

EVOKED POTENTIALS IN THE AUDITORY CORTEX OF THE RAT
DURING POSITIVELY AND NEGATIVELY MOTIVATED CONDITIONING

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To my wife Val
and
daughter Niccola

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ABSTRACT

Experiments were performed to determine the relationship between positive (drinking) and negative (unavoidable shock and conditioned avoidance) motivational states as revealed by changes in the primary amplitude, secondary amplitude and maximal amplitude of the primary-secondary complex of the evoked potential. Evoked potentials were recorded during four different conditioning procedures (unconditioned fear included) in the same rats each with chronically implanted electrodes in the auditory cortex.

In the series of experiments significantly smaller evoked potential amplitudes were found during positive motivation (drinking) than during negative motivational states such as avoidance conditioning, conditioned emotional response (CER) and unconditioned fear. This was a consistent and dependable finding throughout the entire study.

These evoked potential changes were observed in the primary amplitude, secondary amplitude and maximal amplitude of the primary-secondary complex. We found no evidence that the late secondary evoked potential was uniquely affected during conditioning as both significant and non-significant decreases occurred in all three measured components of the evoked potential.

Significant decreases in evoked potential amplitude were recorded during drinking conditioning. These decreases were observed over periods varying from three to nine days prior to the introduction of negative stimuli and the evoked potentials at the end of these periods

invariably exhibited smaller amplitudes than those observed at the beginning of drinking conditioning. Once aversive conditioning had begun the amplitudes of the drinking responses during the stages of Avoidance Learning, Avoidance Learned I, Avoidance Learned II, Early CER and Late CER still decreased but the decrements were no longer statistically significant ($p > .05$). We concluded that there was no evident transfer or feedback of information from the negative to the positive motivational states.

During the initial stages of avoidance conditioning and CER training as well as during the unconditioned fear reaction we observed increased evoked potential amplitudes in conjunction with a fear response which was characterized by inspiratory polypnea, crouching, defecation and piloerection. Because evoked potential amplitudes also decreased as the fear response diminished in strength we concluded that there was a strong relationship between these two measures and that the decrease was likely not an expression of learning but rather one of decreased fear.

During avoidance conditioning evoked potential amplitudes decreased as the percentage of avoidance responses increased but the decrease was not statistically significant ($p > .05$).

In another series of experiments the evoked potentials during Early CER were of larger amplitude than those during early avoidance since the former produced a greater fear response than that observed in the latter. Evoked potential amplitudes recorded during late avoidance (Learned II) were larger than those observed during Late CER.

During drinking conditioning, a few of the animals suddenly stopped lever-pressing and drinking and exhibited signs of fear (inspiratory polypnea, crouching, defecation and piloerection). These behavioural manifestations of unconditioned fear resulted in large evoked potential changes that were similar to those accompanying CER except that the amplitudes of the former were the largest observed in this experimental series.

In one attempt to determine the effect of muscle activity upon evoked potential amplitudes we recorded gross movements during the various stages of avoidance conditioning but found this muscle activity to be of no consequence.

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PART I. A REVIEW OF THE LITERATURE

A. INTRODUCTION

The search for neuroelectric correlates of conditioning began with the work of Durup and Fessard (49). A complete review of this whole field would be far too extensive and our attention will therefore be limited to changes in cortical and subcortical sensory evoked potentials observed during conditioning. We will be concerned with conditioned emotional responses, avoidance, and appetitive conditioned responses and with factors primarily affecting the first two. In particular we will consider the effects of learning and motivation on auditory evoked potentials.

B. BRAIN ELECTRICAL ACTIVITY

1. The Significance of the Electroencephalogram

A consensus is developing that the EEG represents the algebraic sum of hundreds of thousands of synaptic potentials in the many neurons within the field of a gross recording electrode (8, 132, 145, 167). However, the significance and meaning of EEG waves has been confounded by findings from single neuronal cells. Spike discharges of single cell units in the cortex as recorded by microelectrodes increased, decreased, or were quite unaffected during resting EEG rhythm (21), during EEG desynchronization (90, 96, 132), or during conditioning (101). There even appeared to be no relationship between neuronal spike populations and EEG wave activity at cortical as well as at subcortical levels (23, 24).

Several authors found that EEG waves could be recorded where

action potentials had disappeared and when the EEG flattened, synaptic potentials failed also (111, 132). From this it was concluded that surface activity correlates better with transmembrane events (slow synaptic potentials) than with spike generation alone (98).

2. Evoked Potentials and the EEG

The evoked potential has proven useful in that it provides a time-locked response initiated by a stimulus producing a synchronized impulse in an afferent pathway (132). Such impulses modify the continuously occurring cortical EEG activity and the very brief change in the whole picture of such continuous EEG activity before it reverts back, is the evoked potential (13, 132).

Since the evoked potential is a derivative of the EEG, comments on the one usually apply equally well to the other. In this light, the evidence presented by Fox et al. (56) stands opposed to that presented in the previous section on the EEG. They found that the cortical evoked potential was closely related to the sequential activity of a single neuron.

3. The Electrophysiological and Neuroanatomical Basis of the Evoked Potential

Cortical surface macropotentials are generated within the dendrites of pyramidal cells and are mainly postsynaptic in origin (34, 142, 143, 144). It is generally agreed that surface positive potentials are due to depolarization of neuronal somas and basilar dendrites, which act as sinks to apical dendrites, while surface negative evoked potentials

are due to depolarizing postsynaptic potentials generated in apical dendrites which act as sinks to the neuronal somas and basilar dendrites (20, 22, 37, 57, 68, 98, 142). However, cortical surface positivity can also reflect inhibition in the superficial cortical layers while cortical surface negativity has been shown to result from inhibition in the deeper cortical structures (18, 27, 31, 146).

The initial surface positive (deep negative) potential change resulting from a stimulus delivered to the periphery is followed by a longer lasting surface negative wave and where this positive-negative sequence of surface waves occurred, the middle layers of the responding site exhibited a negative slow wave corresponding in phase (time) with the surface positive wave (5, 6, 7, 19, 21, 27, 132, 137, 148, 170). However, inconsistencies have been reported whereby surface negative waves were associated either with excitatory or inhibitory cellular potentials and surface positive waves with cellular excitation (38, 39, 90). It is still unresolved whether evoked potentials recorded from different cortical depths represent the same process or whether they are produced by different generators located in the different layers (20).

The primary short-latency response of the evoked potential (first positive-negative wave) was found to be very sharply localized in the auditory cortex, while the secondary long-latency response (second positive-negative wave) appeared simultaneously over most of the cortex (10, 21, 27, 40, 54, 131, 149, 150). It has been generally accepted that the primary surface positivity depends on the lemniscal specific system (1) while the secondary negativity depends on the multi-synaptic non-specific system (27, 55, 81, 112, 128, 129, 138, 142, 149, 150, 171).

Others have concluded that the positive and negative components of the primary evoked cortical potential belong to two different ascending systems; the positive depending on the specific system and the negative depending on the non-specific system (11, 116).

Section of the brachium of the inferior colliculus (BIC) abolished short-latency auditory activity in the cortical auditory areas (136) but did not affect large auditory potentials from association and sensorimotor cortex (2, 3, 60). However, it has also been shown by others that the extralemiscal route is anything but secondary to the classical pathway (60). These authors suggested that it is irrelevant whether or not impulses are carried to the cortex by way of a specific sensory pathway since responses to clicks are unchanged in the auditory cortex after a lesion of the BIC (60, 62) but that impulses may reach the auditory cortex by pathways other than the BIC (3). Cytological and architectonic arrangement of neurons under the recording electrode is not critical either since essentially the same electrical event was recorded from cortex, caudate nucleus, white matter and reticular formation (62).

From the conflicting reports it is evident that the nature of the evoked potential is extremely complex (152), its significance is largely unknown (182) and its underlying specific components are still poorly understood (50, 87, 152).

C. EVOKED POTENTIALS AND BEHAVIOUR

1. Effects of Conditioning on Evoked Potentials

Galambos and Morgan (59) described work published in a Russian

journal by Artemyev and Bezladnova (1952) which appeared to be the first to relate conditioning to variations in evoked potential amplitude. Another early report which was first presented in 1955 and then written up in a western journal, related conditioning to somesthetic and auditory evoked potentials (100).

It has been shown that disruption of the long latency late components of the evoked potential interfered with learning significantly more than did disruption of the early components (91, 92, 98). In a contrary vein, there is also evidence that the information content of a brief stimulus is carried by the primary portion of the evoked response while the late or secondary components may only supply redundant information to insure detection (52, 112). However, there is general agreement that during the conditioned emotional response (CER), evoked potentials in the primary auditory cortex increased in size (58, 59, 62, 63, 69, 72, 73, 99, 100, 106, 108, 119, 120, 135, 163, 186).

It was presumed that these evoked response amplitude changes were related in some way to the establishment of a motor conditioned response (62). Yet the time courses of these two phenomena differed significantly in that enhanced evoked responses preceded development of the motor conditioned response (16, 25, 34, 35, 43, 69, 74, 89, 98, 124, 133, 151, 157, 163, 172). These EEG changes diminished and disappeared when the conditioning trials were extended beyond the attainment of criterion performance (16, 34, 53, 64), and in some cases, conditioned responses (CRs) were elicited without EEG changes (44, 53, 93).

Worden (181) using appetitive conditioning procedures observed the same sequence of responses in cats during the period of "waiting"

for the acoustic signals and prior to the execution of conditioned motor responses. The evoked potentials reverted to smaller amplitudes when the discriminations were well established (74, 181). Furthermore, Hall and Mark (69) observed that during positive reinforcement procedures not only was there no indication of any changes in evoked potentials as conditioned behaviour was established but that evoked potentials associated with correct or incorrect behavioural responses showed no differences.

It is small wonder then, that some authors have found no significant correlation between evoked response amplitudes and the state of learning (35, 69, 115, 130, 154, 155). Much of the data reviewed does strongly suggest that significant changes in evoked potentials during conditioning do occur and this seems clear enough. However, interpretations of this data have been at variance and except for the dissenting view of a few investigators, the idea has evolved that evoked potentials are somehow associated with conditioning. Consequently, it has been our prime concern to investigate and resolve this area of controversy.

2. Fear, Arousal and the Evoked Potential

A number of authors have asserted that the voltage changes during avoidance conditioning and the CER are strongly correlated with a state of fear or alarm (65, 69, 70, 72, 119, 130, 155). All components of the auditory cortical evoked potential were greatly increased during the CER, although the early components did not exhibit consistent increases (69, 70, 163) and were clearly not related to the conditioning process (70). Late components became significantly larger during conditioning and amplitudes seemed closely related to the strength of the conditioned

response (67, 70). Moreover, acoustically evoked potentials increased in amplitude before the visible emotional response became conditioned. This is not to say that there were no conditioned autonomic components such as increased heart rate and blood pressure during this initial period. A shock UCS brought about significant increases in acoustically evoked potentials independently of any conditioning process (69). Furthermore, Hall and Mark (70) showed that during behavioural manifestations of unconditioned fear the changes in the late components of the evoked potentials were quite similar to those occurring during the conditioned fear response (69, 70). However, there is controversy as to whether it is the positive or negative component of the secondary wave which is characteristically increased during unavoidable shock (67, 106).

Similar variations in amplitude have occurred during avoidance conditioning. As appropriate avoidance behaviour increased in frequency with succeeding trials, the amplitudes of auditory evoked potentials diminished together with the strength of the fear reaction i.e., less crouching, less defecation and decreased piloerection (69, 70).

In studies of conditioning and pseudo-conditioning both associated with shock, there was a lack of increase of evoked response amplitude during avoidance conditioning which immediately followed pseudo-conditioning. During preconditioning sessions when no shock was presented the amplitudes of the evoked potentials exceeded those which occurred during conditioning and pseudoconditioning, suggesting that successive pairing of neutral and noxious stimuli was not the causal agent leading to the acquisition of the conditioned response (65).

During a pseudoconditioning control procedure employed by Buser et al. (28) ambiguous results were obtained. One subject evidenced evoked potential changes similar to those observed during conditioning while another did not. In another type of control experiment, Macadar et al. (115) showed that there was no amplitude difference in evoked potentials between experiments in which shocks were delivered at the beginning or at the end of flash-evoked cortical potentials.

Some researchers have considered the increase in evoked potential amplitude to be an expression of alertness or increased arousal not related to the learning process (26, 44, 65, 89, 92, 140, 172), while others have considered it to be an expression of alertness or alarm which can be a part of learning (34, 106, 163). Consistent with the former position are experiments showing that presentation of positive rewards such as sugar pellets or milk to animals familiarized with a CS, appeared to be comparable to a first shock since it caused them to become thoroughly alert while at the same time the evoked response increased in amplitude (58, 94).

From the studies reviewed in this section and in the previous one, it is abundantly clear that the cause of evoked potential increases during conditioning has not been resolved. The evoked potential changes have been attributed to fear itself, to alertness unrelated to learning, to alertness which could be related to learning, and to conditioning itself. As we have seen, research conducted using conditioning, pseudoconditioning, and preconditioning techniques (28, 65, 115) has provided encouraging results. Although there have been very few such studies and

although this approach appears to have been abandoned, it does hold considerable potential.

It would be enlightening to apply positive (drinking) and negative (avoidance and CER) conditioning techniques in succession, on the same animals. By comparing evoked potentials prior to positive reward with potentials during aversive conditioning over a period of several weeks, it should be possible to obtain a better assessment of the contributions of both fear and conditioning to evoked potential amplitude changes.

3. Evoked Potentials and Habituation

Habituation in electrophysiological terms has been described as a decrement in the amplitude of the evoked potential as a result of repeated stimulation (63, 173). As we have seen in the previous section, some researchers have considered this increase in evoked potential amplitude during conditioning to be an expression of alertness or increased arousal (26, 44, 65, 89, 92, 140, 172). Conversely, a decrease in evoked potential amplitude from this high point could signify decreasing alertness but since this response decrement could be due to habituation quite apart from decreased alertness or conditioning, we felt a need to review this area.

As early as 1951, Artemiev (12) observed that cortical auditory evoked potentials disappeared rapidly as a result of acoustic habituation. Since then it has been shown that progressive reductions occur in the amplitudes of the late components of cortical evoked potentials in the alert animal as a function of repetitive stimulation (63, 67, 69, 82, 86,

88, 105, 109, 120, 121, 135, 173, 174) and that these changes could only be attributed to central neural mechanisms (67, 169, 179) below the cortex (156). Several authors observed that the amplitude of the secondary surface positive component during habituation closely followed the behaviour of the animal and was more closely related to the level of significance of the stimulus than was the primary wave (53, 103, 163). The decrement reported after thousands of clicks did not appear to be related to learning (147, 158) but rather to a deliberate focussing of attention away from the insignificant stimulus (86).

No agreement has been reached with regard to habituation below the cortex (47). As a result of repetitive stimulation, decrements (45, 47, 63, 77, 78, 79, 120, 162, 176), no decreases (67, 85, 109, 121, 184), and inconsistent increases and decreases of evoked potential amplitudes at the cochlear nucleus (122, 178, 182, 184) have been reported. Similar confusion exists with regard to habituation at the inferior colliculus (45, 46, 47, 67, 121, 162, 179). The effects at these subcortical stations are most important and should be considered since they relay and may modulate input to higher centres along the auditory chain.

It appears that the history of habituation studies of cortical auditory evoked potentials has been one of attempts to control the many relevant variables and the problem is still with us. In order to clarify this situation it is necessary to standardize techniques and methods, particularly repetition rate and frequency of sound stimulus. This is also true with regard to precise electrode placement (175), better control of stimulus intensity inputs, levels of arousal and background synchrony as well as absence of movement artifact (50).

4. Gross Muscle Activity and Evoked Potential Amplitude

As already mentioned, the time courses of evoked response amplitude changes in the auditory cortex and motor conditioned responses differ. Because of this observation some researchers have ruled out gross muscle activity or its consequences as the cause of these evoked response changes (63, 69, 70, 151, 178). Others have shown that during motor activity such as running around in the cage, hanging onto a bar, searching movements, cleaning movements etc. the amplitudes of the evoked potentials were decreased (29, 107, 139, 140, 158, 163, 166, 171). Research by Dunlop et al. (48) revealed that movement resulted in marked decreases in the evoked potential amplitude at the cochlear nucleus, inferior colliculus, and medial geniculate body and indicated that a peripheral attenuating mechanism was operating. On the other hand, Karlin et al. (102) found no effects on the averaged evoked potential that could be attributed unequivocally to the motor response itself.

Here is a controversial factor which could and probably does have significant effects on evoked potential amplitudes in most conditioning experiments, but by no means is it near satisfactory resolution. In our own experimental design, we made no attempt to restrict the animals or control for their activity but we did make provisions for recording gross muscle activity and for evaluating its effects upon evoked potential amplitudes.

5. Changes in Evoked Potential Amplitude observed during Middle Ear Muscle Activity

It appears that middle ear muscle activity is coordinated with

general body movement, including yawning, swallowing, and defensive movements in response to painful stimuli (29, 30, 166). Contraction of the tensor tympani and stapedius muscles has been known to reduce the size of cochlear microphonic and cochlear nucleus responses thereby directly affecting auditory input (15, 17, 29, 30, 42, 61, 122, 159, 161). Some workers have implicated the middle ear muscles in the process of acoustic modification (84) and habituation (4, 14, 66), while others have denied and rejected this conclusion (26, 120, 135, 162, 177, 179). Starr (166) on the other hand, indicated that although subcortical pathways were unaffected during movements, cortical evoked responses decreased in amplitude even in the absence of action by these muscles. Zimmerman et al. (187) pointed out that there may be a direct cortical effect on the cochlear nucleus, while more recent work (122) indicated that ablation of the primary auditory cortex had profound effects on the tensor tympani response patterns. The intermittent unpredictable action of the middle ear muscles in resting animals in a constant sound field has only added to this confusion (61).

As we have seen, past research has attributed a whole spectrum of effects to the influence of middle ear muscle contractions. These effects have ranged from consistent, to partial, to intermittent to nil and it is for this reason that we chose not to incorporate any controls for this factor. Although there has been a substantial amount of research in this area, there is a desperate need for more refined methodology before firm conclusions can be drawn about the relationship of middle ear muscles to evoked potentials.

6. Acoustic Variability and its Effects on Evoked Responses

Changes in sound intensity resulting from changes of position in a sound field produce gross evoked potential changes and have confounded attempts to demonstrate a correlation between behavioural changes and auditory evoked potential changes (86, 183). The effects of this intensity variation on evoked potentials have been found to be quite marked on the lower auditory centres such as the cochlear (160, 176) and the cochlear nucleus (123, 182) but were found to be of little consequence at the auditory cortex (182, 185). Because we will be concerned only with cortical potentials, and with the latter results in mind, we decided to use an overhead sound source in our design.

7. Reticular Influences on Evoked Responses

It has generally been accepted that the brain stem reticular formation is an essential mechanism in the development of acoustic habituation (4, 120, 125). The reticular formation exerts an inhibitory influence (76, 77, 80, 110) which has been known to change synchronized cortical discharge into low voltage fast activity (134) and to reduce the amplitude of cortical auditory evoked potentials (118, 169) by selectively blocking incoming sensory impulses at the cochlear nucleus (75, 78, 79, 84, 104, 180). Middle ear muscle contractions effected by reticular stimulation have also been implicated in the decrease of evoked potential amplitudes from the cochlear nucleus (83, 84) but subsequent work by Chin *et al.* (32, 33) failed to substantiate this finding. It would then appear that the modulating effect of the reticular formation is indirect since other workers have not been able to confirm direct control (41, 48, 75, 173).

As early as 1949, it was discovered that lesions of the medial core of the mesencephalic brain stem resulted in greatly altered behavioural and electroencephalographic responses (113, 114). The reticular formation has been implicated in the alteration of potentials evoked by significant stimuli (63, 77, 157). According to some authors lesions in the mesencephalic reticular formation produced emotional disorganization (44, 164, 165, 168) but largely had no effect on the conditioning process (36, 44, 164, 168), while others found an impairment in avoidance conditioning (117). Sprague et al. (165) concluded that animals with midbrain reticular formation lesions were impaired in learning because of sluggishness, distractability and hyper-emotionality.

It is not surprising that initial pairing of CS with UCS activates the reticular formation and leads to widespread cortical excitation (98) since it was discovered that all along the course of the brachium of the inferior colliculus short fibres enter the lateral mesencephalic reticular formation (126, 127). Cortical evoked potential increases and subsequent decreases accompanying conditioned response acquisition and overtraining respectively could result from increasing and decreasing levels of reticular facilitation (53). Here too, the evidence appears to be conflicting. Click-evoked potentials from the midbrain reticular formation showed considerable increases in amplitude during CER (119) while during classical aversive conditioning there were no statistically significant changes in the level of midbrain reticular formation excitability (124). In summary, it can be said that the role of the reticular formation in the learning process is still undecided (117). Our experiments will attempt to further knowledge in this area by studying the

effect on cortical evoked potential amplitudes of a variety of levels of EEG activation based on motivational changes.

8. Overview and Special Considerations

It has been pointed out that the nature of the evoked potential is extremely complex, its significance is largely unknown and its underlying specific components are still poorly understood. Non-specific structures outside the auditory pathway seem to play a central role in the processing of information about an auditory stimulus (62, 94, 95, 97, 100) and the information pertaining to a behavioural decision might even be found in other unanalyzed sections of the waveform (152). Furthermore, the cortical EEG has been dissociated from animal behaviour by lesions, states of fatigue, rewards and drugs (141).

With due consideration to the foregoing, it seems impossible to give a general rule for evoked potential changes during conditioning, not only because they vary with experimental conditions (140, 153) which have not been standardized and techniques which have not been refined, but also because different animals have been found to respond to different aspects of the same stimulus (182). Although cortical evoked potentials do vary with conditioned behaviour and although these changes are reproducible, ultimately it is necessary to show the relationship of these changes to overt behaviour. This condition has not yet been met (152, 155).

Where two or more conditioning procedures had been used in the studies reviewed, they were usually performed on different animals. Comparison of such results had introduced much variance because we know

from our own experiments that responses of different animals subjected to the same conditioning procedures vary considerably (163). On the other hand, we chose to apply all of our conditioning techniques to each animal (controls excluded). Our experimental design allowed us to obtain daily comparisons of evoked potentials prior to drinking and during aversive conditioning (avoidance CER). In this manner we hoped to reduce considerably the variability resulting from separate groupings. By this set-up we were able to compare evoked potentials during drinking conditioning, avoidance, CER and unconditioned fear in the same animals. Moreover, we were able to compare drinking conditioning potentials before initiation of aversive stimuli, drinking conditioning potentials during stages of avoidance conditioning and drinking conditioning potentials during the period of CER training. We anticipated that these latter comparisons would provide us with a measure of control by which we could determine the effects, if any, of aversive stimuli upon evoked potentials during drinking conditioning.

Positive (drinking) and negative (avoidance or CER) motivational states are each connected with specific changes in the evoked potential. In our experiments we altered the test chamber prior to each of drinking conditioning, avoidance conditioning and CER. These changes provided environmental clues that resulted in a background of tonic EEG activation that was either positively motivated by the anticipation of water or negatively motivated by the anticipation of shock. The phasic characteristics (physical intensity of the sound CS) that were superimposed on this tonic background were exactly the same during positive and negative motivation

but their significance was changed by cues provided by the environment i.e., only the state of the animal was changed. The resultant electrophysiological changes could well serve as a tool for evaluating the nervous pathways for these two states.

To the best of our knowledge, this is the first experiment of its kind where evoked potentials were recorded during four different conditioning procedures in the same animals, where the results were cross-correlated by computer and where comparative analyses were carried out on evoked potential amplitudes in relation to the conditioning procedures. It is hoped that this work will provide a small measure of clarification in this area and permit a greater insight into the contributions of conditioning and fear to evoked potential amplitude changes.

PART II. EVOKED POTENTIALS IN THE AUDITORY CORTEX
OF THE RAT DURING POSITIVELY AND NEGATIVELY
MOTIVATED CONDITIONING

A. INTRODUCTION

The purpose of this study was to determine the relationship between conditioned behaviour (learning) and brain activity as revealed by evoked potentials recorded from the auditory cortex of the male rat. In particular it was hoped to demonstrate:

1. The relationship between positive (drinking) and negative (conditioned avoidance and unavoidable shock) motivational states as revealed by the amplitude of the evoked potential.

2. The characteristics of the primary, secondary and overall evoked potential amplitudes in each of these different motivational states.

3. The changes in the evoked potentials with respect to stage of learning in each of these different motivational states.

The hypotheses to be tested were: (a) that the amplitude of the evoked potential varies as a function of the stage of learning the conditioned response; (b) that as the conditioned avoidance response (CR) becomes stronger with training and the strength of the conditioned fear response (i.e., crouching, defecation and piloerection) decreases, the evoked potential amplitude will also decrease from the early to the late stages; (c) that evoked potentials of early conditioned emotional responses (CER) are larger in amplitude than those of the less aversive early avoidance training; (d) that the evoked potentials of Late CER are larger

in amplitude than those of late avoidance and (e) that evoked potentials recorded during positively motivated (water) responding will differ significantly from those recorded during aversive conditioning.

B. METHODOLOGY

1. Subjects

In the experiments described here, nine male albino rats (R37, R38, R39, R40, R41, R42, R44, R45, R46) of the Sprague-Dawley strain were used, a minimum of three and a maximum of six in any one experiment. The rats were six weeks old when conditioning was begun, eight weeks old when electrodes were implanted and ten weeks old when recording was begun. At the end of the recording session which lasted seven weeks, the rats were 17 weeks old.

2. Surgical Procedures

About ten minutes prior to the administration of the anesthetic, each animal was given an intraperitoneal injection of atropine (0.1 mg/100 gms body wt.). This was followed by intraperitoneal sodium pentobarbital (40 mg/Kg body wt.). Midway through the operation ephedrine (0.1 mg/100 gms body wt.) was administered and this was followed by adrenaline (0.1 mg/100gms body wt.) at the completion of electrode implantation.

3. Electrodes

All electrodes were made of platinum-iridium alloy and a total of eight were implanted in each animal, one in each auditory cortex, two unilaterally in the motor cortex, three in the cerebellum and an

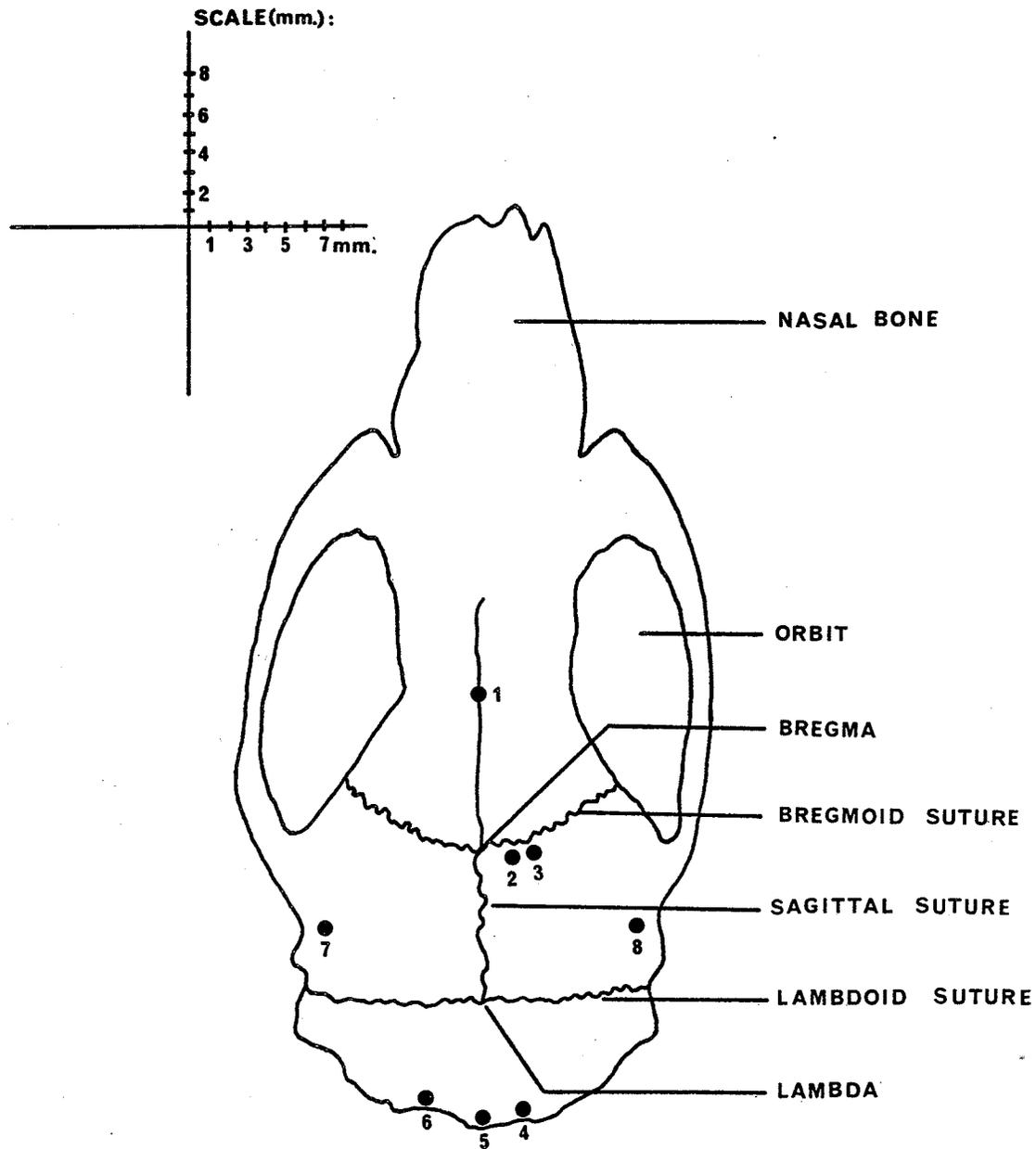


Fig.1 Dorsal surface of rat skull.

Electrode placement: Reference: No. 1; Motor: No. 2, No. 3;
Cerebellum: No. 4, No. 5, No. 6; Auditory: No. 7, No. 8.

indifferent reference electrode in the olfactory tract (Fig. 1). Electrode wires were soldered to eight-pin connectors made from dual in-line integrated circuit sockets. The electrodes were implanted according to Krieg, W. J. S.: Atlas of Coordinates of the Albino Rat. Johnson Scientific Instrument Company, Berwyn, Illinois. With bregma as the (0,0) coordinate, the reference electrode was placed eight mm. rostral to bregma i.e., at (0,8). The electrodes in the motor cortex, 2 and 3, were placed at $(-1/2, 3/2)$ and $(-1/2, 7/2)$ while those in the auditory cortex, 7 and 8, were placed at $(-9/2, -8)$ and $(-9/2, 8)$ in mm. measurements.

4. Electrical Recording and Analysis of Signals

Evoked potentials were amplified by Tektronix Type RML22 low level preamplifiers and X10 amplifiers and then fed into a Didac 800 Computer for signal averaging. Each trace on the Didac oscilloscope screen represented an averaging of 100 conditioned stimulus (CS) presentations or sweeps. Frequencies greater than 10 KC/sec. and less than 0.8 c/sec. were filtered out and a Didac sensitivity scale of 20 K was used for all Polaroid pictures taken. Amplified signals were also recorded on a Grass 8-channel EEG machine. In addition, lever presses, floor vibrations and all gross body movements were also recorded on one of the EEG channels. All signals were routinely monitored on a 4-channel oscilloscope.

Evoked potentials in all experiments were evoked by clicks (CS) that were generated from an EICO square wave Audio Generator Model 377 at a frequency of 30 K, in series with an AEL Laboratory Stimulator Model 104A. In all experiments, aversive and drinking, the CS, of 5 msec.

duration and a frequency of 3 cps was generated across a speaker located 33 inches above the floor of the test chamber. Its intensity within the test chamber was approximately 70 decibels while the background noise (without the clicks) at the same level was in the range of 60 decibels.

5. Training Procedures

a. Appetitive Lever-Pressing

All animals were water-deprived for approximately 23½ hours. Lever-pressing in the test chamber (two Skinner Boxes modified to share a common wall) was established to obtain water, with the CS being presented on a variable interval every 30 to 40 seconds. The CS was presented in 10-second blocks after which water was presented for ten seconds.

All rats were trained to lever-press for water before electrode implantation and re-training procedures were initiated five to seven days after the electrodes were implanted. All animals received an average of 18 to 20 drinking conditioning trials of seven to 14 minute duration over a period of four weeks before evoked potentials were recorded. In all animals, drinking responses and evoked potentials stabilized before further changes in experimental conditions.

b. Instrumental Avoidance

Using the same modified Skinner Box, but now with the solid floor removed to expose the grids and the partition removed to provide two chambers separated by a three inch high wall, avoidance conditioning was begun and continued to an 80% conditioned response criterion and then to overtraining. By means of a three-way switch each grid could be

electrified separately. In addition, the wall could also be electrified. Current was supplied from a Grass S8 Stimulator in series with a Grass Stimulus Isolation Unit Model SIU5 and a Grass Constant Current Unit Model CCULA. The current was fairly constant varying from 0.3 to 0.5 mA D.C., with a frequency of 50 Hertz, pulse duration of five msec. and a train of one second in length.

During initial avoidance conditioning, the CS was again presented in ten-second blocks followed by the unconditioned stimulus (UCS) until the avoidance response occurred. If a conditioned response (CR) occurred within the ten-second limit the CS was terminated immediately. The CS intertrial interval ranged from eight to 30 seconds. As the latency for the CR to appear decreased with conditioning, the number of trials needed to produce a trace of 100 sweeps increased.

c. Unavoidable Shock (CER)

During conditioned emotional response (CER) elaboration, the environmental stimuli were again changed. The partition was replaced and the rat was placed in that half not containing the drinking lever. In addition a special retaining wall was placed over the top of the Skinner Box, doubling its total height and thereby preventing the animal from jumping out. The CS again was presented in ten-second blocks after which an UCS of 0.3 to 0.5 mA D.C. was presented regardless of the response made by the rat. The CS intertrial interval ranged from ten to 20 seconds and all gross movements during the CS were recorded on a separate channel of the EEG machine.

d. Training and Recording Sequence

The usual daily procedure for six of the animals (R37, R38, R39, R40, R41 and R42) consisted of a drinking session followed by a session of aversive training (avoidance or CER). In this manner we had daily comparisons of positive and negative motivational states. Three of the animals (R44, R45, R46) served only as drinking controls for a month after which they were each subjected to drinking and only one aversive situation i.e., R46 had daily sessions of drinking followed by unavoidable shock, R45 had daily sessions of drinking followed by avoidance conditioning and R44 had daily sessions of drinking followed by punishment.

With R37, R38 and R40 the block of avoidance trials was followed by the block of unavoidable shock trials whereas with R41 and R42 avoidance conditioning preceded as well as superceded the block of unavoidable shock trials.

Training, conditioning and recording of all animals was completed within a span of seven weeks. R37, R38, R39, R40, R41 and R42 had daily sessions of drinking followed by aversive conditioning such that within the seven-week period these six animals had each been subjected to extinction, punishment, unavoidable shock and avoidance conditioning. See fig. 2 for a complete summary of recording sessions for all the animals. Each symbol represents one daily session. On some days two or more different conditioning procedures were employed consecutively (drinking, extinction, punishment, avoidance or CER) and this is illustrated by appropriate symbols lined up in a vertical fashion.

Results of the extinction and punishment trials with R37, R38, R40, R41 and R42 are not included in this report and the results of R39

are incomplete as he lost his electrode in the early stages of avoidance conditioning.

6. Statistical Methods Applied

A considerable portion of the data was statistically evaluated by means of the student t-test (unpaired). To the remainder we successively applied analysis of variance and Duncan's new multiple-range test as outlined by Steel, R. G. D. & J. H. Torrie (1960). : Principles and Procedures of Statistics. McGraw-Hill Book Company, Inc., New York, Toronto, London.

Fig.2 Summary Table of Training and Recording Sessions

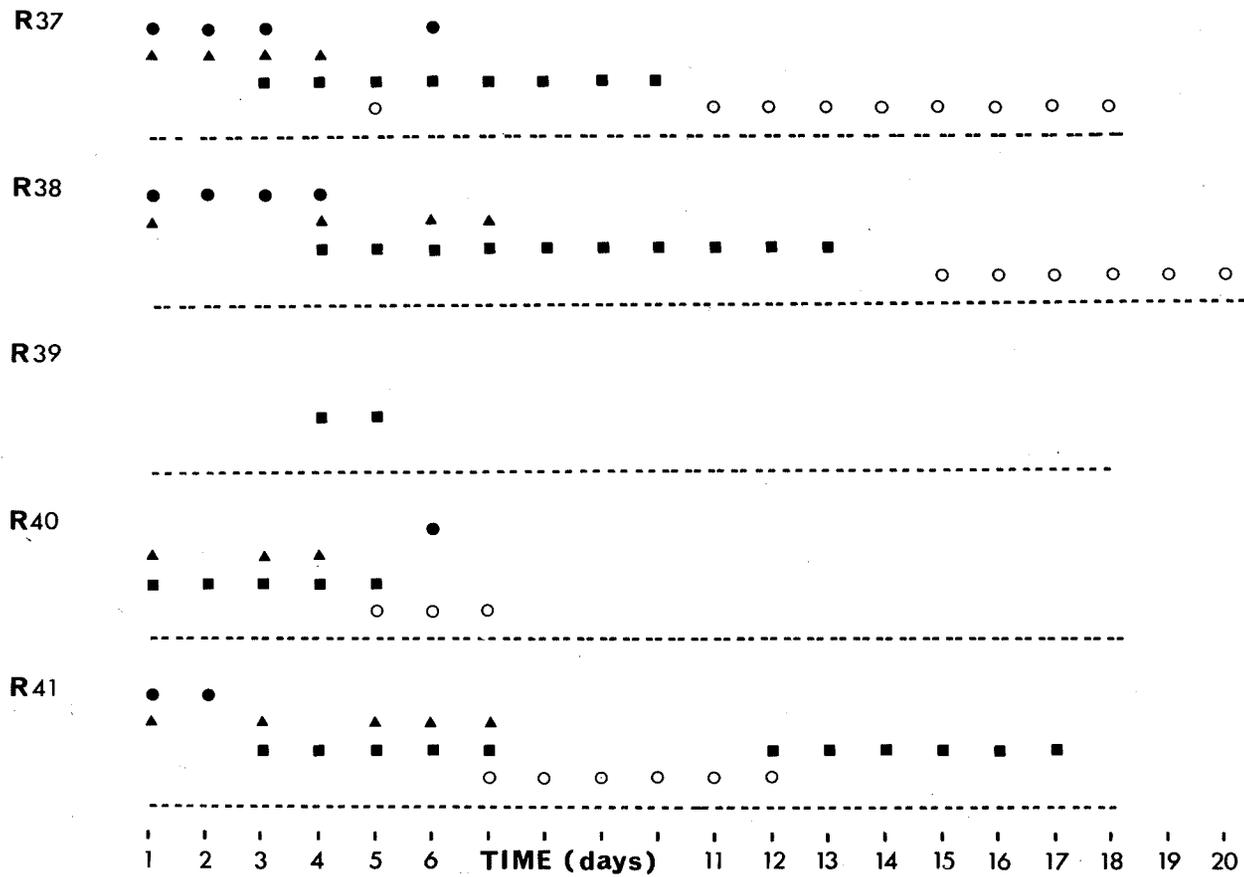
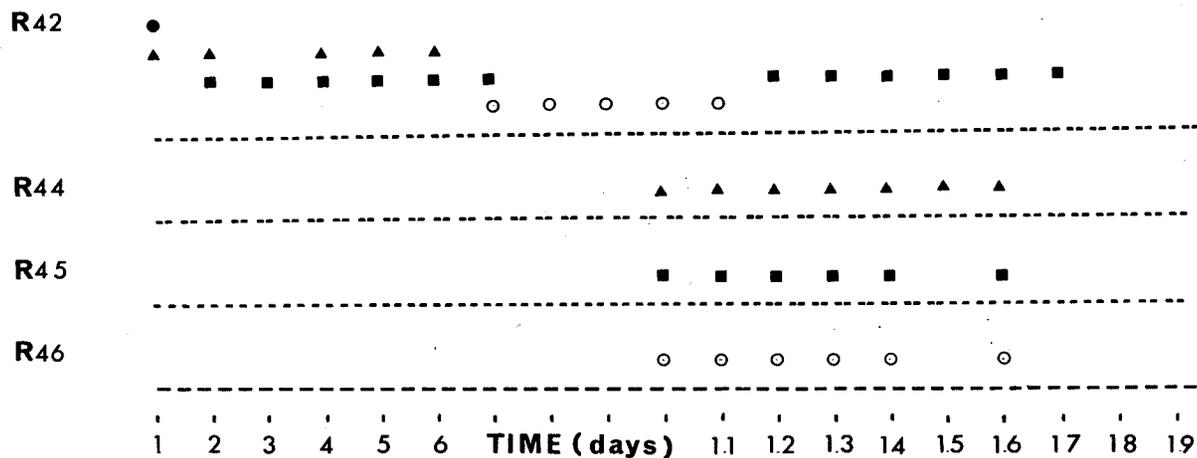


Fig.2 continued



LEGEND:

- Extinction:** ● ●
- Punishment:** ▲ ▲
- Avoidance:** ■ ■
- CER:** ○ ○

Each Symbol represents one daily session. Where several conditioning procedures were employed consecutively on the same day, the symbols are lined up in a vertical fashion. The time scale indicates consecutive recording sessions which may or may not represent consecutive calendar days as the animals were generally not run on weekends. The time scale is aligned in such a manner that it also gives the training sequence of each animal relative to every other animal. Conditioned drinking responses were recorded every session in every animal.

C. RESULTS

1. Definition and Nomenclature of segments of the Evoked Potential Measured

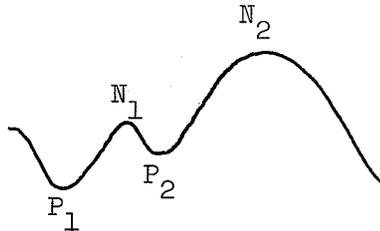


Fig. 3 A typical evoked response from the auditory cortex

Although the physiological bases of early and late components of evoked potentials (responses) have been reviewed it would be expedient now to make a distinction in terms of nomenclature. The initial surface-positive deflection P_1 in fig. 3 is followed by three peaks of alternating polarities (N_1 , P_2 , N_2). The early components P_1 and N_1 will be called the primary components of the evoked potential or the primary evoked potentials and their amplitudes have been measured as the voltage difference between the two peaks P_1 and N_1 . Similarly the late components P_2 and N_2 will be called the secondary components of the evoked potential or the secondary evoked potentials and their amplitudes have been measured as the voltage difference between the two peaks P_2 and N_2 . However, the maximal amplitude deflection of the evoked potential can be between P_1 and N_1 , P_1 and N_2 , P_2 and N_1 or between P_2 and N_2 .

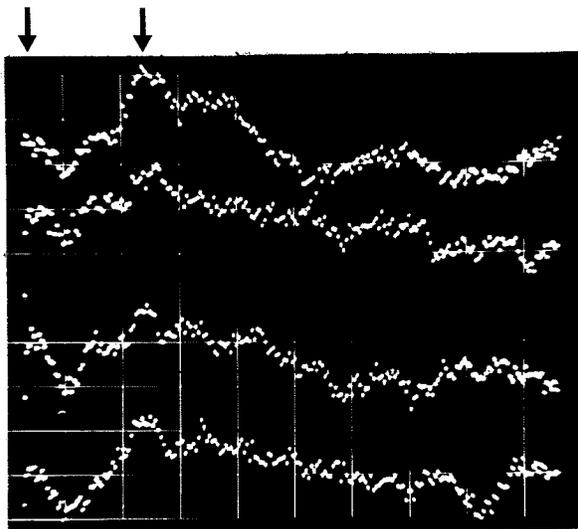
2. Evoked Potentials during the CS Period which precedes and is continuous with Lever-Pressing prior to Water Reward

In three animals (R37, R45 and R46) where complete data was

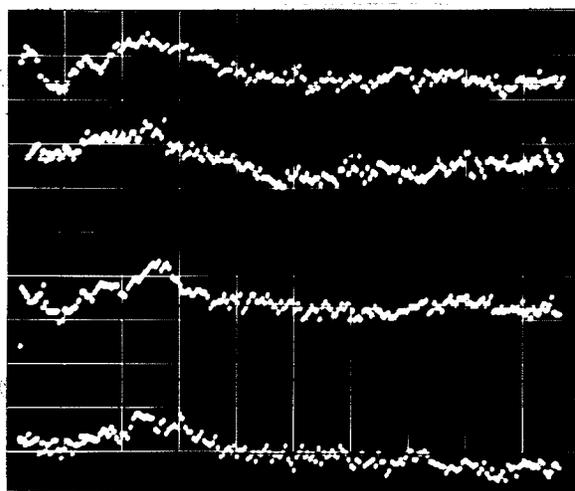
available, evoked responses to the CS preceding water reward decreased during the seven-week period (fig. 4 and fig. 5). However, the decreases in evoked potential amplitudes of R37 (table I and table II) are remarkably similar to those of R45 (table III) and R46 (table IV); the decreases being greater during the CS period preceding lever-pressing for water reward within the block of CER conditioning trials than during the CS period preceding lever-pressing for water reward within the block of avoidance conditioning trials. The primary and secondary evoked potentials in R37 and R46 during drinking conditioning within the CER block as compared to evoked potentials during earlier drinking conditioning which was not followed by aversive trials, showed a decrease significant at the .01 level (table I and table IV). However, primary evoked potentials in R37 and R45 during drinking conditioning within the avoidance block as compared to evoked potentials during earlier drinking conditioning, showed a decrease in amplitude that was significant only at the .05 level (table II and table III).

However, once aversive conditioning had begun the drinking means during CER, Avoidance Learning, Avoidance Learned I and Avoidance Learned II (table V and fig. 6) showed no statistically significant changes ($p > .05$). The control animals, R45 and R46 showed the same trend (table VI, table VII, fig. 7 and fig 8). A comparison of fig. 7 and fig. 8 indicates that the greatest decrease in evoked potential amplitudes occurred initially, before aversive conditioning began. R38 (fig. 9) is typical of the control animals, showing no significant change in the drinking response between avoidance conditioning and CER conditioning ($p > .05$ by the Duncan Test).

(a)
Evoked potentials during the CS period preceding and continuous with lever-pressing prior to water reward and within the block of drinking conditioning only. we are concerned only with that portion of the evoked response that is found within the arrows.



(b)
Evoked potentials during the CS period prior to water reward and within the block of avoidance conditioning trials.



(c)
Evoked potentials during the CS period prior to water reward and within the block of CER trials.

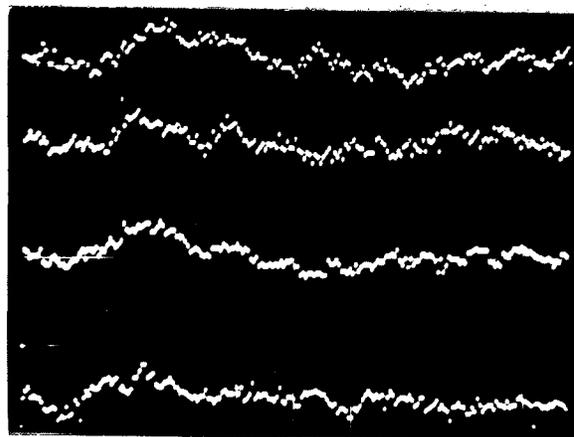
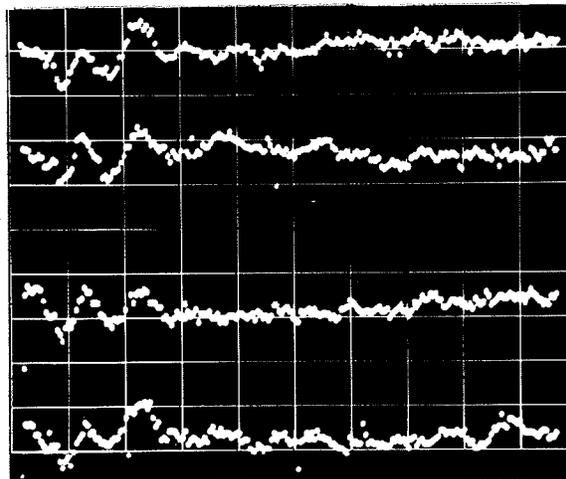


Fig. 4 Drinking evoked potentials during drinking conditioning, avoidance conditioning and CER training (R37).

(a)
Evoked potentials during the CS
period preceding and continuous
with lever-pressing prior to
water reward and within the block
of drinking conditioning only.



(b)
Evoked potentials during the CS
period prior to water reward and
within the block of CER trials.

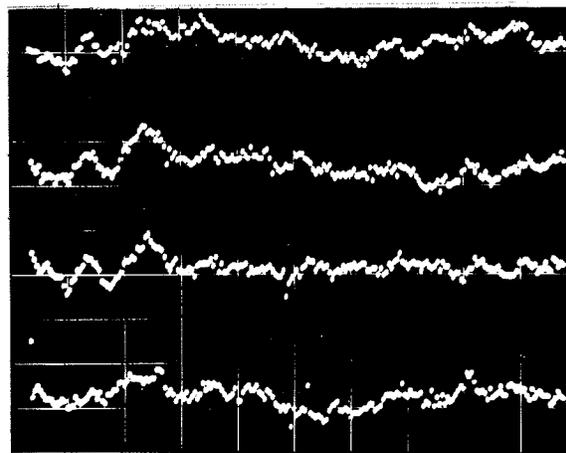


Fig. 5 Drinking evoked potentials during drinking conditioning
and CER training (R46).

TABLE I

COMPARISON OF EVOKED POTENTIALS DURING THE CS PRIOR TO DRINKING WITHIN THE BLOCK OF DRINKING CONDITIONING ONLY AND EVOKED POTENTIALS DURING THE CS PRIOR TO DRINKING WITHIN THE BLOCK OF CER TRIALS (R37)

Evoked potential amplitude prior to drinking exclusively				Evoked potential amplitudes prior to drinking within the block of CER trials			
Date	Prim. (μV)	Sec. (μV)	Max. (μV)	Date	Prim. (μV)	Sec. (μV)	Max. (μV)
June 27*	38.5	48.5	75.6	Aug. 24	24.3	34.2	44.9
July 2*	42.1	47.8	72.7	25	23.7	31.3	41.8
				26	25.0	25.7	40.6
Mean	40.3	48.2	74.2		24.3	30.4	42.4
S. D.	2.5	0.5	2.1		0.7	4.3	2.2
S. E.	1.8	0.3	1.5		0.4	2.5	1.3
d. f.	3	3	3		3	3	3
t-value	11.2	5.5	16.1		11.2	5.5	16.1
Probability	<.01	<.01	<.01		<.01	<.01	<.01

* The values of the evoked potential amplitudes for each day usually represent a mean of 100 CS presentations

S. D. = Standard deviation

S. E. = Standard error

d. f. = Degrees of freedom

TABLE II

EVOKED POTENTIALS DURING THE CS PRIOR TO DRINKING WITHIN THE BLOCK OF DRINKING
CONDITIONING AND WITHIN THE BLOCK OF AVOIDANCE CONDITIONING (R37)

Evoked potential amplitude prior to drinking exclusively				Evoked potential amplitudes prior to drinking within the block of Avoidance Learned I trials			
Date	Prim. (μV)	Sec. (μV)	Max. (μV)	Date	Prim. (μV)	Sec. (μV)	Max. (μV)
June 27	38.5	48.5	75.6	Aug. 12	33.5	35.7	57.0
July 2	42.1	47.8	72.7	12	25.7	42.0	52.7
				13	37.1	39.9	62.7
				14	27.1	29.2	43.5
Mean	40.3	48.2	74.2		30.9	36.7	54.0
S. D.	2.5	0.5	2.1		5.4	5.6	8.1
S. E.	1.8	0.3	1.5		2.7	2.8	4.0
d. f.	4	4	4		4	4	4
t-value	2.26	2.7	3.29		2.26	2.7	3.29
Probability	< .05	< .05	< .025		< .05	< .05	< .025

The values of the evoked potential amplitudes for each day usually represent a mean of 100 CS presentations.

TABLE III

EVOKED POTENTIALS DURING THE CS PRIOR TO DRINKING, WITHIN THE BLOCK OF DRINKING
CONDITIONING AND WITHIN THE BLOCK OF AVOIDANCE CONDITIONING (R45)

Evoked potential amplitudes prior to drinking exclusively				Evoked potential amplitudes prior to drinking within the block of avoidance conditioning			
Date	Prim. (μV)	Sec. (μV)	Max. (μV)	Date	Prim. (μV)	Sec. (μV)	Max. (μV)
July 7	32.1	43.5	46.4	Aug. 14	27.6	26.6	35.1
7	28.5	29.9	39.9	17	21.4	30.7	41.4
24	30.7	27.8	37.1	18	18.6	32.8	34.9
Aug. 4	27.8	27.1	36.3	19	25.7	17.8	34.2
5	23.5	38.5	44.2	22	22.8	25.7	39.2
6	32.1	26.4	42.8	24	23.5	23.5	32.1
7	19.6	27.5	35.6				
Mean	27.8	31.5	40.3		23.3	26.2	36.2
S. D.	4.7	6.7	4.2		3.2	5.3	3.5
S. E.	1.8	2.5	1.6		1.3	2.2	1.4
d. f.	11	11	11		11	11	11
t-value	1.98	1.57	1.93		1.98	1.57	1.93
Probability	<.05	>.05	<.05		<.05	>.05	<.05

The values of the evoked potential amplitudes for each day usually represent a mean of 100 CS presentations.

TABLE IV

EVOKED POTENTIALS DURING THE CS PRIOR TO DRINKING WITHIN THE BLOCK OF
 DRINKING CONDITIONING AND EVOKED POTENTIALS DURING THE CS PRIOR
 TO DRINKING WITHIN THE BLOCK OF CER TRIALS (R46)

Evoked potential amplitudes prior to drinking exclusively				Evoked potential amplitudes prior to drinking within the block of CER trials			
Date	Prim. (μV)	Sec. (μV)	Max. (μV)	Date	Prim. (μV)	Sec. (μV)	Max. (μV)
July 7	34.2	41.4	44.9	Aug. 14	29.2	35.6	41.4
24	39.9	42.1	51.3	17	28.5	34.9	42.8
Aug. 4	32.1	38.5	47.1	18	24.2	37.1	44.2
5	39.9	42.1	47.8	19	29.9	34.9	39.2
6	25.7	40.6	41.3	22	28.5	39.2	45.6
7	34.2	44.9	48.5	24	23.5	31.4	34.2
Mean	34.3	41.6	46.8		27.3	35.5	41.2
S. D.	5.3	2.1	3.4		2.7	2.6	4.1
S. E.	2.2	0.9	1.4		1.1	1.1	1.7
d. f.	10	10	10		10	10	10
t-value	2.88	4.46	2.57		2.88	4.46	2.57
Probability	<.01	<.01	<.025		<.01	<.01	<.025

The values of the evoked potential amplitudes for each day usually represent a mean of 100 CS presentations.

TABLE V

* MEANS OF EVOKED POTENTIALS RECORDED DURING THE CS PERIOD PRIOR TO DRINKING AND WITHIN THE BLOCKS OF CER TRAINING, AVOIDANCE LEARNING, AVOIDANCE LEARNED I, AND AVOIDANCE LEARNED II

PRIMARY EVOKED POTENTIALS

Condition	Number	Mean	Standard Deviation	Number of observations
CER I & II	2	31.8	10.4	29
Av. Learning	5	34.1	8.5	6
Av. Learned I	9	36.2	12.5	9
Av. Learned II	4	33.4	8.8	13

Cross correlations 2-5, 2-9, 2-4, 5-9, 5-4, 9-4 were not significant at the 5% level.

SECONDARY EVOKED POTENTIALS

Condition	Number	Mean	Standard Deviation	Number of observations
CER I & II	4	31.2	6.6	29
Av. Learning	8	36.4	13.7	6
Av. Learned I	5	31.4	8.9	9
Av. Learned II	2	30.8	6.8	13

Cross correlations 4-8, 4-5, 4-2, 8-5, 8-2, 5-2 were not significant at the 5% level.

MAXIMAL EVOKED POTENTIALS

Condition	Number	Mean	Standard Deviation	Number of observations
CER I & II	4	47.4	6.8	29
Av. Learning	5	49.0	9.0	6
Av. Learned I	7	51.0	10.6	9
Av. Learned II	3	46.6	7.1	13

Cross correlations 4-5, 4-7, 4-3, 5-7, 5-3, 7-3 were not significant at the 5% level

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

Fig. 6

Once aversive conditioning had begun, the means of the drinking amplitudes during avoidance and CER showed no statistically significant changes ($p > .05$).

Fig. 6

Means of evoked potentials recorded from R37, R38, R39, R40, R41 and R42 during the CS period prior to drinking and within the blocks of CER training, Avoidance Learning, Avoidance Learned I and Avoidance II.

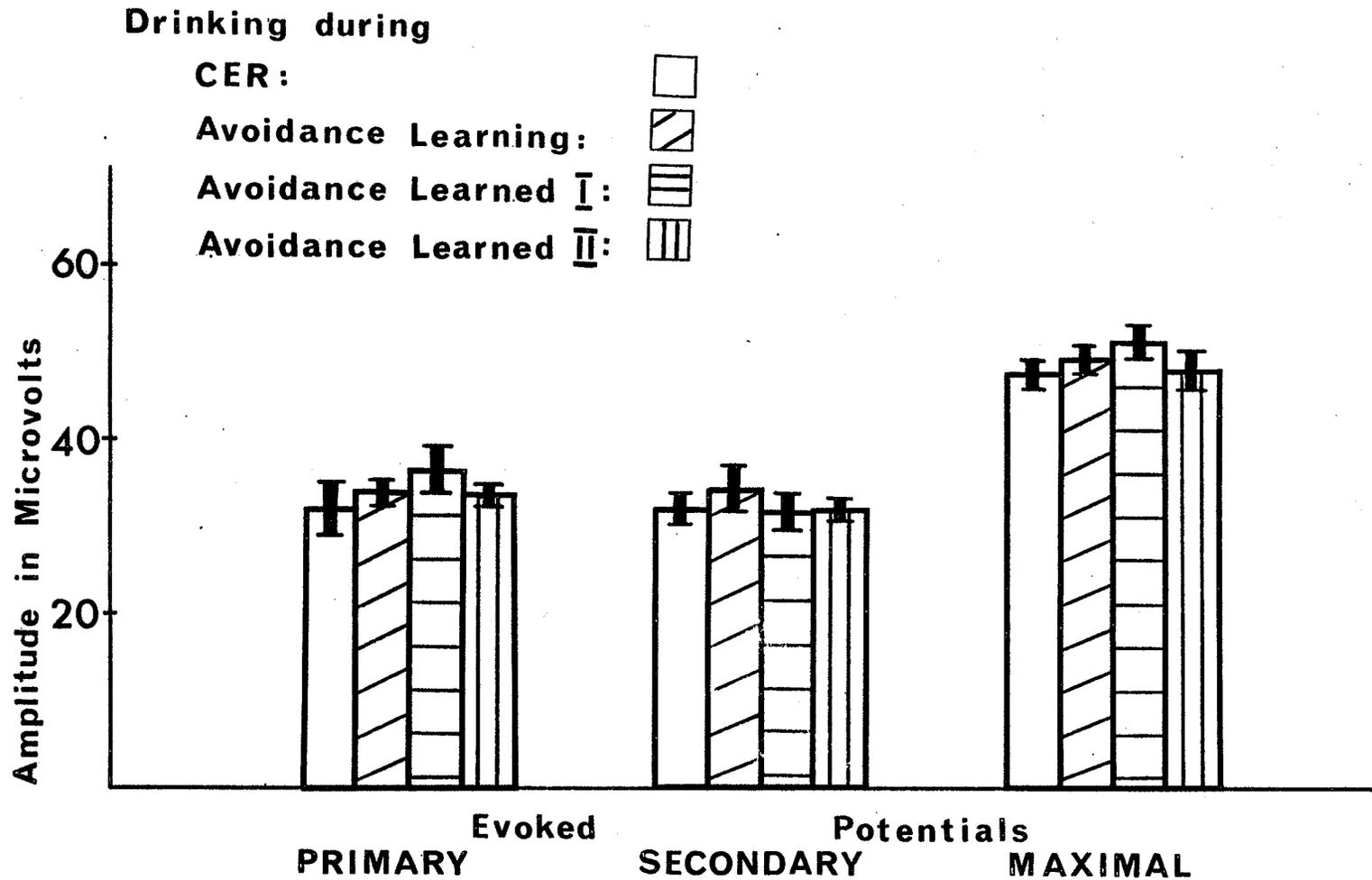


TABLE VI

STATISTICAL COMPARISON OF EVOKED POTENTIALS DURING THE CS PERIOD PRIOR TO DRINKING,
WITHIN THE STAGE OF AVOIDANCE LEARNING AND WITHIN THE STAGE OF AVOIDANCE LEARNED I (R45)

Evoked potential amplitudes prior to drinking within the stage of Avoidance Learning				Evoked potential amplitudes prior to drinking within the stage of Avoidance Learned I			
Date	Prim. (μ V)	Sec. (μ V)	Max. (μ V)	Date	Prim. (μ V)	Sec. (μ V)	Max. (μ V)
Aug. 14	27.6	26.6	35.1	Aug. 19	25.7	17.8	34.2
17	21.4	30.7	41.4	22	22.8	25.7	39.2
				24	23.5	23.5	32.1
Mean	24.5	28.7	38.3		24.0	22.3	35.2
S. D.	4.4	2.9	4.4		1.5	4.1	3.7
S. E.	3.1	2.0	3.1		0.9	2.4	2.1
d. f	3	3	3		3	3	3
t-value	0.19	1.86	0.86		0.19	1.86	0.86
Probability	>.05	>.05	>.05				

TABLE VII

STATISTICAL COMPARISON OF EVOKED POTENTIALS DURING THE CS PERIOD PRIOR TO DRINKING,
WITHIN THE STAGE OF EARLY CER TRAINING AND WITHIN THE STAGE OF LATE CER TRAINING (R46)

Evoked potential amplitudes prior to drinking within the stage of Early CER training				Evoked potential amplitudes prior to drinking within the stage of Late CER training			
Date	Prim. (μV)	Sec. (μV)	Max. (μV)	Date	Prim. (μV)	Sec. (μV)	Max. (μV)
Aug. 14	29.2	35.6	41.4	Aug. 19	29.9	34.9	39.2
17	28.5	34.9	42.8	22	28.5	39.2	45.6
18	24.2	37.1	44.2	24	23.5	31.4	34.2
Mean	27.3	35.9	42.8		27.3	35.2	39.7
S. D.	2.7	1.1	1.4		3.4	3.9	5.7
S. E.	1.6	0.6	0.8		1.9	2.3	3.3
d. f.	4	4	4		4	4	4
t-value	0	.3	.92		0	.3	.92
Probability	> .05	> .05	> .05		.	.	.

Fig. 7

Evoked potential amplitudes during the CS prior to drinking within the block of only drinking conditioning and evoked potential amplitudes during the CS prior to drinking within the block of avoidance conditioning (R45). Evoked potential amplitudes for each day usually represent a mean of 100 CS clicks.

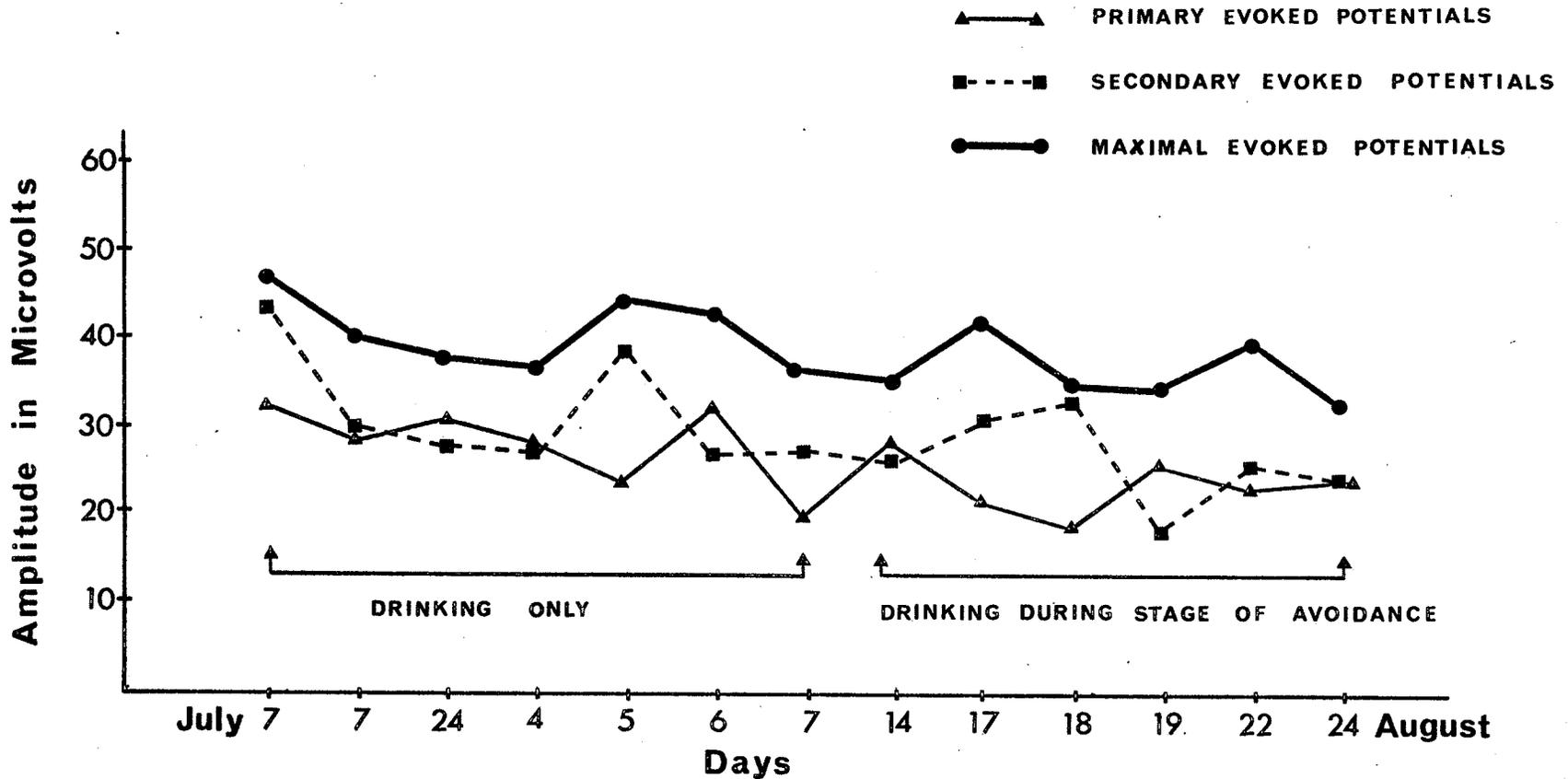


Fig.8

Evoked potential amplitudes during the CS prior to drinking within the stage of only drinking conditioning and evoked potential amplitudes during the CS prior to drinking within the stage of Unavoidable Shock (R46). Evoked potential amplitudes for each day usually represent a mean of 100 CS clicks.

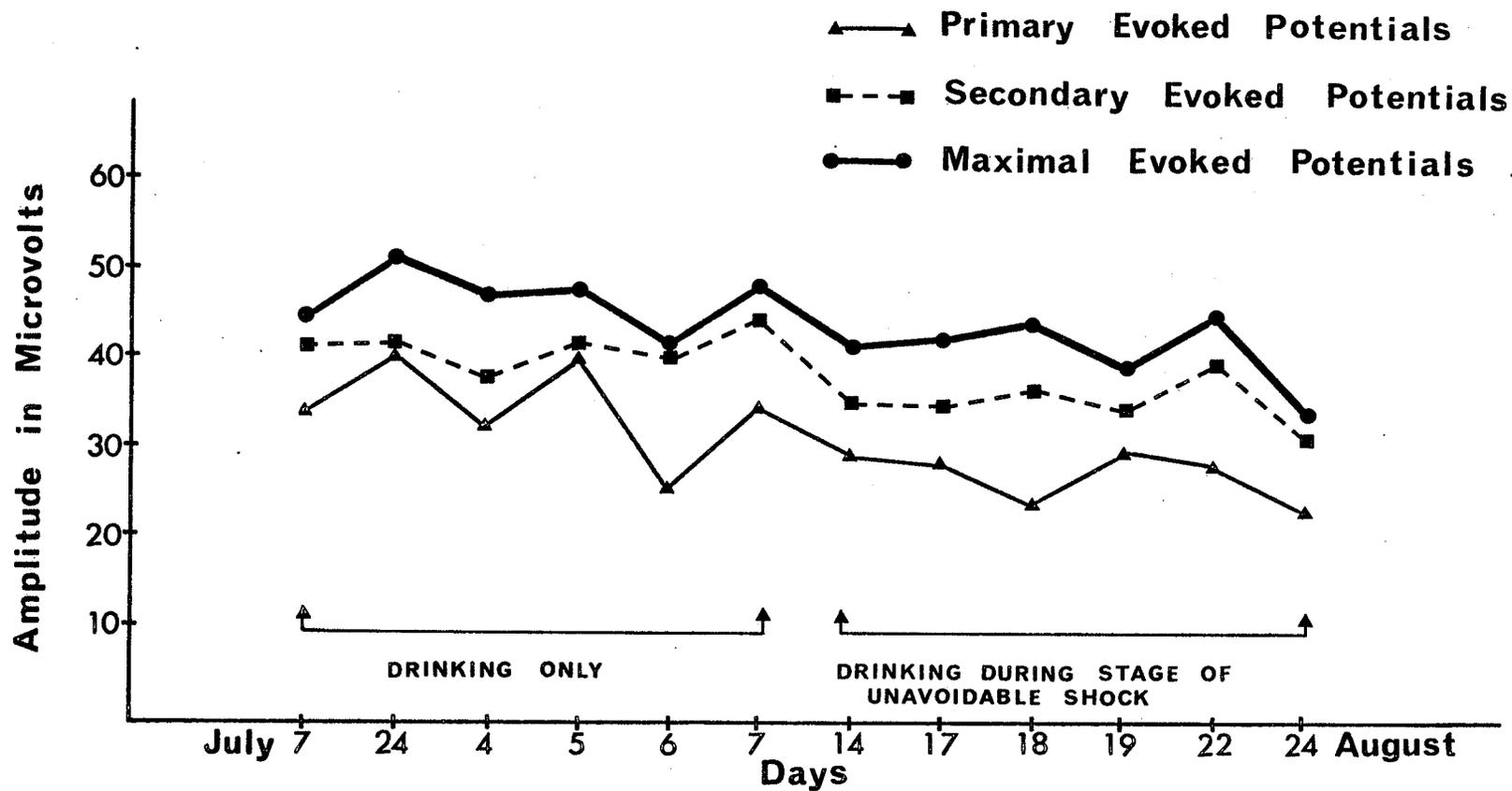
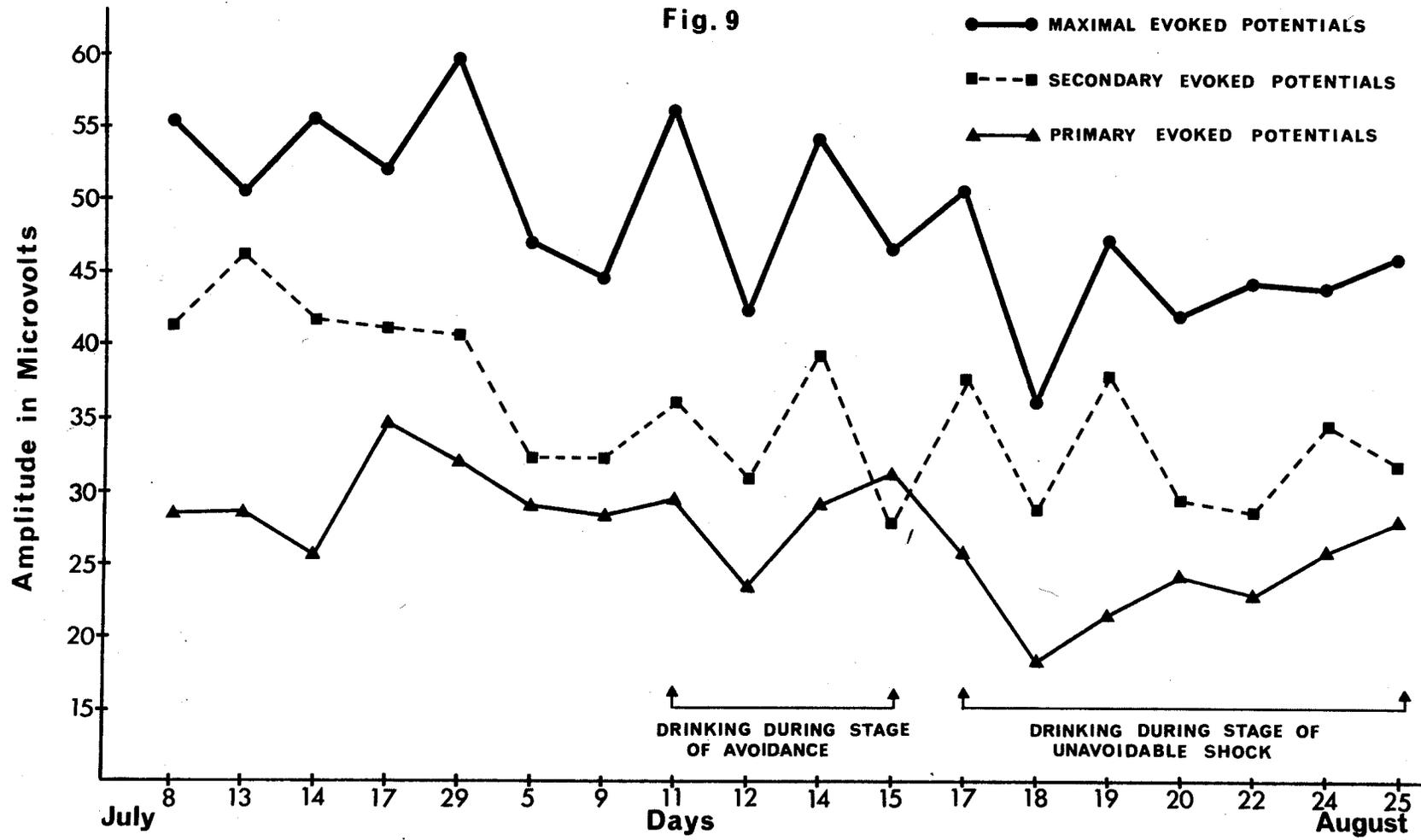


Fig. 9

Evoked potential amplitudes during the CS prior to drinking within the stage of avoidance conditioning and evoked potential amplitudes during the CS prior to drinking within the stage of Unavoidable Shock conditioning (R38).

Evoked potential amplitudes for each day usually represent a mean of 100 CS clicks.

Fig. 9



In a similar fashion, the potentials evoked by a CS prior to drinking in each animal during the period of avoidance conditioning (fig. 10 and fig. 11) and during the period of CER conditioning (fig. 12) showed sometimes visible but not significant decreases in amplitude ($p > .05$).

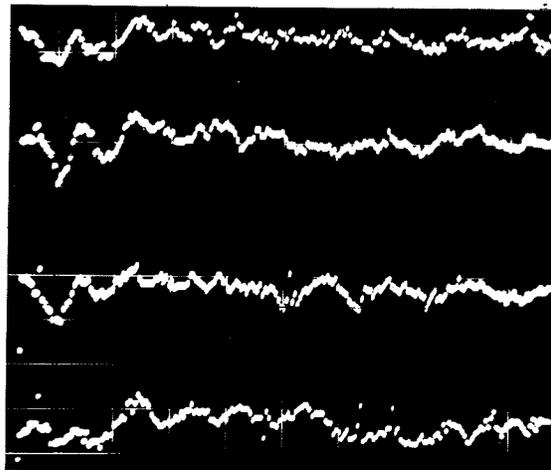
Of considerable interest is the comparison between fig. 11(b) and fig. 13(c). The former represents the drinking response during the period of avoidance overtraining (80%+ correct responses) while the latter represents the avoidance response during the same session. It is evident that the evoked potentials during drinking and during avoidance in this single session are similar with regard to amplitude and configuration. Unless one were "in the know", it would be easy to mistake fig. 13(c) for a drinking response. This becomes easier to comprehend when one compares fig. 13(c) with fig. 14, the latter representing a drinking response which is larger in amplitude than the previous avoidance response. This similarity was evident only in R41 but might also have occurred in the other animals if conditioning trials had been continued further.

3. Acoustically Evoked Potentials during Avoidance Conditioning

The data from the conditioned avoidance experiment was divided into three sections: Learning (before 80% CR criterion), Learned I (after 80% CR criterion) and Learned II (overtraining i.e., 80%+ CR).

A comparison of figs. 13 and 15 with figs. 16, 17 and 18 would indicate that there is a visible decrease in evoked response amplitude with increased learning in each animal i.e., the evoked response amplitudes were smaller during Learned II than during Learning. However, a

(a)
Evoked potentials prior to drinking
during period of avoidance conditioning
when 80% response criterion is
reached.



(b)
Evoked potentials prior to drinking
during period of avoidance over-
training (80%+).

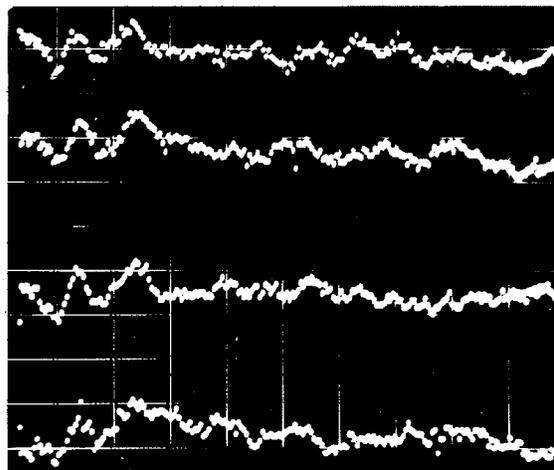
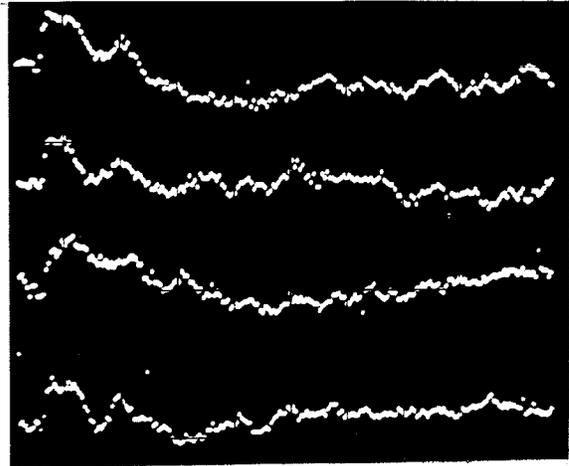


Fig. 10 Potentials evoked by CS preceding lever-pressing for
water during the period of avoidance conditioning (R42).

(a)

Potentials evoked by a CS preceding and continuous with lever-pressing for water reward during early avoidance conditioning (criterion not reached).



(b)

Potentials evoked by a CS preceding and continuous with lever-pressing for water reward during avoidance overtraining (80%+ correct responses)

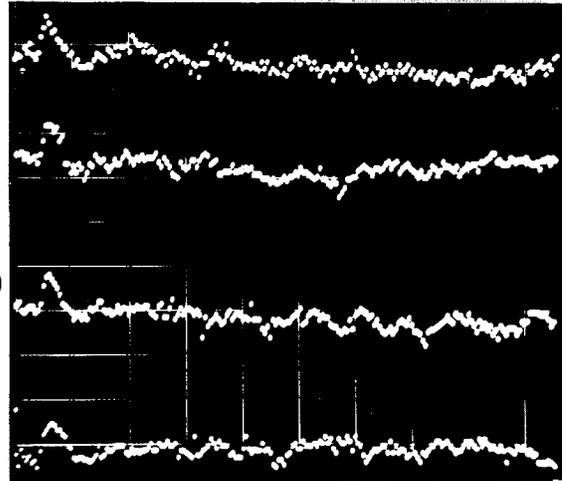
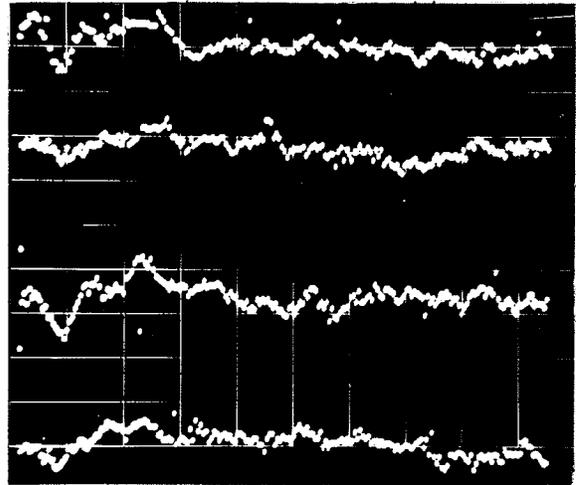


Fig. 11 Potentials evoked prior to drinking during the period of avoidance conditioning (R41).

(a)

Evoked potentials prior to drinking during the stage of early CER training.



(b)

Potentials evoked by a CS prior to drinking reward during the stage of stable CER.

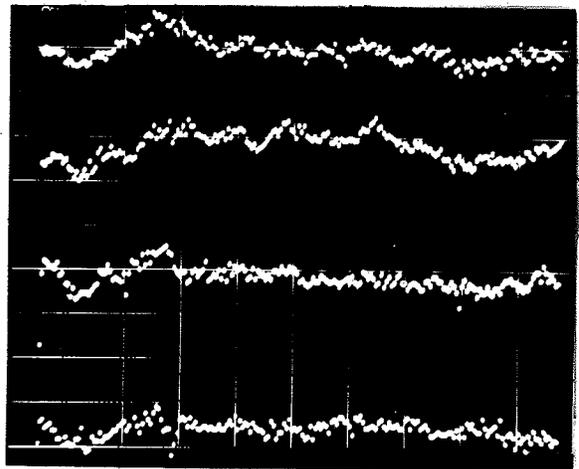
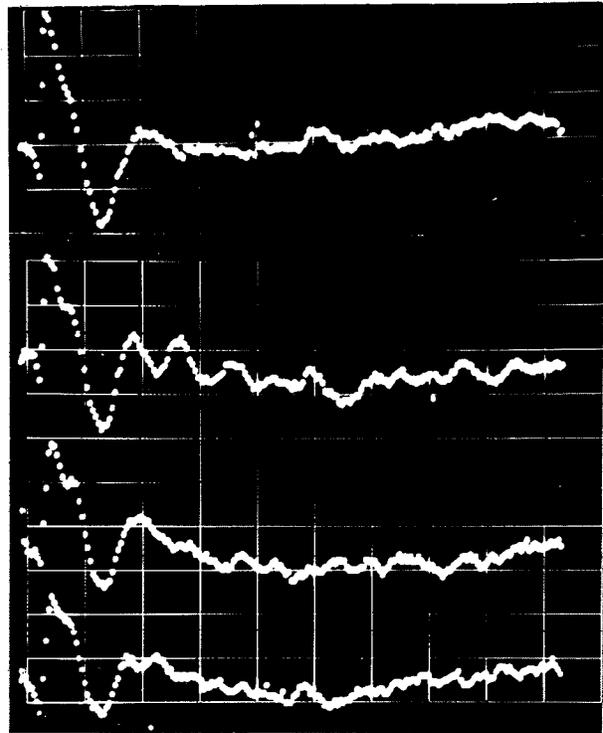


Fig. 12 Potentials evoked by a CS preceding lever-pressing for water during early CER and during stable established CER (R37).

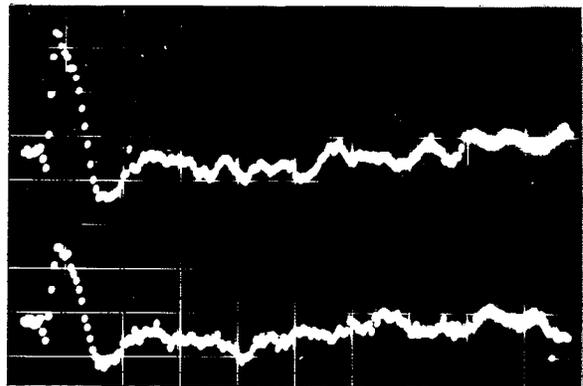
(a)

Evoked potentials during early avoidance conditioning (before 80% criterion was reached). Note the decrease in response amplitude from upper to lower trace during this particular session.



(b)

Evoked potentials during a later stage of avoidance conditioning when an 80% criterion has been reached.



(c)

Evoked potentials during a late stage of avoidance conditioning i.e., during criterion overtraining (80%+ correct response).

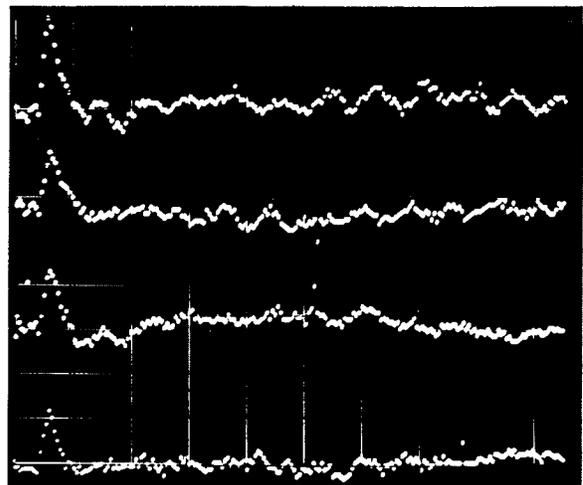
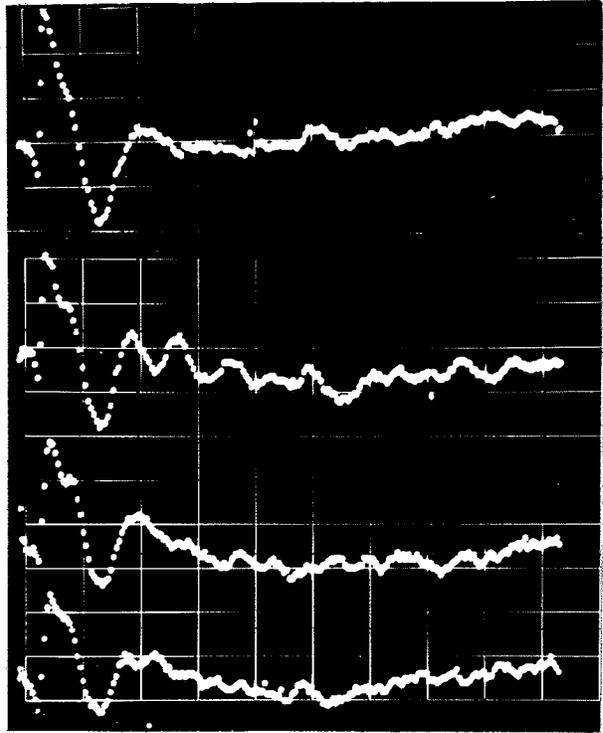


Fig. 13 Evoked avoidance responses (R41).

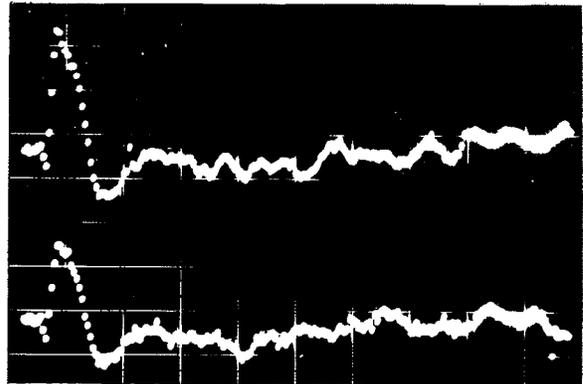
(a)

Evoked potentials during early avoidance conditioning (before 80% criterion was reached). Note the decrease in response amplitude from upper to lower trace during this particular session.



(b)

Evoked potentials during a later stage of avoidance conditioning when an 80% criterion has been reached.



(c)

Evoked potentials during a late stage of avoidance conditioning i.e., during criterion overtraining (80%+ correct response).

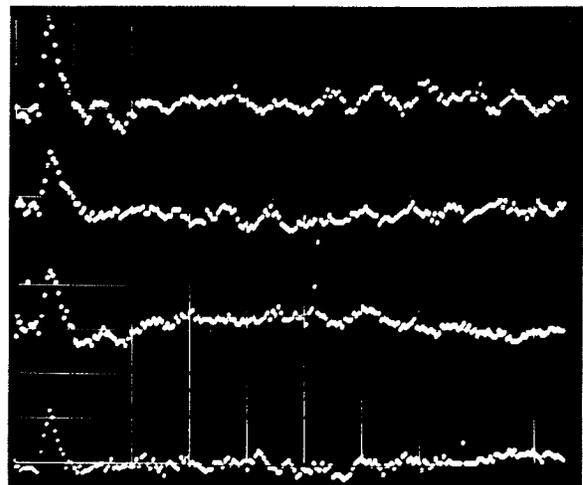
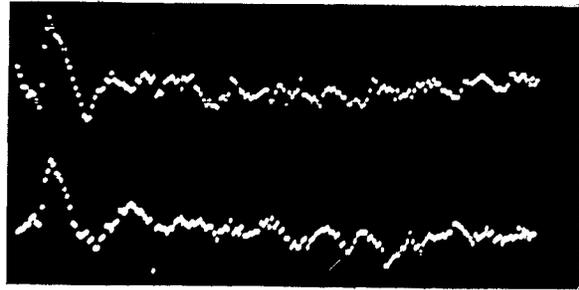


Fig. 13 Evoked avoidance responses (R41).

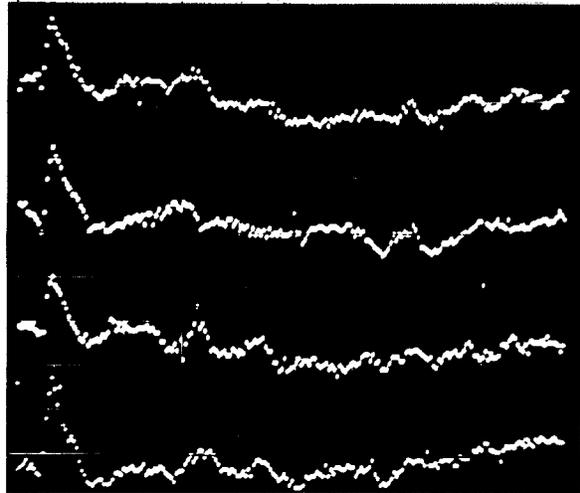
(a)

Potentials evoked by a CS prior to drinking during a period of avoidance training (Aug. 6, 1970).



(b)

Potentials evoked by a CS prior to drinking during a period of CER training (Aug. 18, 1970).



(c)

Potentials evoked by a CS prior to drinking during another period of avoidance training (Aug. 19, 1970).

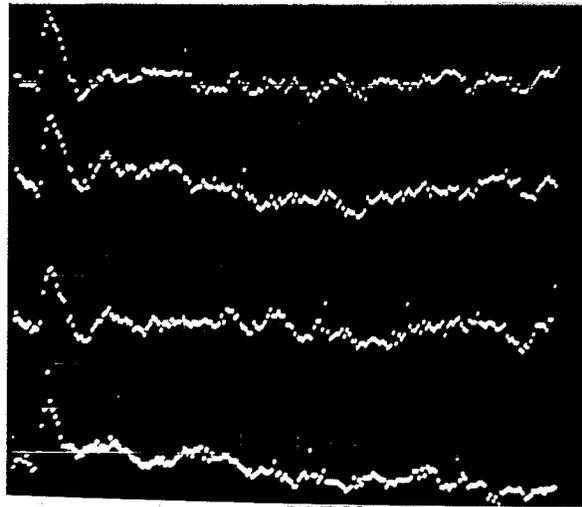
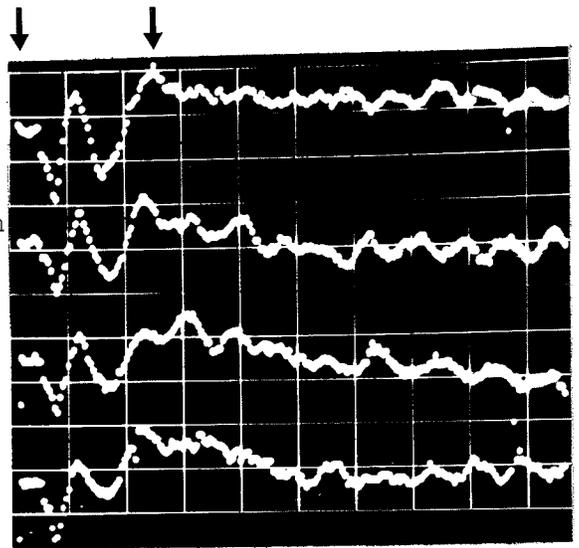


Fig. 14 Potentials, evoked by a CS preceding drinking, and recorded over a two-week interval during three different stages of aversive conditioning (R41).

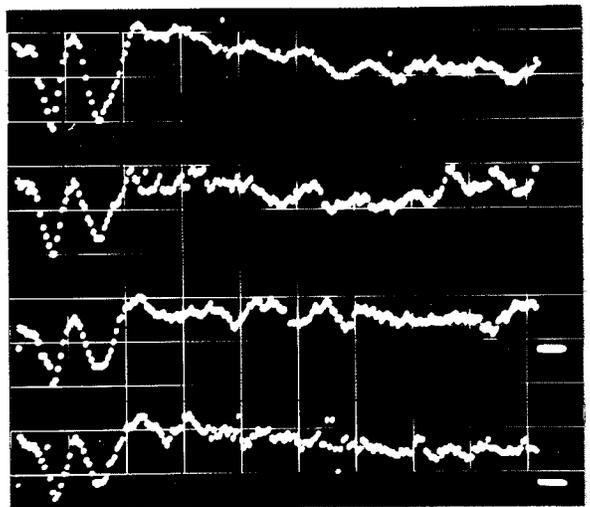
(a)

Evoked potentials during early avoidance conditioning (before 80% criterion was reached). We are concerned only with that portion of the evoked response that is found between the arrows.



(b)

Evoked potentials during avoidance conditioning following attainment of an 80% criterion performance.



(c)

Evoked potentials during criterion overtaining (80%+ correct avoidance responses).

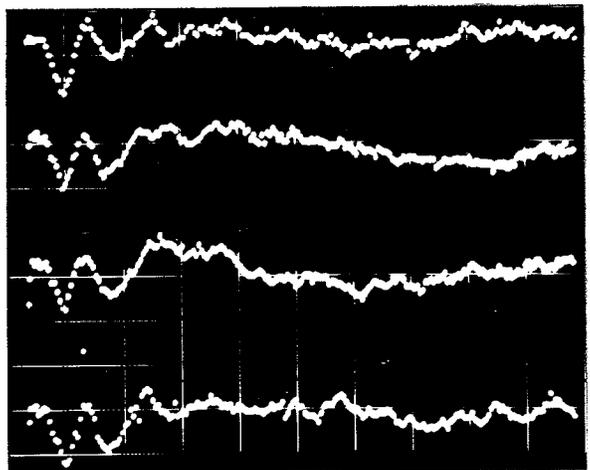


Fig. 15 Evoked avoidance responses (R42).

Fig. 16

Evoked potential amplitudes during avoidance conditioning (R41)

Evoked potential amplitudes for each day usually represent a mean of 100 CS clicks.

Legend: Learning - < 80% correct responses
Learned I - 80% correct responses
Learned II - > 80% correct responses

Fig. 16

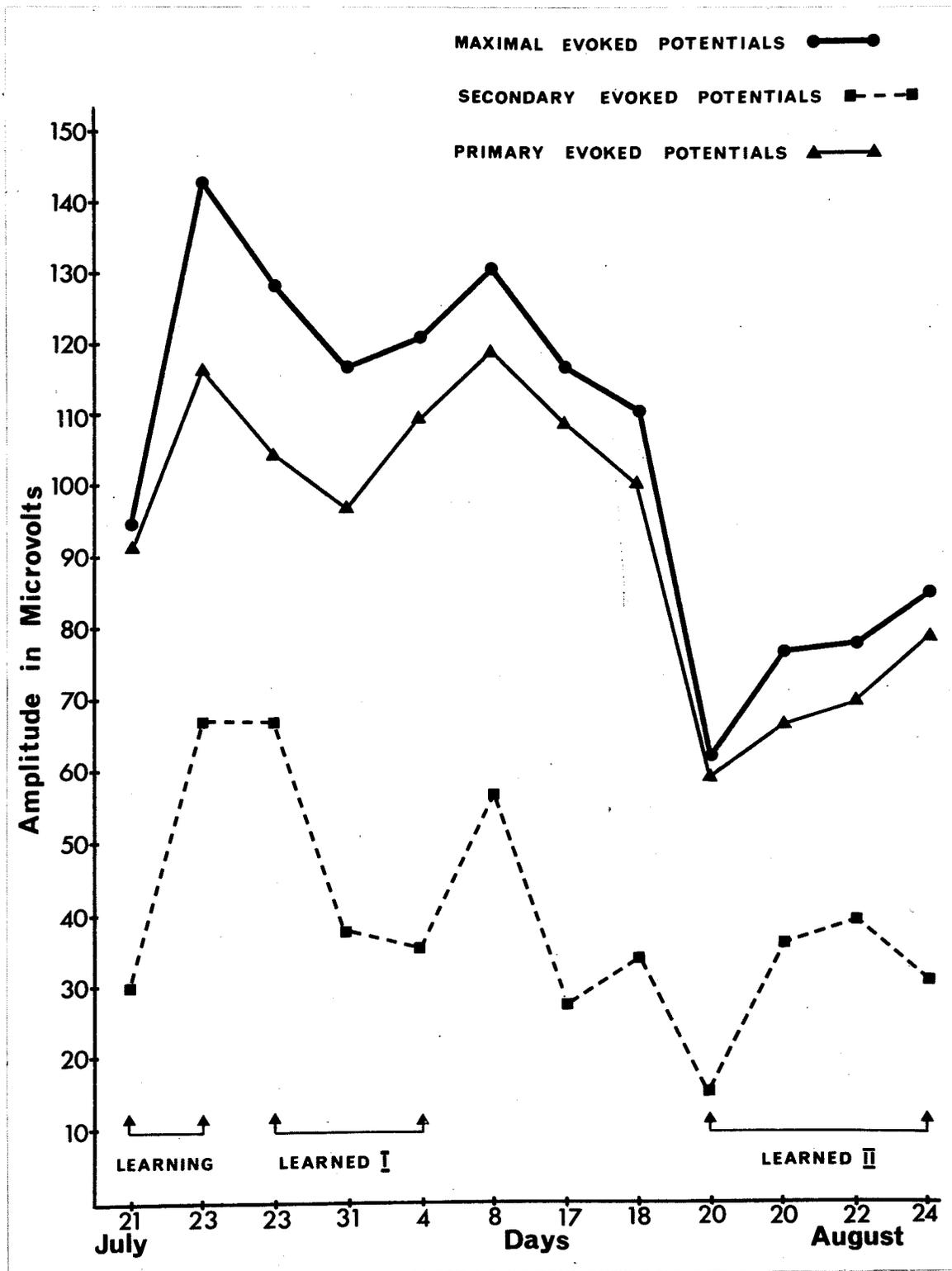


Fig. 17

Evoked potential amplitudes during avoidance conditioning
(R42)

Legend:

Escape	-	no learned responses
Learning	-	< 80% correct responses
Learned I	-	80% correct responses
Learned II	-	criterion overtraining (80% + avoidance)

Amplitudes for each day usually represent 100 CS clicks

Fig.17

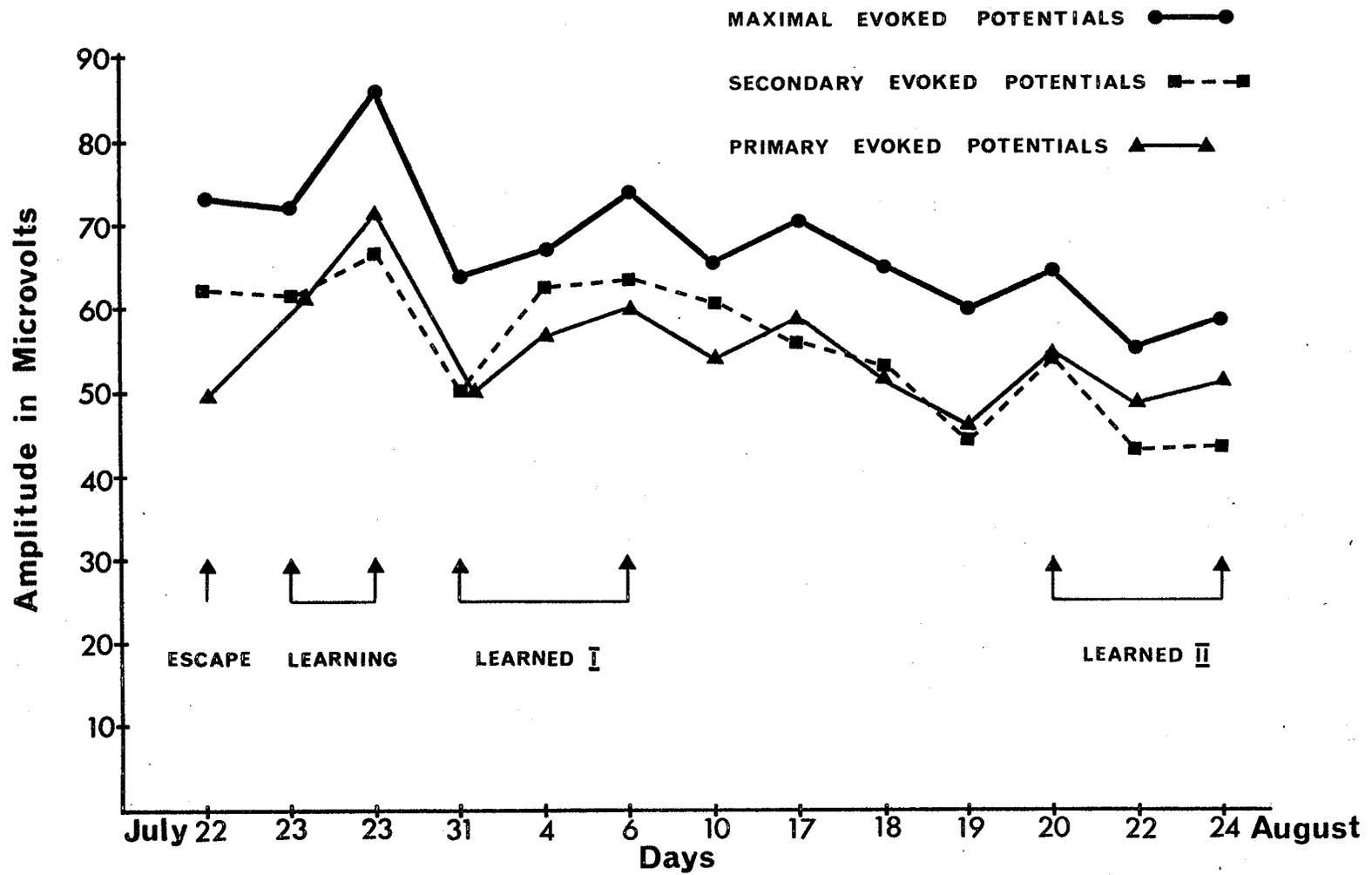
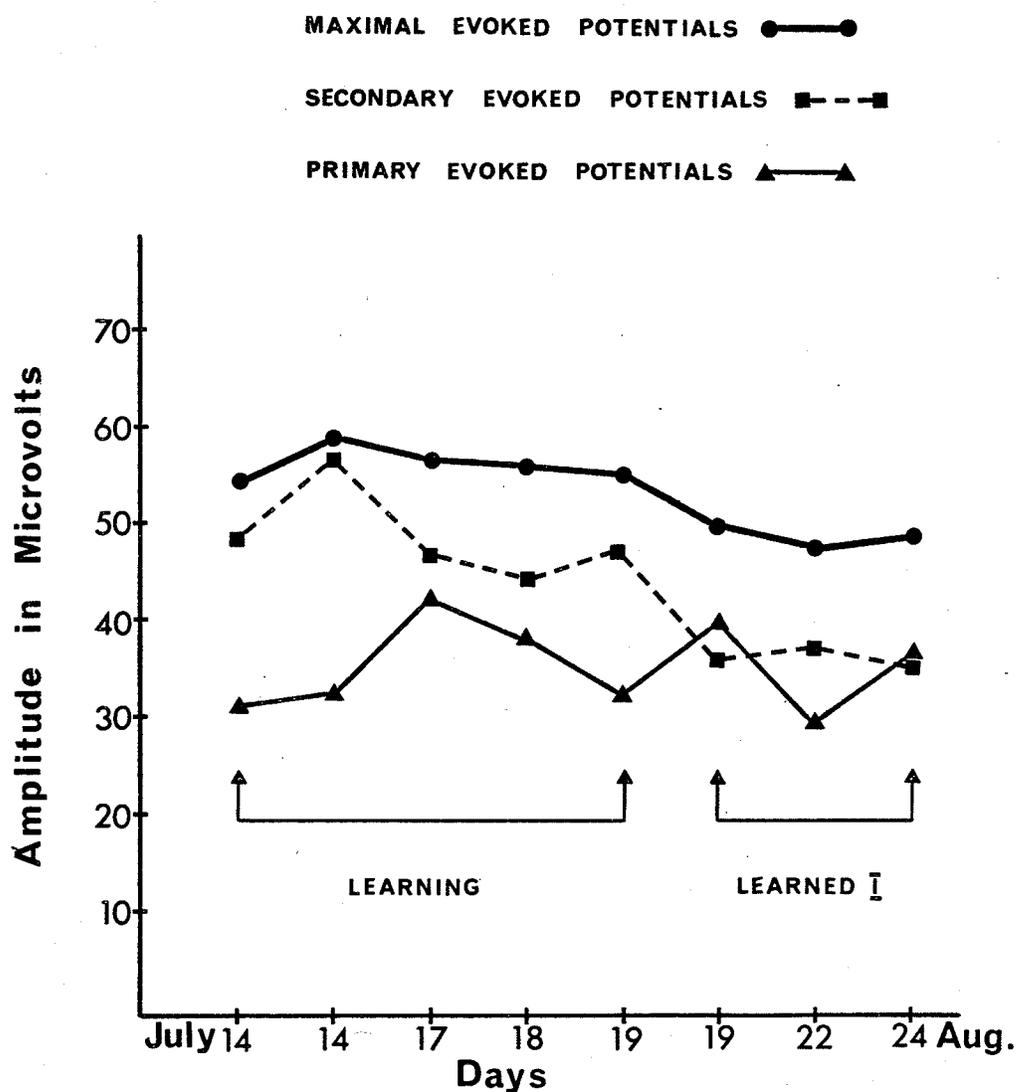


Fig.18

Evoked potential amplitudes during avoidance conditioning (R45). Amplitudes for each day usually represent a mean of 100 CS clicks.

Legend: Learning - < 80% avoidance responses
Learned I - 80% avoidance responses



correlation of means from all the animals by the Duncan New Multiple Range Test (table VIII) revealed that these visible differences were not statistically ($p > .05$) demonstrable.

It was observed that during conditioning of the avoidance response, the strength of the fear reaction (crouching, defecation, and piloerection) decreased as the percentage of correct responses increased. The latency for the CR decreased and the animals executed more avoidances during the same time span (tables IX, X and XI). In addition, the number of changes in position increased as the percentage of correct responses increased. The most obvious changes in position were standing up on the hind legs and avoiding and these were used as an index of gross activity (tables IX, X and XI). By means of the unpaired t-test it was shown that the only significant increase in this activity occurred between the Learning and the Learned II phases ($p < .025$). When this statistic is correlated with the previous finding that there was no significant difference ($p > .05$) in evoked response amplitude between Learning and Learned II (table VIII), it is difficult to escape the conclusion that the effect of gross muscle activity on auditory evoked potential amplitude is negligible. Fig. 19 summarizes the combined evoked potential and activity data.

4. Acoustically Evoked Potentials during Unavoidable Shock Conditioning (CER)

Early in CER conditioning during the CS interval the animals remained motionless and appeared frightened. Increased depth of breathing was readily observed in all animals. After a few sessions these gross changes in behaviour became apparent as soon as the animals were placed into the CER section of the Skinner Box and before the presentations of

TABLE VIII

MEANS* OF EVOKED POTENTIALS RECORDED DURING THE LEARNING, LEARNED I AND LEARNED II STAGES OF AVOIDANCE CONDITIONING (R37, R38, R40, R41, R42, R45)

	Mean (μ V)	Standard Deviation (μ V)	Number of Observations	Mean (μ V)	Standard Deviation (μ V)	Number of Observations	Probability
	Learning			Learned I			
Primary amplitude	58.6	26.2	11	54.5	24.4	18	p > .05
Secondary amplitude	57.8	12.0	11	53.8	12.1	18	p > .05
Maximal amplitude	79.5	24.0	11	76.1	23.3	18	p > .05
	Learning			Learned II			
Primary amplitude	58.6	26.2	11	46.8	15.4	15	p > .05
Secondary amplitude	57.8	12.0	11	49.5	9.1	15	p > .05
Maximal amplitude	79.5	24.0	11	67.5	9.8	15	p > .05
	Learned I			Learned II			
Primary amplitude	54.5	24.4	18	46.8	15.4	15	p > .05
Secondary amplitude	53.8	12.1	18	49.5	9.1	15	p > .05
Maximal amplitude	76.1	23.3	18	67.5	9.8	15	p > .05

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

TABLE IX

CONDITIONED AVOIDANCE RESPONSES DURING LEARNING
(R 37, R38, R40, R41, R42)

Rat	Date	* Series of CS presentations	Avoidances	Standing up during CS	Changes in position during CS	Average changes in position	Average avoidances
37	Aug. 5	31	23	0	23	13.8	13.8
37	11	18	16	0	16		
38	July 17	25	16	7	23	11.5	8
40	20	30	5	8	13	6.5	2.5
41	21	25	9	0	9	3.8	2.8
41	23	12	1	2	3		
42	23	18	14	0	14	14.0	14.0
Mean		22.7	12			9.9	8.2
S. D.						4.6	5.6
S. E.						2.0	2.5

* During any one session, the total series of CS presentations usually consists of 100 or 200 CS clicks, such that one series of CS presentations can theoretically contain from 1 to 30 clicks. This of course varies with avoidance response latency. The final results (Average avoidances) are standardized per 100 CS clicks.

TABLE X

CONDITIONED AVOIDANCE RESPONSES DURING LEARNED I
(R37, R38, R40, R41, R42)

Rat	Date	* Series of CS presentations	Avoidances	Standing up during CS	Changes in position during CS	Average changes in position	Average avoidances
37	Aug. 13	38	33	2	35		
37	14	37	32	1	33	17.3	15.5
37	14	18	14	4	18		
38	July 29	44	33	0	33	16.5	16.5
40	31	45	26	0	26	8.7	8.7
41	July 23	24	1	2	3		
41	31	18	16	0	16	11.3	10.7
41	Aug. 4	34	30	0	30		
42	July 31	19	14	0	14	12.5	12.5
42	Aug. 4	41	22	0	22		
Mean		31.8	22.1			13.3	12.8
S. D.						3.6	3.3
S. E.						1.6	1.5

* See Table IX

TABLE XI

CONDITIONED AVOIDANCE RESPONSES DURING LEARNED II
(R37, R38, R40, R41, R42)

Rat	Date	* Series of CS presentations	Avoidances	Standing up during CS	Changes in position during CS	Average changes in position	Average avoidances
37	Aug. 14	55	46	5	51		
37	15	39	34	0	34	16.7	16.1
37	16	18	16	0	16		
38	Aug. 14	96	91	0	91		
38	15	22	22	0	22	20.6	20.6
38	16	18	17	0	17		
40	Aug. 4	17	11	0	11	10.5	10.5
40	10	35	20	0	20		
41	Aug. 20	40	40	4	44		
41	22	17	16	1	17	20.0	18.3
41	24	21	19	2	21		
42	Aug. 20	17	15	1	16		
42	22	22	19	0	19	18.0	15.7
42	24	19	13	6	19		
Mean		31.1	27.0			17.3	16.2
S. D.						4.1	3.8
S. E.						1.8	1.7

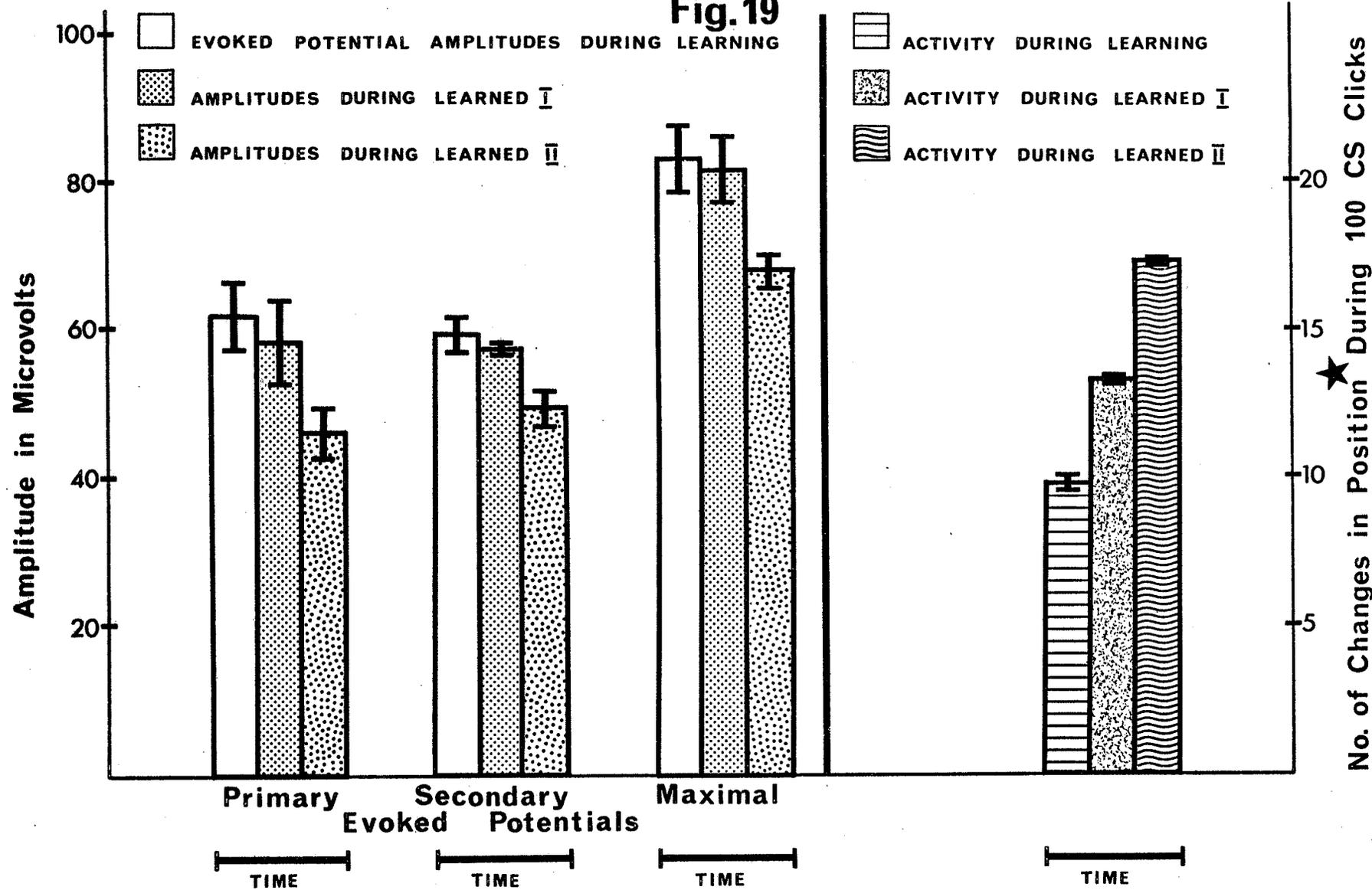
* See Table IX

Fig. 19

Evoked potentials and simultaneously recorded gross movements
within the CS interval during three stages of avoidance
responding

★ avoidances plus standing up

Fig. 19



the CS.

The same parameters of shock level were maintained throughout this experiment, and the animals adapted to this shock level as conditioning progressed into the later stages. During Late CER the animals showed more interest in their environment, doing more exploring and standing up during the CS. At the same time the initial increases in depth of breathing were no longer visibly apparent.

At the outset of CER conditioning the evoked potentials increased in amplitude over several sessions before decreasing (fig. 20) or else they decreased gradually from an original high (fig. 21). As CER conditioning progressed and as the evoked potentials decreased in amplitude it appeared that the decrease were similar to that observed during avoidance conditioning (figs. 20, 21, and 22) and with most of the animals the decrease was apparent with simple observation. Furthermore, means obtained by the successive application of analysis of variance and Duncan's New Multiple Range Test (table XII) revealed significant differences between the secondary evoked potentials ($p < .05$) and between the maximal evoked potentials ($p \ll .01$).

5. Acoustically Evoked Potentials during Fear Behaviour

Beginning after the initiation of aversive conditioning and occurring randomly throughout the drinking sessions, were periods when some of the animals (R37, R38 and R41) appeared very "frightened". During these periods there were no apparent changes in the environmental stimuli that would have precipitated this behaviour. The animals stopped lever-pressing, "froze", defecated and exhibited visibly increased rate

Fig. 20

Evoked potential amplitudes during early and late stages of Unavoidable Shock conditioning (R37). Amplitudes for each day usually represent a mean of 100 CS clicks.

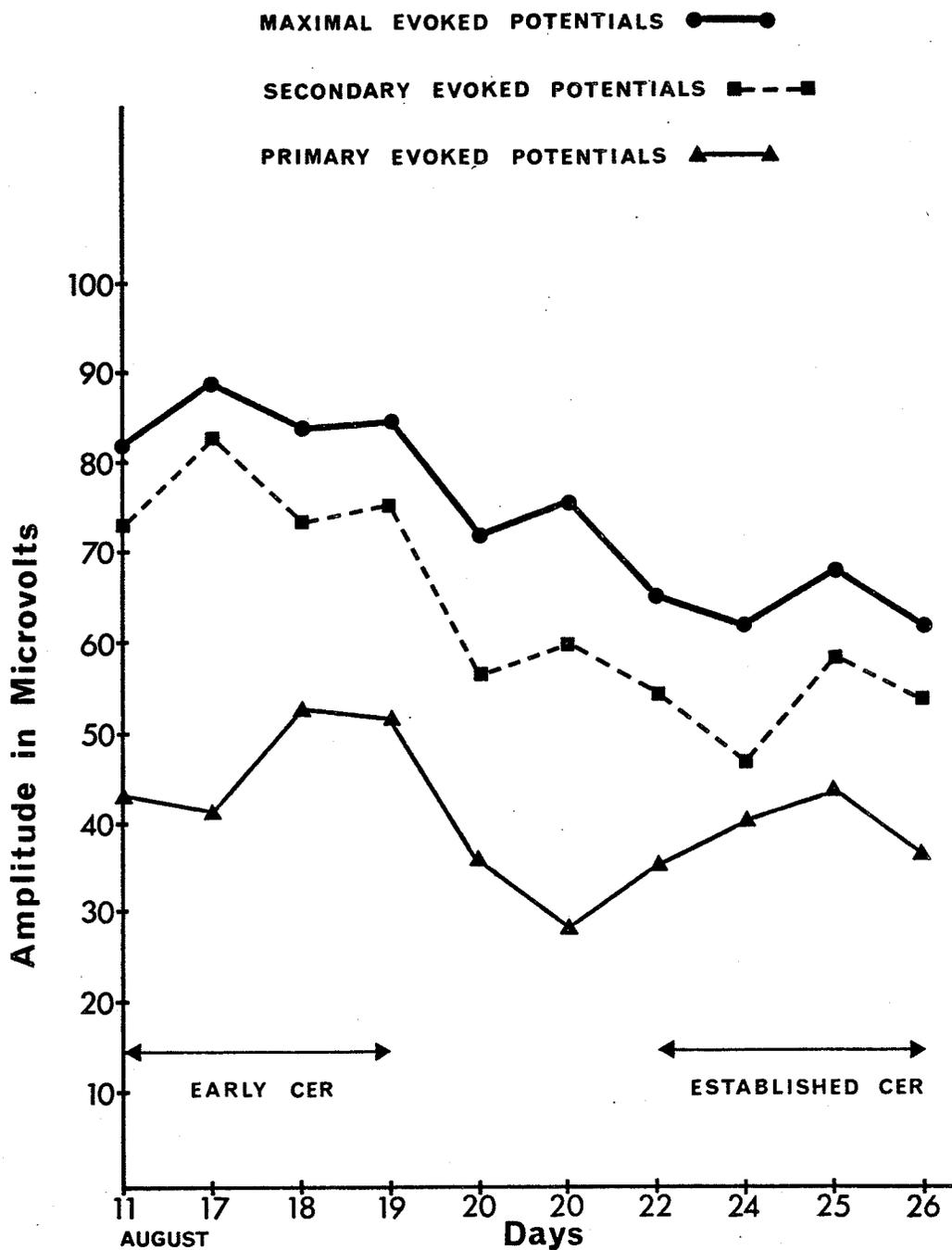
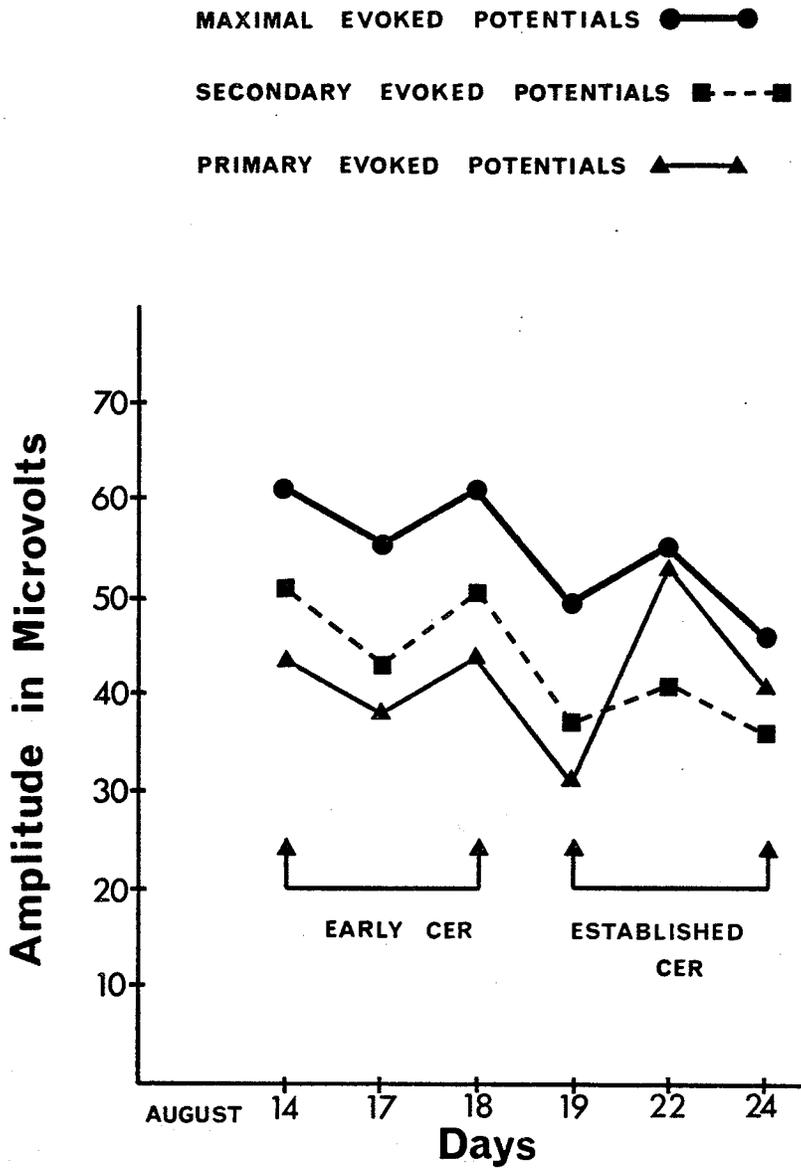
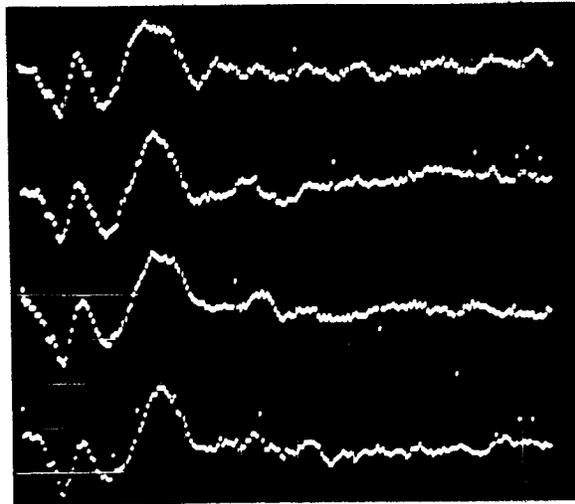


Fig. 21

Evoked potential amplitudes during early and late stages of Unavoidable Shock conditioning (R46). Amplitudes for each day usually represent a mean of 100 CS clicks.



(a)
Evoked potentials during Early CER



(b)
Evoked potentials during stable
established CER conditioning

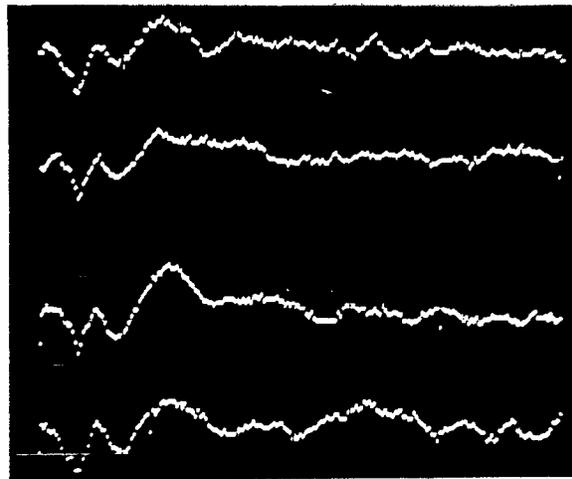


Fig. 22 Evoked potentials during Unavoidable Shock Conditioning
(R37)

TABLE XII

MEANS* OF EVOKED POTENTIALS RECORDED DURING EARLY AND LATE STAGES OF UNAVOIDABLE SHOCK CONDITIONING (R37, R38, R40, R41, R42, R46)

	Early CER			Late CER			Probability
	Mean (μV)	Standard Deviation (μV)	Number of Observations	Mean (μV)	Standard Deviation (μV)	Number of Observations	
Primary amplitude	56.0	28.1	21	42.3	6.7	10	p > .05
Secondary amplitude	59.2	12.5	21	47.7	7.7	10	p < .05
Maximal amplitude	88.7	29.8	27	63.2	8.6	14	p << .01

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

of breathing (inspiratory polypnea) as well as piloerection. At this time the auditory evoked potential amplitudes were the highest ever observed during this series of experiments (fig. 23). Invariably, continual presentation of the CS and water caused a decrease in evoked potentials and a resumption of lever-pressing and drinking.

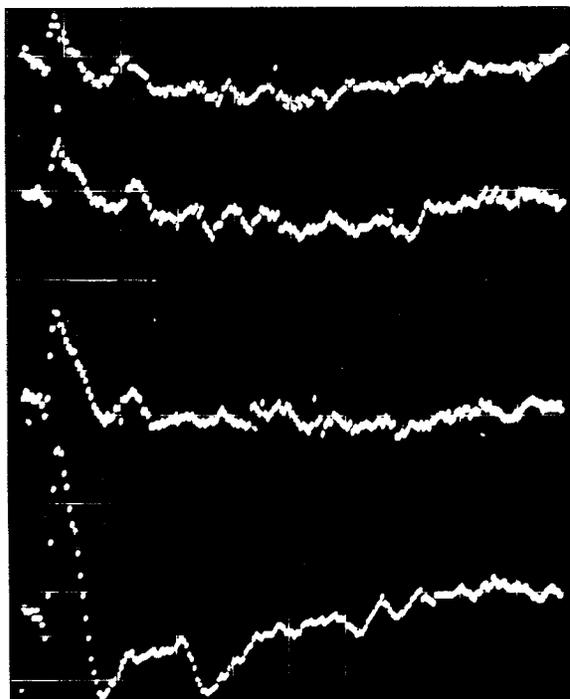
6. Overview of Results and Other Special Considerations

During three stages of avoidance conditioning there was a decrease in evoked potential amplitude from Learning to Learned II but this decrease was not significant. Although a considerable increase ($p < .025$) in gross movement by the animals was recorded during these same sessions, its effect was not apparent. In R41 at some stages of conditioning, the evoked potentials to the CS prior to water reward were higher in amplitude than the late avoidance responses. Generally, however, significantly smaller amplitudes were observed prior to drinking than during aversive conditioning (table XIII). In our studies this has been a consistent finding and can be readily observed in tables XIV and XV where potentials evoked by a CS preceding drinking are compared with those during Avoidance Learning and Avoidance Learned II. Similar results are shown in tables XVI and XVII where potentials evoked by a CS prior to drinking are compared with those during Early and Late CER training. As compared to drinking conditioning the changes in potential evoked during Early CER (table XVI) are highly significant ($p \ll .01$) in all three measured components and are only exceeded in amplitude by those recorded during the fear response (tables XIII and XVIII).

Evoked responses to the CS preceding water reward decreased all

(a)

Spontaneous fear development (R41). Note that the increase in evoked potential amplitudes between the second and fourth traces occurred during the same recording session. At this time there were no apparent changes in environmental stimuli.



(b)

Unconditioned fear development in R37. As in part (a), these four traces were recorded consecutively in the same session. Note that the evoked potential amplitudes decrease consistently from trace 1 to trace 4. The animal resumes lever-pressing in trace 4.

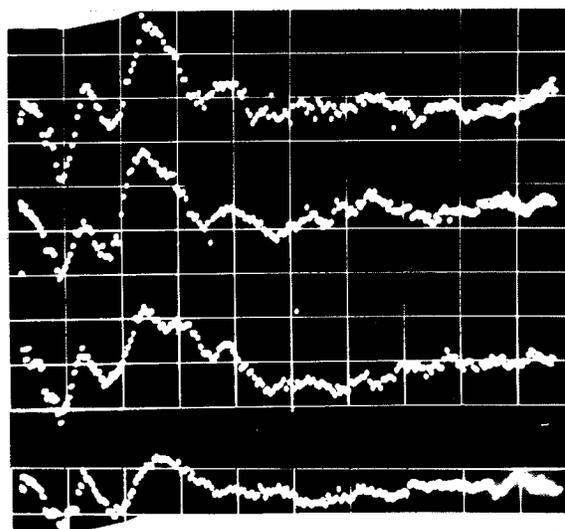


Fig. 23 Evoked potentials during unconditioned fear (R41 and R37)

TABLE XIII
 MEANS* OF POTENTIALS EVOKED BY A CS DURING AVOIDANCE,
 CER, SPONTANEOUS FEAR, AND PRIOR TO DRINKING

Experimental Condition	Maximal EP - AMPL (μV)	Secondary EP - AMPL (μV)	Primary EP - AMPL (μV)
Fear-behaviour	91.6 ⁺	51.5 ⁺	67.5 ⁺
CER-early	88.7 ^{+o}	59.2 ^{+#}	56.0 ⁺
AVOID-early	79.5 ⁺	57.8 ⁺	58.6 ⁺
AVOID-late	67.5	49.5 ⁺	46.8 ⁺
CER-late	63.7 ^o	47.7 ^{+#}	42.3 ⁺
DRINK	52.0	36.0	35.6

+ Sig. diff. from DRINK EP's at or beyond $p = .01$

Sig. diffs. at or beyond $p = .05$

o Sig. diffs. at or beyond $p = .01$

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

TABLE XIV

* MEANS OF POTENTIALS EVOKED BY A CS PRECEDING DRINKING WITHIN THE STAGE OF AVOIDANCE LEARNING AND MEANS OF POTENTIALS EVOKED DURING AVOIDANCE LEARNING

	Positive Motivation (Drinking conditioning)			Negative Motivation (Avoidance Learning)			Probability
	Mean (μV)	Standard Deviation (μV)	Number of Observations	Mean (μV)	Standard Deviation (μV)	Number of Observations	
Primary amplitude	34.1	8.4	6	58.6	26.2	11	p < .01
Secondary amplitude	36.3	13.7	6	57.8	12.0	11	p < .01
Maximal amplitude	49.0	9.0	6	79.5	24.0	11	p < .01

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

TABLE XV

* MEANS OF POTENTIALS EVOKED BY A CS PRECEDING DRINKING WITHIN THE STAGE OF AVOIDANCE LEARNED II AND MEANS OF POTENTIALS EVOKED DURING AVOIDANCE LEARNED II

	Positive Motivation (Drinking conditioning)			Negative Motivation (Avoidance Learned II)			Probability
	Mean (μV)	Standard Deviation (μV)	Number of Observations	Mean (μV)	Standard Deviation (μV)	Number of Observations	
Primary amplitude	33.4	8.7	13	46.8	15.4	15	p > .05
Secondary amplitude	30.8	6.7	13	49.5	9.1	15	p \ll .01
Maximal amplitude	46.6	7.1	13	67.5	9.8	15	p < .01

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

TABLE XVI

MEANS* OF POTENTIALS EVOKED BY A CS PRECEDING DRINKING WITHIN THE EARLY STAGES OF UNAVOIDABLE SHOCK AND MEANS OF POTENTIALS EVOKED DURING THE EARLY STAGES OF UNAVOIDABLE SHOCK CONDITIONING

	Positive Motivation (Drinking conditioning)			Negative Motivation (Early CER)			Probability
	Mean (μV)	Standard Deviation (μV)	Number of Observations	Mean (μV)	Standard Deviation (μV)	Number of Observations	
Primary amplitude	31.8	10.4	29	56.0	28.1	21	p \ll .01
Secondary amplitude	31.2	6.6	29	59.2	12.5	21	p \ll .01
Maximal amplitude	47.4	6.8	29	88.7	29.7	27	p \ll .01

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

TABLE XVII

MEANS* OF POTENTIALS EVOKED BY A CS PRECEDING DRINKING WITHIN THE LATE STAGES OF UNAVOIDABLE SHOCK AND MEANS OF POTENTIALS EVOKED DURING THE LATE STAGES OF UNAVOIDABLE SHOCK CONDITIONING

	Positive Motivation (Drinking conditioning)			Negative Motivation (Late CER)			Probability
	Mean (μV)	Standard Deviation (μV)	Number of Observations	Mean (μV)	Standard Deviation (μV)	Number of Observations	
Primary amplitude	31.8	10.8	29	42.3	6.7	10	p > .05
Secondary amplitude	31.2	6.6	29	47.7	7.7	10	p < .01
Maximal amplitude	47.4	6.8	29	63.7	8.6	10	p < .01

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

TABLE XVIII

MEANS* OF POTENTIALS EVOKED BY A CS PRECEDING DRINKING PRIOR TO THE FEAR RESPONSE
AND MEANS OF POTENTIALS EVOKED DURING THE FEAR RESPONSE

	Positive Motivation (Drinking conditioning)			Negative Motivation (Fear Response)			Probability
	Mean (μV)	Standard Deviation (μV)	Number of Observations	Mean (μV)	Standard Deviation (μV)	Number of Observations	
Primary amplitude	33.4	8.7	13	67.5	14.7	13	$p \ll .01$
Secondary amplitude	30.8	6.8	13	51.5	18.7	13	$p \ll .01$
Maximal amplitude	46.6	7.1	13	91.6	18.6	13	$p \ll .01$

* The means were obtained by the successive application of analysis of variance and Duncan's new multiple-range test.

through the seven-week period. However, once aversive conditioning had begun, these drinking CS-evoked responses, whether they preceded stages of CER or avoidance conditioning, showed no statistically significant decreases.

Evoked potential amplitudes decreased during CER as they did during avoidance conditioning but the changes in the former were more marked. Between the early and late stages of CER training, there were substantial decreases in amplitude in the secondary ($p < .05$) and maximal evoked potentials ($p \ll .01$) but not in the primary ($p > .05$). During unconditioned fear the changes were much more dramatic both in amplitude and in rapidity of development. The evoked potential amplitudes were the highest recorded during this series of experiments; they increased very rapidly for no apparent reason and declined in most cases almost as quickly.

Our results do not show whether it is the primary amplitude, secondary amplitude or maximal amplitude of the primary-secondary complex of the evoked potential that exhibits the characteristic changes during conditioning. As compared to drinking response amplitudes before initiation of aversive conditioning, there were equivalent decreases in all three during the CS prior to drinking within the CER blocks ($p < .01$) and primary and maximal decreases ($p < .05$) as well as primary, secondary and maximal decreases ($p < .05$) during the CS prior to drinking within the avoidance conditioning stages. There were no decreases in these three portions of the evoked potential during avoidance conditioning ($p > .05$) and significant changes during CER in the secondary ($p < .05$) and maximal ($p \ll .01$) but not in the primary evoked potentials ($p > .05$).

An overall review and comparison of the data presented is shown in table XIII. It can be observed that the drinking amplitudes of table XIII vary slightly from those of fig. 6. The data of fig. 6 was selected and was not all-inclusive whereas the drinking response amplitudes of table XIII included those prior to extinction and punishment. (The extinction and punishment data are not included in this presentation). The mean differences between these two sets of data are small enough to be ignored.

D. DISCUSSION

Some authors (53, 67, 70, 86, 103) have concluded that the late or secondary evoked potentials show characteristic amplitude changes during conditioning. We have observed both significant and non-significant decreases occurring simultaneously in primary evoked potential amplitudes, in secondary evoked potential amplitudes and in maximal amplitudes of the primary-secondary evoked potential complex during conditioning. Because all three of these components of the evoked potential showed influences we could make no conclusion concerning the relative importance of evoked potential changes in the primary, secondary or maximal amplitudes. We have no evidence which would lead us to the conclusions of other authors that only the late secondary component is significantly affected.

The voltage changes during avoidance and CER appear to be strongly correlated with a state of fear or alarm (34, 106, 163). As soon as the animal is put into the CER situation and even before presentation of the CS, the rate of breathing is visibly increased (inspiratory polypnea) and the evoked potentials are increased in amplitude. Because of the low intensity of shock, the animals became adapted as conditioning progressed into the later stages; both the fear response (freezing, defecation, inspiratory polypnea and piloerection) and the amplitudes of the evoked potentials decreased with time. From this we were able to conclude that the amplitude of the evoked potential is related to the strength of the CER.

During initial avoidance conditioning the evoked potential increased in amplitude. With further conditioning they either decreased

from this high point or else they increased still further for a few days before decreasing. Our work certainly confirms the finding that evoked response amplitude changes precede the development of the motor conditioned response (16, 25, 34, 35, 43, 74, 89, 98, 124, 151, 163). The evoked response amplitudes decreased as the percentage of avoidance responses increased but the decrease was not statistically significant ($p > .05$). We certainly did not get the amplitude attenuation reported by some (16, 34, 53, 64, 93). Individually, however, this is not the case. R41 (fig. 13) exhibited a five-fold decrease between early and late avoidance evoked potential amplitudes such that drinking evoked responses at this point were of larger amplitude than the avoidance evoked potentials. Because of this finding and because only one animal in seven exhibited a significant decrease ($p < .01$) in evoked response amplitude during avoidance conditioning we conclude that the decrease likely is not an expression of learning but rather one of decreased fear (9, 163).

Changes in the evoked potentials during the unconditioned fear response (increased rate of breathing or inspiratory polypnea, crouching, defecation and piloerection) support our conclusion that learning may not be the cause of evoked potential amplitude decreases during conditioning. The evoked potential amplitudes during this fear response were the highest recorded in all of our experimental sessions and yet we were unable to ascertain the condition(s) which brought about these increases. Because of their rapid rise and almost as rapid decline and because the conditions which changed were too subtle to be detected, one has to ask, if learning is assumed, what can be learned so rapidly and dissipate so readily? One cannot answer this without speculating.

The initial CER trials produced a greater fear response than that observed in early Avoidance Learning. The latter situation provided an escape which the former did not. Similarly, Late CER should produce a greater fear response than Learned II Avoidance since the CER provides no escape whereas during Learned II the animal is avoiding the aversive stimulus more than 80% of the time. Table XIII certainly bears out part of this but some of the results are not as predicted, since evoked potential amplitudes of late avoidance (Learned II) are larger than those of Late CER. Havlicek (71) found that when the shock intensity was high, the animals did not become adapted and the evoked potential remained constant and at a high amplitude level. Consequently, we feel that if the levels of shock intensity would have been higher, the animals would not have adapted and the evoked potential amplitudes during Late CER would have been higher than those of Avoidance Learned II. This, however, can be borne out and verified only by further experimentation. As for unconditioned fear we can only speculate why the amplitudes of the evoked potentials are highest. We do offer the possibility that uncertainty and fear of the unknown is greater than fear of the known (51).

We concluded that the marked decrease in evoked potential amplitude during drinking conditioning prior to the initiation of aversive stimuli may have been due to habituation since some of the signs of this amplitude decrease were similar to those observed during repetitive stimulation (63, 67, 69, 82, 86, 88, 105, 109, 120, 121, 135, 173, 174). The evoked potential amplitudes decreased during drinking conditioning before introduction of aversive stimuli, decreased during drinking conditioning within the stages of avoidance conditioning and decreased during drinking

conditioning within the period of CER training. Because of this, we were able to rule out as insignificant the effects of aversive stimuli upon the evoked potential amplitude during the drinking situation i.e., the transfer effect appeared to be nil.

Our results did prove that, in general, significantly smaller amplitudes were observed prior to positive reward than during aversive conditioning. This has been a consistent and dependable finding throughout this study. All of the drinking responses showed a remarkable stability throughout this seven-week session. Once aversive conditioning had begun the drinking amplitudes during CER, Avoidance Learning, Avoidance Learned I and Avoidance Learned II showed no statistically significant changes. However, comparison of these same drinking responses with amplitudes of potentials evoked during Avoidance Learning, Avoidance Learned I, Avoidance Learned II, Early CER, Late CER and unconditioned fear revealed consistently significant increases. We conclude that smaller evoked potential amplitudes are observed when the animals are positively motivated than when they are negatively motivated.

It has been seen that evoked potentials decrease in amplitude when animals are aroused by means of positive motivation such as drinking. Work by Havlicek (71) revealed that potentials recorded from highly motivated rats (water-deprived for 48 hours) are smaller in amplitude than those recorded from less motivated rats (water-deprived for 24 hours). Prewatering the animals (either 24- or 48-hours deprived) reduced the level of motivation and resulted in increased evoked potential amplitudes (71). However, when the animals are aroused and negatively motivated by

fear as during CER and avoidance the evoked potentials increase in amplitude. Why this happens is not known. We can only speculate that perhaps two different mechanisms or nervous pathways are responsible for these opposite trends (73).

Some authors have said that both general body movements and middle ear muscle activity can result in decreased evoked potential amplitudes (29, 107, 139, 140, 158, 163, 166, 171) while others have ruled out this possibility (63, 69, 70, 102, 151, 178). In support of the latter view, our data leads us to the conclusion that if gross body movements do have an effect on evoked potential amplitudes from the auditory cortex, then this effect must be limited and not significant.

It is felt that because of the obvious need for more experimental work on CER with regard to shock intensities and because we have no way of determining what contribution to the evoked potential, no matter how minimal, is made by each of unconditioned fear, alertness, novelty of situation, or learning, in any one conditioning paradigm, it would be wise to use caution before making any sweeping statements.

Even though its contribution is unknown, learning may be a factor influencing evoked potential amplitude. At the present there is simply not enough evidence to rule out this effect as some authors have done (130, 154, 155). Our studies lead us to the firm conclusion that during avoidance and CER training there is a strong relationship between evoked potential amplitude and conditioned fear.

E. SUMMARY

Experiments were performed to determine the relationship between positive (drinking) and negative (unavoidable shock and conditioned avoidance) motivational states as revealed by changes in the primary amplitude, secondary amplitude and maximal amplitude of the primary-secondary complex of the evoked potential. Evoked potentials were recorded during four different conditioning procedures (unconditioned fear included) in the same rats each with chronically implanted electrodes in the auditory cortex.

1. In the series of experiments significantly smaller evoked potential amplitudes were found during positive motivation (drinking) than during negative motivational states such as avoidance conditioning, CER and unconditioned fear. This was a consistent and dependable finding throughout the entire study.

2. These evoked potential changes were observed in the primary amplitude, secondary amplitude and maximal amplitude of the primary-secondary complex. We found no evidence that the late secondary evoked potential was uniquely affected during conditioning as both significant and non-significant decreases occurred in all three measured components of the evoked potential.

3. Significant decreases in evoked potential amplitude were recorded during drinking conditioning. These decreases were observed over periods varying from three to nine days prior to the introduction of negative stimuli and the evoked potentials at the end of these periods invariably exhibited smaller amplitudes than those observed at the

beginning of drinking conditioning. Once aversive conditioning had begun the amplitudes of the drinking responses during the stages of Avoidance Learning, Avoidance Learned I, Avoidance Learned II, Early CER and Late CER still decreased but the decrements were no longer statistically significant ($p > .05$). We concluded that there was no evident transfer or feedback of information from the negative to the positive motivational states.

4. During the initial stages of avoidance conditioning and CER training as well as during the unconditioned fear reaction we observed increased evoked potential amplitudes in conjunction with a fear response which was characterized by inspiratory polypnea, crouching, defecation and piloerection. Because evoked potential amplitudes also decreased as the fear response diminished in strength we concluded that there was a strong relationship between these two measures and that the decrease was likely not an expression of learning but rather one of decreased fear.

5. During avoidance conditioning evoked potential amplitudes decreased as the percentage of avoidance responses increased but the decrease was not statistically significant ($p > .05$).

6. In another series of experiments the evoked potentials during Early CER were of larger amplitude than those during early avoidance since the former produced a greater fear response than that observed in the latter.

7. Evoked potential amplitudes recorded during late avoidance (Learned II) were larger than those observed during Late CER.

8. During drinking conditioning, a few of the animals suddenly

stopped lever-pressing and drinking and exhibited signs of fear (inspiratory polypnea, crouching, defecation and piloerection). These behavioural manifestations of unconditioned fear resulted in large evoked potential changes that were similar to those accompanying CER except that the amplitudes of the former were the largest observed in this experimental series.

9. In one attempt to determine the effect of muscle activity upon evoked potential amplitudes we recorded gross movements during the various stages of avoidance conditioning but found this muscle activity to be of no consequence.

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