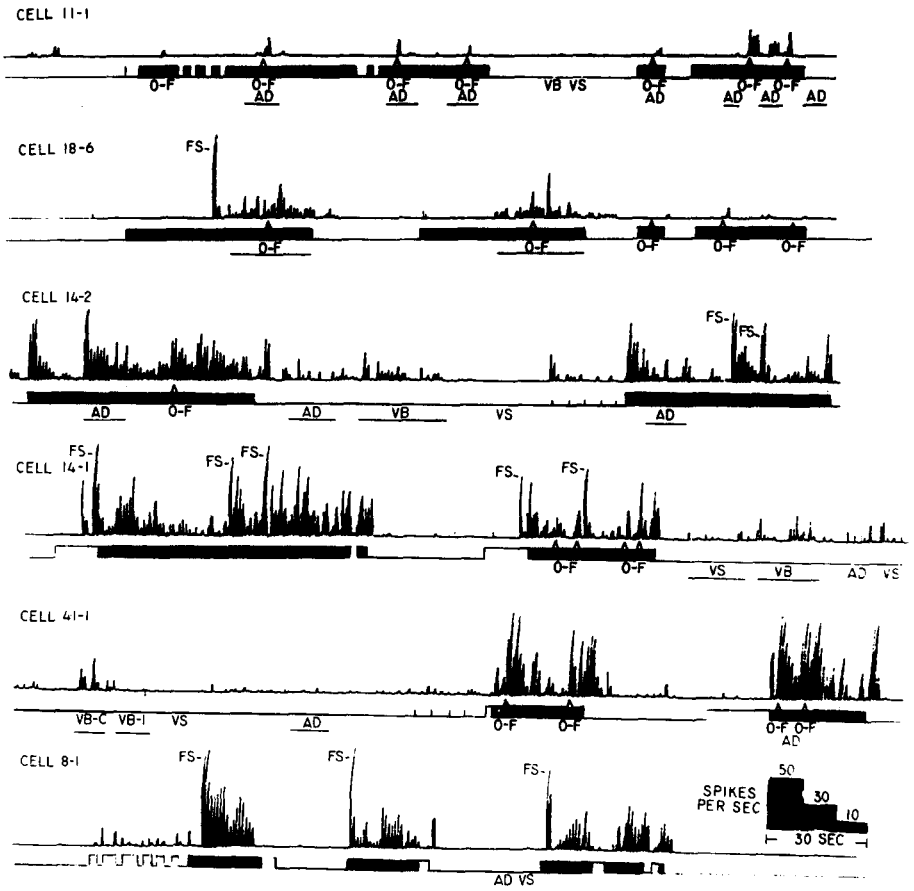


Fig. 2. Ratemeter records of 6 cells with maximal firing rates during fight sequences. The height of each vertical line is proportional to the average rate during a 1 sec epoch. 'FS' indicates footshock artifacts. The event marker line indicates opening of the partition and the dark area indicates the occurrence of mutual upright postures. Note that all partition openings do not lead to mutual upright postures. Letter notations indicating manipulations are identical to those used in Table I. Other notations under the marker line indicate the occurrence of fighting (upright approach, paw strike and gape) by the opponent (O-F).

Footshock was not required for the cells to respond. Fight sequences occurred spontaneously upon opening of the partition or were elicited by handclap startle stimuli in at least some of the recordings from 5 of the 7 cells. Fight sequences were always elicited by footshock during the recording from two of the cells. There were no apparent differences in the cells' activity during fight sequences elicited by footshock and those occurring without it (see Fig. 2, cells 18-6 and 14-2 for examples).

In a number of cases the responsiveness of the cells to sensory stimulation appeared to increase immediately after an episode of fighting. Continuation of firing at a reduced rate for several seconds following a fight sequence was observed in 5 of the 7 cells; this continuation perhaps reflected increased responsiveness to chamber stimuli. For example, cell 12-2 often showed an enhanced rate of firing after the

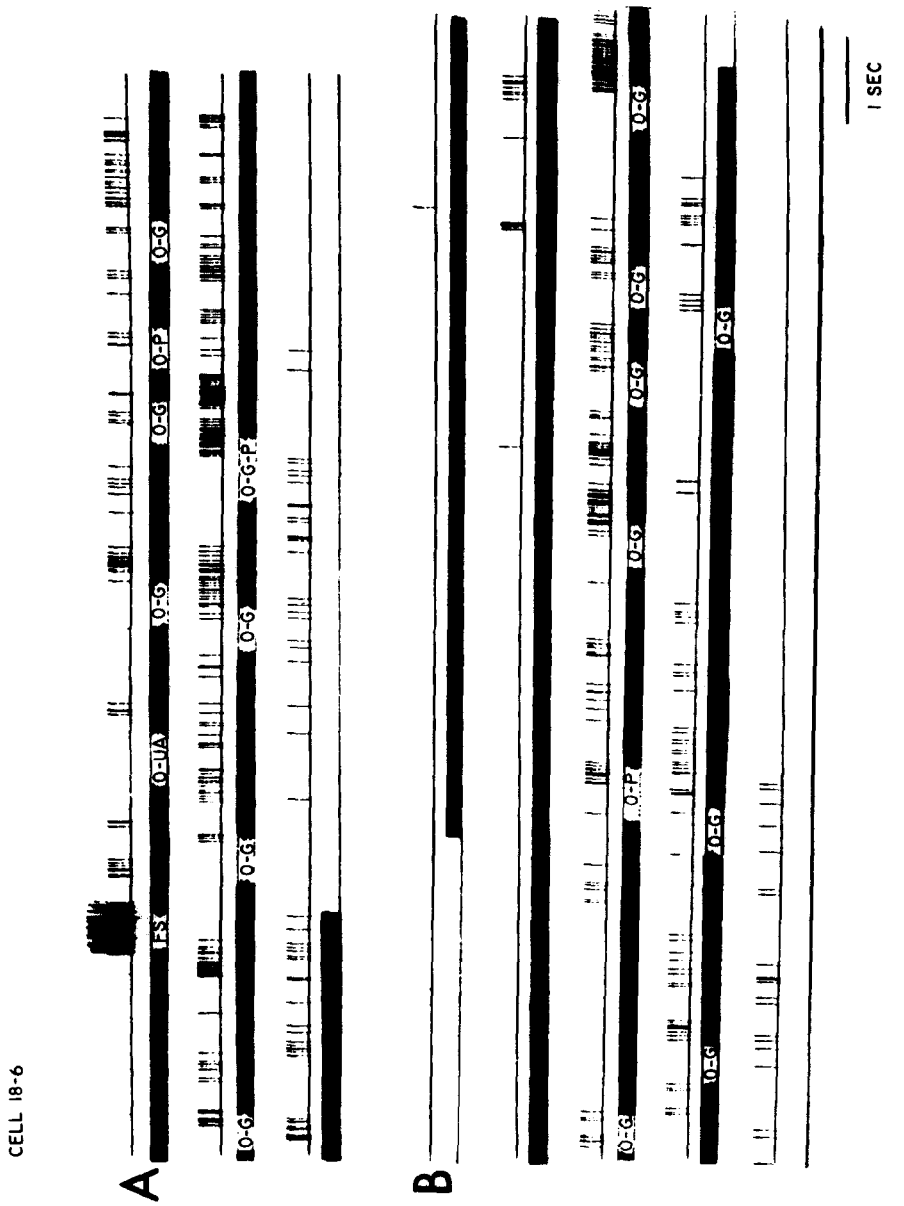


Fig. 3. Detailed writeouts of the activity of cell 18-6 showing increased activity correlated with various fighting behaviors of the opponent animal. Data correspond to the first two fight sequences depicted for this cell in Fig. 2. Each tracing depicts the discriminated activity of the unit represented by standard pulses. The event marker is used as described in Fig. 2. Letter notation indicates opponent upright approach (O-UA), opponent gape (O-G), opponent paw strike (O-P), and footshock artifact (FS).

partition was closed following a confrontation with the other animal, and on one occasion a visual stimulus similar to those which produced only small responses prior to fighting episodes produced a dramatically increased response, in excess of 100/sec, after a fighting episode.

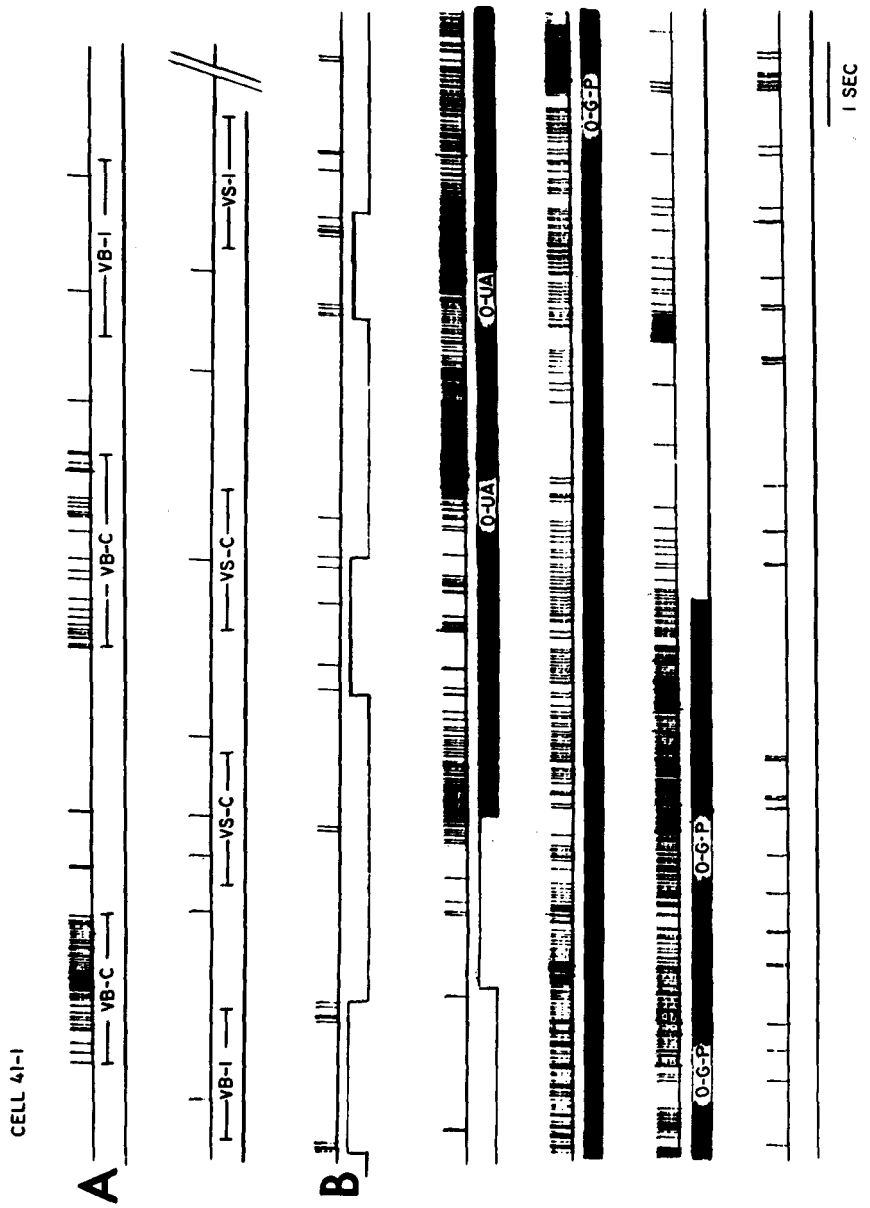


Fig. 4. Detailed writeouts of the activity of cell 41-1 showing increased activity during control sensory stimulation and maximal activity correlated with fighting behavior of the opponent animal. The data correspond to the sensory controls and first fight sequence for this cell depicted in Fig. 2. Letter notations and event markers the same as in Figs. 2 and 3.

Tape recordings of the activity of these units were carefully studied to determine if the increases in firing during the fight sequences were due to the intrusion of activity of other cells into the recordings or to irritation which could be caused by movements of the electrode. The intrusion of activity from other units appeared unlikely from the maintenance of a minimal interspike interval and constancy of spike waveform.

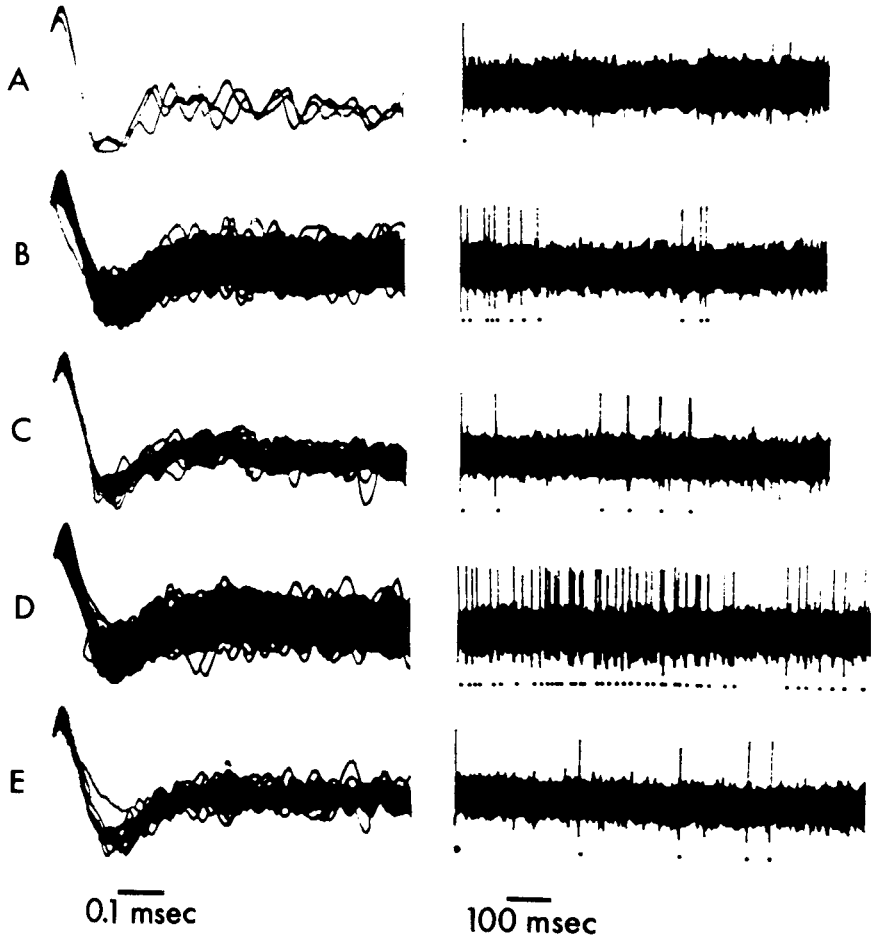


Fig. 5. Stability of spike amplitude and waveform during different behavioral conditions for cell 18-6 (illustrated in Figs. 2 and 3). Left column shows superimposed traces of all spikes during different behavioral epochs. Each sweep was triggered by the leading phase of a spike. Note absence of spikes for remainder of trace indicating that the recording was from one cell. Right column shows cell firing during a 1.0 sec sample from each behavioral epoch. Dots under the spikes indicate that the spike fell within the amplitude and time windows of the discriminator. Note the consistent spike amplitude and waveform across behavioral epochs, again suggesting that recording was from only one cell. The behavioral epochs were as follows: A: from the first partition opening to the footshock presentation. B: from just after the foot shock to closing of the partition. C: from partition closing of first fight sequence to partition opening of second fight sequence. D: second partition opening to second partition closing. E: second partition closing to third partition opening. The peak-to-peak amplitude of this spike was 400 $\mu$V, negative up.

The possibility of cell irritation appeared unlikely from the maintenance of relatively constant spike amplitude and waveform. Fig. 5 shows superimposed tracings of all unit activity from the detailed writeout of cell 18-6. This figure illustrates the maintenance of constant spike waveform and amplitude and minimal interspike interval even during the most intense phases of the behavior.

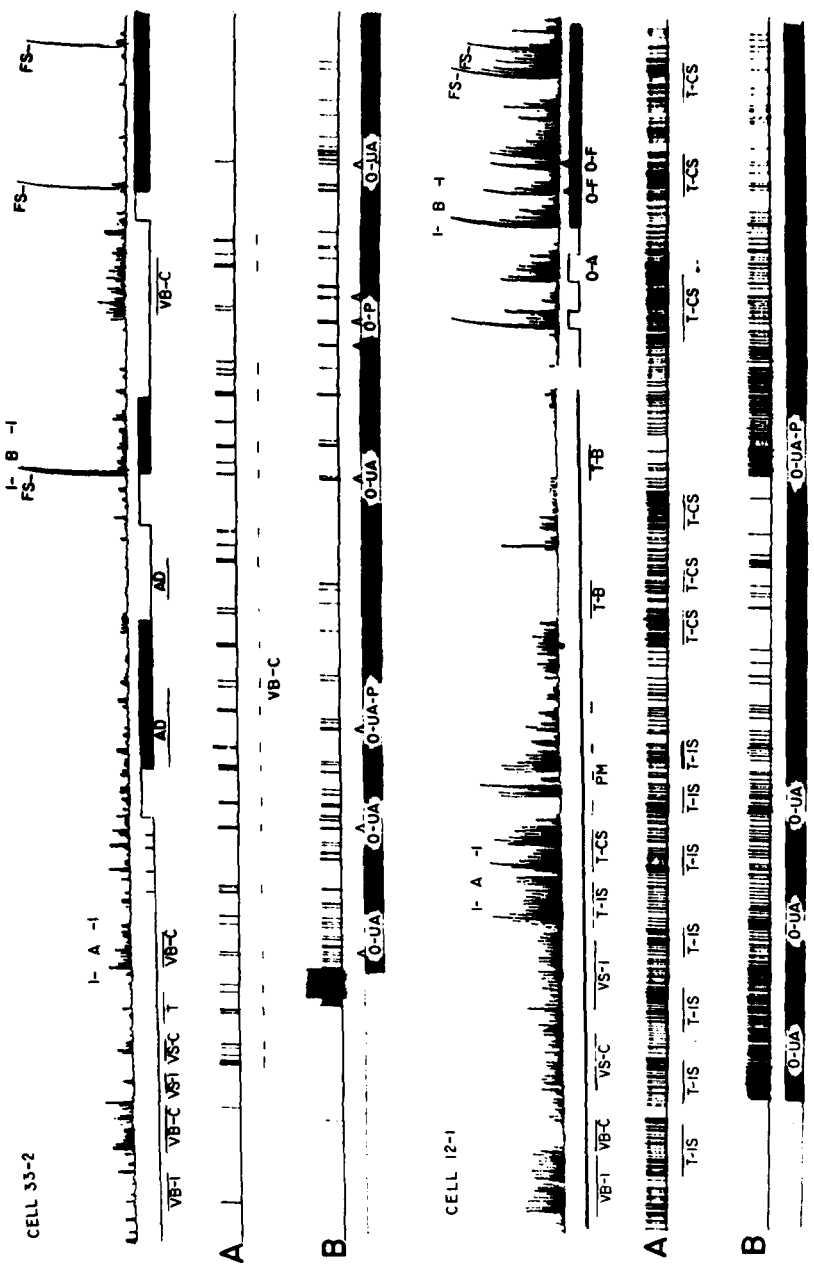


Fig. 6. Ratemeter and detailed writeouts for two cells with increases in firing during fighting that are explicable in terms of sensory correlations. Cell 33-2 fired to contralateral vibrissae manipulations (panel A) and during fighting when contact with the contralateral vibrissae was made by the opponent's vibrissae (indicated in panel B by notations of the opponent's behavior). Note that the event marker indicating a closed partition has been omitted in panel A to show a series of contralateral vibrissae stimulations (VB-C). Cell 12-1 increased firing during tactile stimulation (panel A) of the ipsilateral (T-IS) and contralateral snout (T-CS) and during fighting when the opponent's vibrissae came into contact with the recording animal's snout (indicated in panel B by notations of the opponent's behavior). Origin of detailed writeouts (A and B panels) are indicated by bracketed letters above the ratemeter writeouts. Letter notations and event markers are the same as in Figs. 2 and 3.

*Category II*

Cells whose increases in firing during fight sequences were apparently the result of sensory aspects of the behavior situation were most frequently found in the tectum and tectum-tegmentum junction of the lateral midbrain. These cells usually reached maximal rates during contralateral visual or vibrissal stimulation. Data from two such cells are shown in Fig. 6; from cell 33-2 whose firing increased primarily during contralateral vibrissal stimulation; and from cell 12-1 whose firing rate increased to touching the snout. Initial "baseline" rates of these cells were quite variable, apparently due to the extreme sensitivity of some of the cells to environmental stimuli, including vibrissal or tactile contact of the animal with the cage. In several cases the cells showed cessation of firing to ipsilateral stimulation: cell 35-2 stopped firing during visual, vibrissal and tactile stimulation of the ipsilateral side and during partition movement impinging on that side. Cell 18-1 stopped firing during ipsilateral vibrissal stimulation and cell 12-1 during tactile stimulation of the back.

*Category III*

Cells whose increase or decrease in firing rate during fight sequences were correlated with motor aspects of the behavior were located in the tegmentum ventrolateral to the central gray and in the regions of the red nucleus or third nerve nuclei. The increase or decrease in these cells' firing were correlated with movements involving the contralateral paw, the head, or body movements involved in rearing. During a fight sequence, cells related to rearing fired as the animal went into the upright posture, but did not fire during maintenance of the upright posture or during the boxing movements of the forepaws from an upright stance. The correlation of the activity of these units with motor acts does not imply that these units are motor cells; proprioceptive input associated with the movements would obviously produce similar results.

*Category IV*

The fourth category of cells, those which did not increase in firing rate during fighting, included several types of cells. Cells 18-4 (shown in Fig. 7), 42-2 and 24-2 appeared to fire in conjunction with exploratory activity and sniffing, but stopped firing altogether as soon as the partition was opened and the animals confronted each other. Exploratory sniffing was also suppressed at this time. These cells frequently did not fire following return of the partition for a considerable period of time; resumption of firing corresponded with a resumption of sniffing behavior. Cells 35-1 and 35-3 were strongly responsive to the approach of the opponent animal when the animals were on all-fours and the opponent was in the contralateral visual field. These cells also fired to contralateral tactile and visual stimuli, apparently in the lower or rear portion of the visual field and the posterior portions of the body. The cells did not respond during fight sequences; the appropriate sensory fields were probably not stimulated by the opponent during fighting. Cell 38-1 was unique. It was maximally responsive to visual stimuli when the animal was resting quietly, but apparently identical stimulation of the visual field was ineffective when the animal

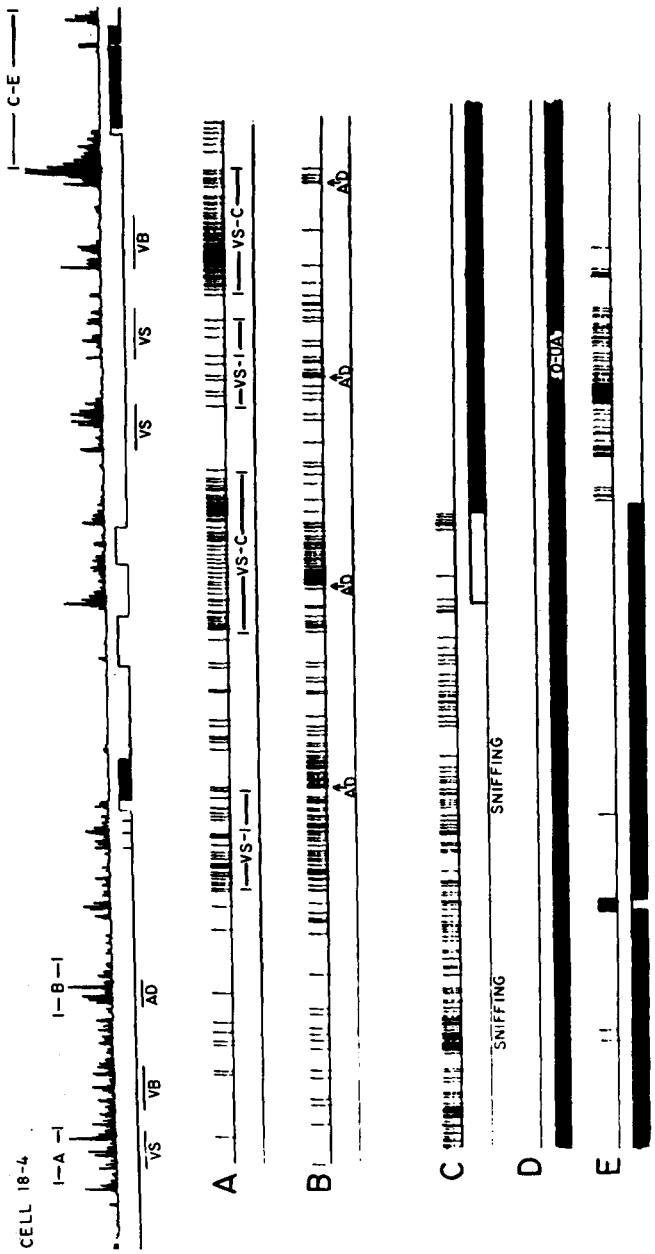


Fig. 7. Ratemeter and detailed writeouts for cell 18-4 which did not fire during fighting behavior despite responsiveness during vibrissal and auditory stimulation and during sniffing behavior. Origins of detailed writeouts are indicated by bracketed letters above ratemeter writeouts. Letter notations and event markers are the same as in Fig. 2 and 3.

was in the upright posture confronting its opponent. The lack of firing by these cells during fight sequences is further evidence against the possibility that the increase in firing of cells which fired maximally during fighting was due to irritation of the cell by electrode movement; particularly when cells of both types occurred in the same animal as is true for example with animals 18 and 42.

## DISCUSSION

Results from the cells which fired maximally during fighting behavior are consistent with the hypothesis that these cells are involved in the integrative neural activity necessary for pain-induced fighting behavior in the rat. First, they fired maximally during fighting behavior and their activity could not be explained simply in terms of sensory or motor components of the behavior. Second, they were located in the midbrain central gray and adjacent reticular formation, regions implicated in the control of the behavior[5,9]. Third, their characteristic sensitivity to vibrissal and tactile stimuli is consistent with the critical role these stimuli normally play in the elicitation of defensive upright posture and boxing[15,16]. And fourth, the data are similar in critical respects to the data of Adams[1] on affective defense behavior derived from single unit recording in the midbrain of the cat.

Although the maximal firing of these cells during boxing behavior is consistent with the hypothesis that these cells are involved in the integration of the behavior, the data in themselves do not compel this conclusion. Some subtle aspect of the sensory stimulus presented by the opponent rat or some subtle aspect of the motor response of the subject conceivably could account for the maximal firing during the fight sequence. This is an ever-present difficulty in chronic single unit studies, and cannot be totally overcome by any single procedure. However, the method of slow-motion videotape analysis provides a high degree of behavioral resolution and the opportunity for repeated evaluations of hypothetical correlations between unit activity and behavior. Together, these features enabled classification of unit activity to be made with confidence in all but a few cases. Thus, the absence of an obvious correlation between sensory or motor events during fighting behavior and the differential levels of activity between fighting sequences and control procedures have led us to conclude that those cells which fire maximally during fighting behavior are elements of an integrative mechanism for pain-induced fighting rather than elements of mechanisms for sensory processing or motor organization and execution.

Alternatively, the increased firing rates of these cells during fight sequences may reflect the arousal-eliciting properties of the aversive situation. Such an interpretation is suggested by the characterization of this midbrain region as part of the reticular activating system[12]. This interpretation encounters immediate difficulty in explaining the minimal rates of activity of these cells when the rats are merely separated by the partition, or together but not engaged in phasic aspects of fighting behavior. The fear-inducing and arousing properties of the entire situation appear to be high and would seem to increase only in degree during a fight sequence. By incorporating a phasic dimension, the explanatory ability of the arousal interpretation can be improved,

but such a modification would be the first in a series of specifications leading to the concept of specific motivational integration.

As an alternative to the arousal hypothesis, Schwartzbaum[13] related multiple unit activity in the midbrain reticular formation to the 'extensive and intensive dimensions of movement'. Applied to the present data, a phasic movement interpretation would relate the increases during fight sequences to movement patterns associated with fighting behavior and the range of firing rates to the extent of muscular involvement and intensity of movement. Such a close correlation between the firing rates of these cells and movement patterns of the recording animal were not observed; relatively high firing rates were frequently observed in response to movements of the opponent animal which were not accompanied by apparent movement of the recording animal. Other cells in the maximally firing group showed high rates of firing throughout fight sequences, even during periods when the animals remained stationary in the upright posture. Furthermore, some units in the same region showed increased rates during sniffing and head turning (Fig. 7) but did not discharge during fight sequences.

The response of the fighting-related cells to vibrissal and tactile stimulation is consistent with data showing that such stimulation is critical for elicitation of the upright posture and boxing behavior. Vibrissal sensation has been shown to be necessary for the upright posture and boxing of naive[16], but not of experienced[15], subjects in the footshock test situation.

The hypothesis that the midbrain central gray and surrounding reticular formation are critically involved in the integration of fighting behavior does not imply a single function for this anatomically complex region. Nor does the hypothesis imply that cells in other midbrain areas must be inactive during the behavior. As shown in the present study, many cells in the tectum which respond to various sensory stimuli continue to respond to those stimuli during the fighting behavior, as do cells in motor regions. In some cases, however, such as that of cell 38-1, there may be suppression of "normal" sensory responding during the fighting behavior.

Results from the present experiment are for the most part consistent with those reported in previous studies on the sensory properties of midbrain cells in the anesthetized or paralyzed rat[6,8]. In agreement with the results of others[4], we observed cells in the tectum which were responsive to vibrissal and tactile stimuli as well as visual and auditory stimuli. In agreement with the studies of others, cells in the midbrain reticular formation were found to be primarily responsive to contralateral[6] somatosensory stimuli and other sensory modalities.

The chronic unit recording technique used here has provided information that could not be obtained from a restrained preparation. Cells have been classified not only in terms of sensory response but also in relation to motor activity and in relation to one motivated behavior pattern. However, the necessary incompleteness of testing presents obvious difficulties. It is not possible to test the responsiveness of the cell during all possible motor patterns and motivated behaviors. By testing the cells during fighting, we bias our classification schema towards the finding of cells related to that behavior and related motor activity. By testing cells during another type of complex behavior, we might obtain a different view of midbrain cells.

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