

HIPPOCAMPAL ELECTRICAL ACTIVITY IN THE MONKEY DURING DELAYED ALTERNATION PROBLEMS

DOUGLAS P. CROWNE¹, AUDREY KONOW, KARL J. DRAKE AND KARL H. PRIBRAM

Department of Psychology, University of Waterloo, Waterloo, Ontario (Canada), and Neuropsychology Laboratories, Stanford University School of Medicine, Stanford, Calif. 94305 (U.S.A.)

(Accepted for publication: April 18, 1972)

A well known effect of lesions of frontal granular cortex and of all limbic structures including the hippocampus is the impairment of the classical delayed spatial alternation problem (Pribram *et al.* 1952, 1962, 1966; Mishkin and Pribram 1955; Mishkin 1964; McFaney and Butter 1969). Not every alternation performance, however, shows a decrement from frontal cortex or medial forebrain lesions. Orbitofrontal and amygdala lesions impair go/no-go alternation to a greater extent than they impair classical alternation (Pribram *et al.* 1966) while monkeys with dorsolateral frontal lesions are able to learn go/no-go alternation (Mishkin and Pribram 1955). In addition, several recent experiments clearly establish that go/no-go alternation is learned *more* readily by animals with hippocampal lesions than by their controls; this finding has been reported for rats (Means *et al.* 1970), cats (Brown *et al.* 1969) and monkeys (Mahut 1971). In two other experiments with hippocampally damaged monkeys, delayed spatial alternation was impaired while delayed go/no-go alternation was neither impaired nor facilitated (Brown and Chino 1971; Bush *et al.*, in preparation).

There is a paradox in the fact that the two delayed alternation problems should be so differently affected by frontolimbic lesions, and

our present concern is with one of the limbic structures involved—the hippocampus. The current accounts of hippocampal function cannot readily accommodate the facts of drastic impairment of spatial alternation and the enhancement or at least absence of impairment of go/no-go alternation. The intent of the present experiment is to investigate the paradox by a comparative analysis of hippocampal electrical activity during the learning of delayed go/no-go and spatial alternation tasks. This analysis involves three major questions: (1) Do systematic frequency changes in hippocampal electrical activity occur during the learning of the two alternation problems? (2) Are there differences or commonalities at certain specific frequencies between the two problems? (3) Are there differences at specific frequencies between trial categories on go/no-go alternation (*i.e.*, between go and no-go trials), and are there differences between correct and incorrect responses on the two problems?

At a basic level, this experiment deals with another issue. A rhythmical slow activity (theta) is observable in the electrical activity of the hippocampus of subprimate mammals during orienting and attention (Grastyán 1959; Radulovački and Adey 1965), some stages of learning (Adey *et al.* 1960; Elazar and Adey 1967) and skeletal movement (Black *et al.* 1970; Vanderwolf 1971). Theta rhythm is not evident in the raw EEG recorded from the primate hippocampus, and the earlier conclusion of Green (1960) was that "In the monkey... the theta rhythm [is] virtually impossible to see, excepting under conditions likely to produce extreme emotional

¹ This research was conducted while the first author held a Special Research Fellowship from the National Institutes of Health, U.S. Public Health Service in the Neuropsychology Laboratories, Department of Psychiatry, Stanford University School of Medicine. Portions of the data analyses were supported by U.S. Public Health Service Grant No. MH 19720 and National Research Council of Canada Grant No. A8262.

reactions" (p. 1382). While spectral analyses of limbic activity in the monkey have now established that rhythmical slow activity is present and that coherence functions derived from auto-spectra are related to orienting and to learning (Berkhout *et al.* 1969; Campeau *et al.* 1971), the occurrence of primate hippocampal theta rhythm and its relation to behavior need to be investigated in more detail.

METHOD

Subjects

Three experimentally sophisticated Rhesus monkeys were chronically implanted with bipolar electrodes (0.01 in. diam. nichrome wire, 0.5 mm tip exposure, and 1.0 mm separation between exposed tips), 5 in each hippocampus and two control electrodes in inferotemporal cortex. The hippocampal electrodes were implanted stereotaxically using coordinates derived from Olszewski (1952). Since the hippocampus reacts to electrode penetration with local seizure activity, the electrical activity of each electrode was monitored during implantation to assure further accurate placement. The criterion for final tip location was agreement between stereotaxic coordinates and the appearance of seizure activity.

From preliminary examination of EEG records, two hippocampal electrodes showing the clearest presence of rhythmical slow activity and one of the inferotemporal placements were selected for each monkey. The stereotaxic coordinates for the hippocampal electrodes recorded from in each animal were as follows:

Monkey No. 327: Right, AP 0, L 10.0, H - 2.0, and Left, AP - 0.1, L 10.0, H - 2.4.

Monkey No. 328: Left, AP + 6.2, L 11.6, H - 5.4, and Left, AP + 10.0, L 12.0, H - 6.5.

Monkey No. 329: Right, AP - 0.9, L 10.0, H - 2.0, and Left, AP - 5.1, L 12.0, H 0.0.

Histological verification of these placements is not available since additional experiments are being conducted with the animals.

Apparatus

The behavioral testing was done in the Discrimination Apparatus for Discrete Trial Analysis (DADTA, Pribram 1969), an automated,

computer-controlled discrimination learning device. DADTA essentially consists of a small enclosure which has on one wall a 4 × 4 array of illuminable plexiglas panels which are also response keys; in the center under the bottom row is a food cup to which banana pellets (Noyes, 190 mg) are dispensed. Stimuli are displayed on the panels from the rear by miniature projectors. Stimulus presentation, registration of responses, delivery of reinforcement, and the recording and timing of responses are all programmed by a PDP-8 computer.

Procedure

Alternation tasks. All of the animals had extensive pre-operative experience in the DADTA on a variety of discrimination problems including delayed response tasks. Post-operatively, they were trained on three problems in the following order: delayed go/no-go discrimination; delayed go/no-go alternation; and delayed spatial alternation.

Delayed go/no-go discrimination was included both as pre-training for the more difficult go/no-go alternation task and because animals with hippocampal lesions show a deficit on successive discrimination (Isaacson *et al.* 1966). The data of this problem are not reported here.

The delayed go/no-go alternation problem required the monkey to alternate go and no-go (inhibiting the panel press response for 5 sec) to the same stimulus display. On this task (and on delayed spatial alternation as well) each trial began with the illumination in red of the two center panels on the bottom row. These were "initiate" panels, and pressing either one of them brought on the task stimuli (numeral 2s) in the two center panels of the second row from the top. The monkey had to press either of these panels within 5 sec on trial 1, refrain from pressing for 5 sec on trial 2, and so on. A banana pellet was delivered to the food cup immediately following correct go responses and at the end of the 5 sec inhibit period on correct no-go trials. The delay interval was 7 sec.

Go and no-go errors resulted in a time out period of 10 sec during which the house light was turned off. A correction procedure was used with errors resulting in the re-presentation of the trial until a correct response was made.

Fifty correct trials a day were given. With the use of the correction procedure, a very large number of trials was typically required during the early stages of learning since the monkeys tended to make repeated perseverative errors. Learning was continued to a criterion of 90% correct over 3 days of a criterion block. Errors were calculated on the basis of initial errors; that is, consecutive perseverations of the same error were not counted.

On the delayed spatial alternation task the monkey had to alternate presses of left and right panels: the two center panels in the second row from the top. As above, each trial commenced with the illumination of the initiate panels, and pressing either one of them produced numeral 4s in the stimulus panels. The delay interval and error time out periods were the same as on the previous problem, and a correction procedure was again used. Errors or failure to make a choice within 5 sec resulted in the dark time out and repetition of the same trial.

EEG recording and analysis. All testing was done with the monkeys restrained in a primate chair. The electrical activity from the three electrodes was continuously recorded on magnetic tape throughout the monkeys' performance on every third day except near criterion when daily EEG recordings were taken. Synchronization pulses marked the occurrence of stimulus onset and the monkey's response. The three channels of analog data were digitized at a sampling rate of 200 samples per sec on a PDP-8 computer, and frequency analyses were then performed for each trial by means of the Fast Fourier Transform.

Two time periods were examined: the 1.28 sec immediately following stimulus presentation and a matching 1.28 sec "control" period beginning half way through the 5 sec duration of each trial. The Fast Fourier Transforms were averaged over individual trials in the following categories of response: go/no-go alternation: go correct, no-go correct, go incorrect, no-go incorrect; spatial alternation: left-right correct, left-right incorrect. These day averages were then averaged over blocks of 3 days selected from three points in the course of learning: (1) criterion performance; (2) at the point of change from chance to above-chance levels of perfor-

mance (i.e., between 65 and 80% correct); and (3) at a chance level, when the animal's performance contained as many initial errors as correct responses. Finally, averaged power spectra were computed over animals. For individual animals, the averaged power spectra of each of the three blocks are based on 150 spectral plots, and the averages over animals thus represent 450 observations.

RESULTS

A sample of the EEG record from the two hippocampal electrodes and the inferotemporal lead during a correct no-go trial is shown in Fig. 1. Activity in the theta range does not appear clearly in this segment, nor in others we have examined, and the hippocampal activity during the early part of the trial cannot be differentiated from that later in the trial (as it can from the spectral analyses as discussed below). The power spectrum analyses presented in Fig. 2, 3 and 4, however, establish that the principal frequency components of hippocampal electrical activity in the monkey lie in the range of 2-8 c/sec. These spectral plots are all cut off at approximately 14 c/sec since there was little hippocampal activity at frequencies beyond this point and no systematic differences associated with learning.

Rows *A* and *B* of Fig. 2 show the power spectrum plots of the two hippocampal electrodes averaged over the three animals for the criterion block and Blocks 2 and 3. Each individual figure contains the spectral density plots of correct trial categories on both problems. Note that on the spatial alternation problem left and right responses were collapsed since spatial locus did not make a difference. Considering the data of the go/no-go alternation problem first, there is a very pronounced difference at criterion between go and no-go trials within a 3-5 c/sec bandwidth, with the no-go trials showing more activity at these frequencies. During Block 2, when learning had moved above chance, the differences between go and no-go trials are still evident but considerably reduced in magnitude, while at the chance level of performance of Block 3 (when the monkeys were making as many initial errors as correct responses) there was no difference between go and no-go trials.

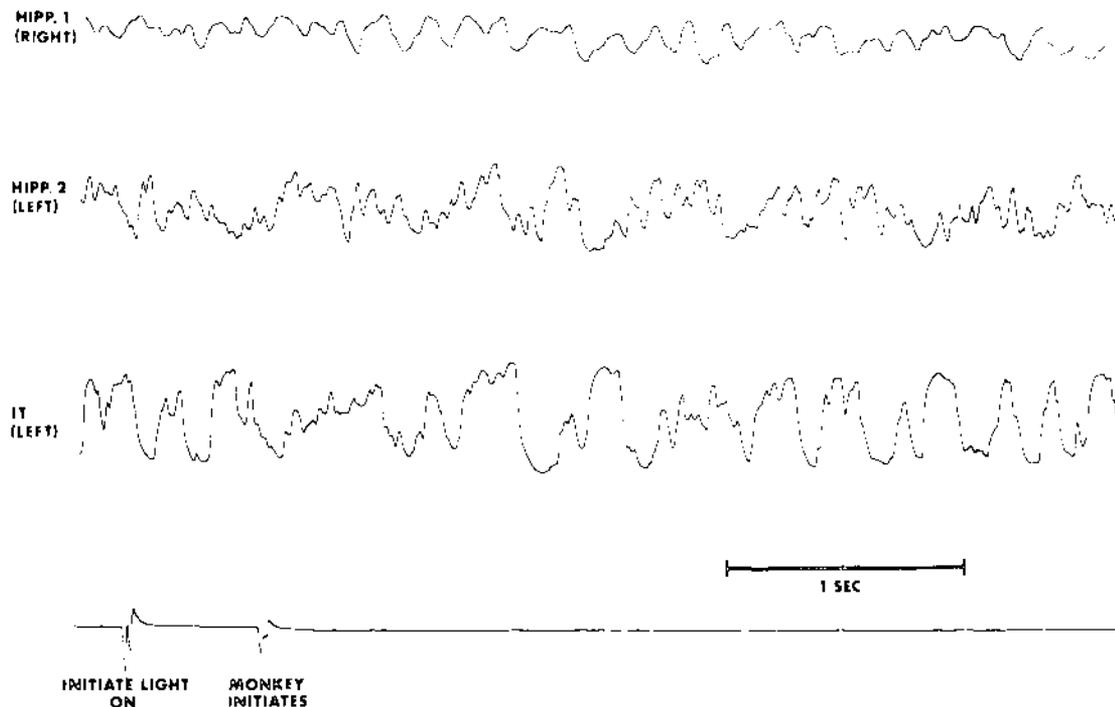


Fig. 1. Hippocampal and inferotemporal cortex electrical activity during delayed go/no-go alternation (monkey No. 327; criterion day 3, trial no 4; no-go correct). Bottom channel is event recorder. Calibration: 1 mv/mm.

Comparing the power spectra on the go/no-go alternation and spatial problems, the hippocampal activity shown at criterion on the spatial alternation task is like that observed on no-go trials of the go/no-go problem. Between 3 and 5 c/sec, the spectral density plot for left-right correct trials parallels very closely the plot for no-go correct trials and is quite clearly different from the go trials. During Block 2, theta rhythm on left-right correct trials does not differ from go trial activity on one hippocampal electrode (row *A*) and shows the same reduced difference as that seen between go and no-go trials on the other hippocampal placement (row *B*). Block 3 shows no differences in theta rhythm between the two problems.

The changes that appear in the course of learning in theta rhythm (*i.e.*, between 3 and 5 c/sec) involve an increase on no-go trials from Block 3 to Block 2 to criterion and a parallel decrease on go trials. On the spatial alternation problem, the trend is for theta to increase over blocks, reaching a maximum at criterion; this is seen on the first hippocampal electrode (row *A*) but not on the second (row *B*). All three animals

show the progressive increase in theta on the first electrode but only one does on the second lead.

The spectral plots of an individual monkey are shown in row *A* of Fig. 3. The differences between trial categories on the go/no-go problem and the between-problem differences are consistent over electrodes and over animals, with the exception of one monkey that failed to show the go/no-go difference and the failure of the second hippocampal lead to show the elevation of theta rhythm on left-right correct trials at criterion in one monkey. The consistency of the findings extends to the daily averages of individual monkeys which make up each block, and there are no exceptions to the block averages to be found on any day.

Theta rhythm on incorrect trials of the go/no-go problem is concordant with the nature of the animal's response. There is a close similarity of activity in the 3-5 c/sec range on go correct and no-go incorrect trials at criterion and a clear difference between the power spectra on these trials, when the monkey made a go response, and the spectra of no-go correct and left-right correct and incorrect trials. Rhythmical slow activity on

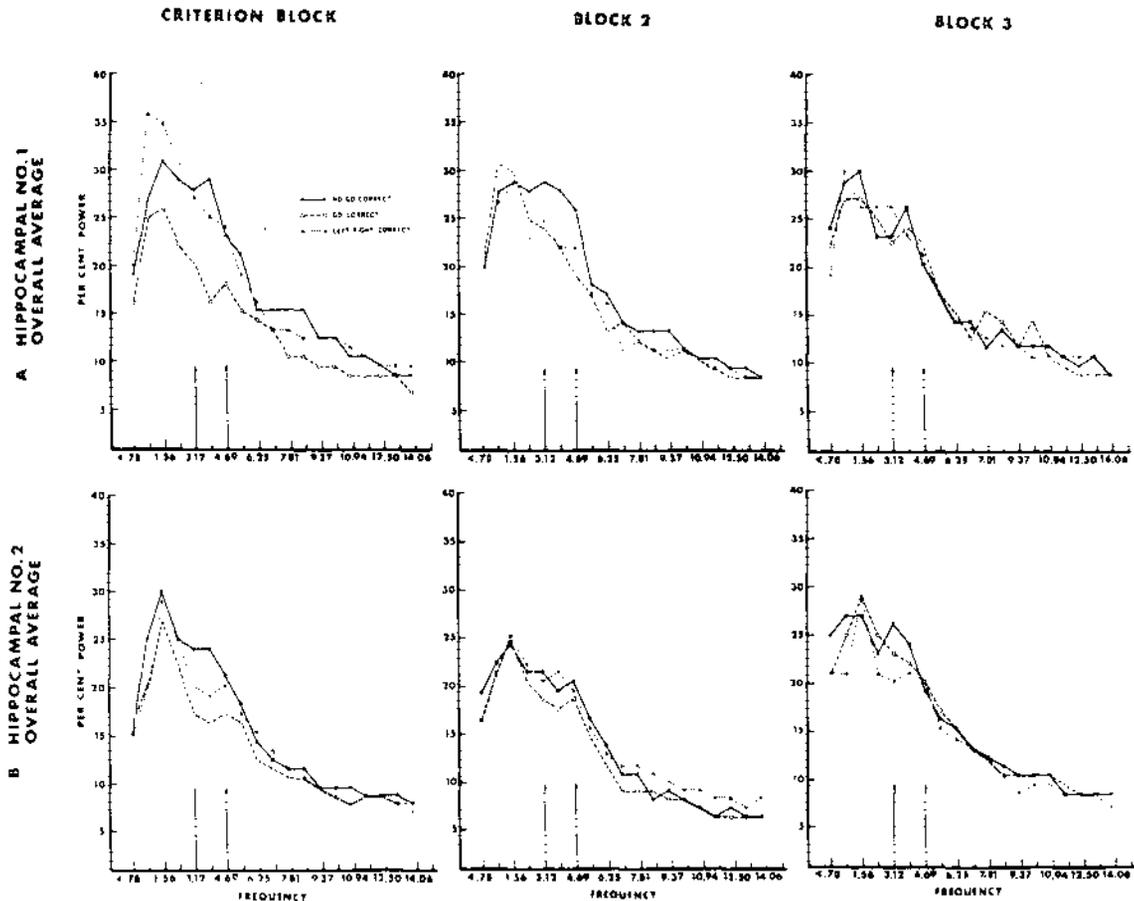


Fig. 2. Spectral density plots averaged over days and animals for the hippocampal (A and B) electrodes. Each individual figure shows Fast Fourier Transforms of activity during 1.28 sec following stimulus onset on go correct and no-go correct trials of the go/no-go problem and left-right correct trials of the spatial alternation task. Arrows on abscissa indicate the theta bandwidth within which reliable effects are found.

left-right alternation errors at criterion is intermediate between no-go correct and left-right correct and the go correct and no-go incorrect categories. These results are shown in row B of Fig. 3. A spectral plot is not shown for go incorrect errors during the criterion block since incorrect responses of this type were not made at this final stage of learning.

During Block 2, the power spectrum of no-go incorrect trials is, as at criterion, more like the spectrum of go correct trials. Go incorrect trials closely resemble no-go correct in the proportion of theta rhythm. There is no difference in 3-5 c/sec activity between correct and incorrect spatial alternation trials, and theta on both categories appears to be more like electrical activity on go correct trials at this stage of learn-

ing. Consistent with the findings on correct responses presented above, there are no systematic differences in theta on incorrect trials in Block 3.

The spectral plots of electrical activity from inferotemporal cortex (row A of Fig. 4) differ from the power spectra of the hippocampal electrodes in a much higher proportion of fast activity which is not shown in the figures. The activity recorded from inferotemporal cortex further differs from hippocampal activity in the absence of the delayed alternation effects. In no case was any inferotemporal difference observed between trial categories, problems, or stages of learning.

Power spectra recorded during the control period—the 1.28 sec starting from the middle of each trial—do not show any consistent differ-

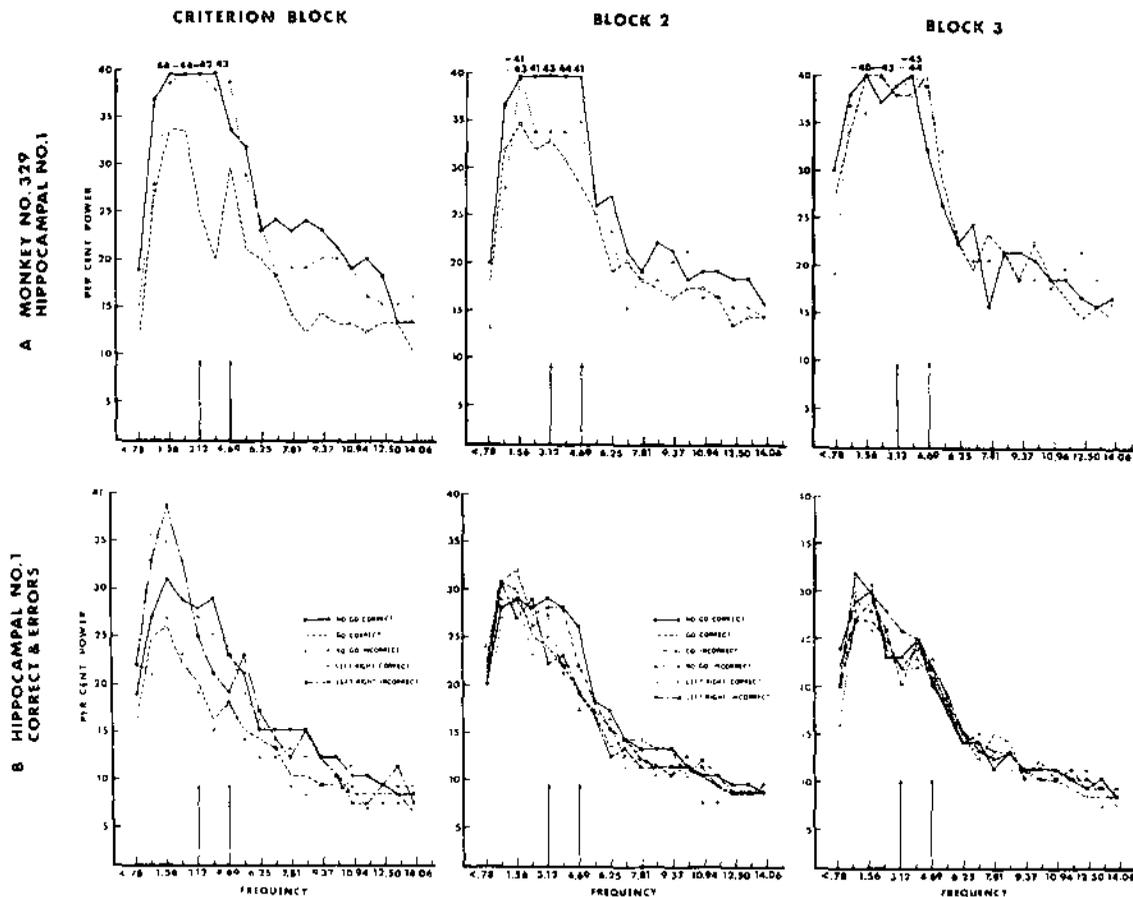


Fig. 3. Averaged spectral density plots for the hippocampal electrodes during the go/no-go and spatial alternation problems. *A*: Monkey No. 329 at criterion, Block 2 and Block 3. Each individual figure shows spectral plots of go correct and no-go correct trials of go/no-go problem and left-right correct trials on spatial alternation. *B*. Correct and incorrect trials on each of the two problems.

ences. These spectral plots are in row *B* of Fig. 4. It appears, then, that theta comes into play and differentiates between the responses called for on the different types of trials during the process of response selection immediately following stimulus onset.

We may note, finally, that despite the spectral peaks which appear between 1 and 2 c/sec on some leads, there are no systematic differences, and the only effects to be observed are found between 3 and 5 c/sec.

DISCUSSION

The appearance and differentiation of hippocampal theta rhythm over the course of learning is, from the present data, no less characteristic of

the monkey than it is of subprimate species. Power spectrum analysis is required to see primate theta activity and the course of its changes during learning, but it is clearly a dominant feature of the electrical activity of the monkey hippocampus and is systematically related to the learning of alternation problems.

These findings are consistent with those of Adey *et al.* (1960) and Elazar and Adey (1967) in showing the relation of trains of theta rhythm to learning. The difference in theta between correct and incorrect responses within a trial category (*i.e.*, go or no-go) close to and at criterion represents a considerable similarity with the Adey *et al.* and Elazar and Adey studies. Changes in spectral peaks over learning were not observed in the present experiment, nor did we find com-

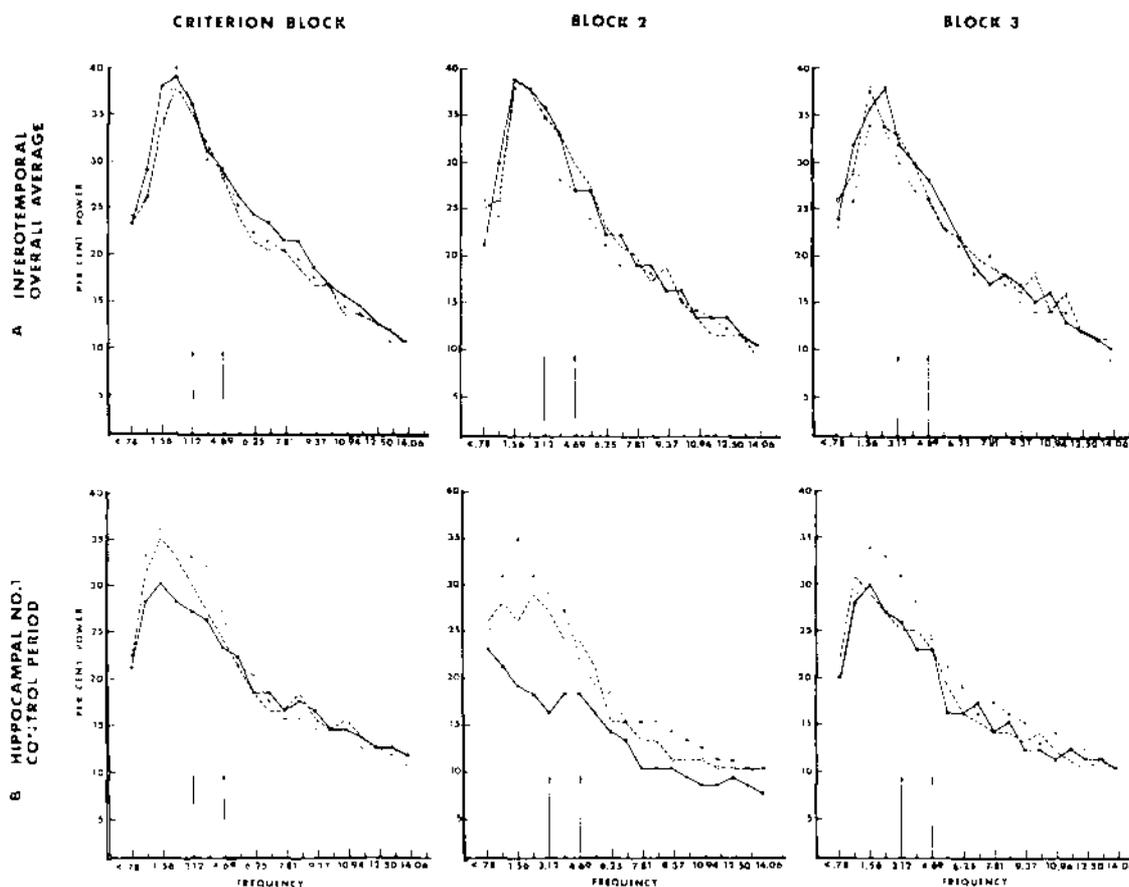


Fig. 4. Averaged spectral density plots from the three blocks of the two alternation problems. A: Inferotemporal electrode. B: Hippocampal electrode activity recorded during the 1.28 sec control period beginning 2.5 sec through each trial.

parable frequency shifts between periods or "epochs" during the time course of individual learning trials. These differences may be due to the more complex electrical activity of the monkey as compared to the cat and other subprimate species or to procedural differences between the experiments. For example, trials requiring the monkey to make a response (go or left right alternation) were executed very rapidly and the sampling period for the recordings of the hippocampal EEG was shorter than that of the Adey *et al.* and Elazar and Adey studies. Further, several episodes were recorded in those studies (*i.e.*, pre-stimulus, stimulus, approach and post-stimulus), while in this experiment samples were taken for computer analysis following stimulus onset and 2.5 sec later. Yet another distinction concerns the difference between a brightness discrimination and alternation problems which

reflect the effects of frontolimbic damage.

The Fourier transforms of hippocampal EEG that we report are similar in general form to the intensity spectra of Berkhout *et al.* (1969) recorded from a monkey during delayed visual matching. They found a high proportion of activity in the hippocampal power spectra to lie in the low frequency range, although in the theta bandwidth they did not find autospectral differences related to learning. In the latter case, perhaps the inconsistency between Berkhout *et al.* and the present experiment may lie in differences in the degree of hippocampal participation in the tasks represented in the two studies.

The electrical activity of the hippocampus during the learning of the two alternation problems suggests a solution to the paradox of the lesion deficit on spatial alternation and the absence of a deficit on go/no-go alternation. To

be noted first is the fact that the monkeys learned the three problems in a standard order: go/no-go discrimination, go/no-go alternation and spatial alternation. This sequence may be seen to constitute the development of an increasingly differentiated and complex hierarchy of responses, in the development of which a critical feature is involved in the learning of go/no-go problems, especially the alternation problem. The most difficult aspect of go/no-go problems for the monkey appears to be learning to program the no-go part—to inhibit the panel press response. During the early trials of the go/no-go alternation problem, the monkeys perseverated for very large numbers of trials in making go responses, frequently ceasing to respond at all since the same trials continued to be presented until a correct (no-go) response was made. While such quitting was rewarded once, it typically took the monkeys some time to make the go response required next. It should be emphasized that no-go is not the passive withholding of a response; observation of the monkeys' behavior clearly revealed an active process—reaching out, almost pressing the panel and then withdrawing—which continued throughout the no-go period.

The go/no-go alternation problem may be soluble by animals with hippocampal lesions because the early learning of this task follows the course above. Although the hippocampally damaged animal lacks anticipatory control of the no-go response, his natural tendency to quit following repeated no-go errors provides distinctive experience in learning to inhibit responses, which helps to differentiate no-go from go trials.

In the learning of the delayed spatial alternation problem, the alternation of left and right responses must, as a result of the data obtained in the current studies, be viewed as a differentiation of no-go response selection—that is, what the monkey has to learn is *not* to go to the place he went before, not to perseverate this response to a single panel.

The contribution of the present electrophysiological data to this interpretation stems from the close similarity of theta on left right alternation to theta activity on the no-go trials of the go/no-go problem. Go responses appear

to involve increasingly less activity in the frequency range of 3–5 c/sec as learning progresses; the suggestion is that they become relatively automatic at advanced stages of learning and do not require active hippocampal control. No-go trials (and left right alternation), however, demand a high degree of modulation or control, which becomes increasingly evident in the greater proportion of theta as criterion is approached. In this connection, the recent suggestion of Vanderwolf (1971) that "... the hippocampal formation takes part in the programming of an intended act but... no actual behavior occurs until the program is activated by the diencephalic trigger" (p. 95–96) is relevant. Presumably, as responses (the go response) become relatively automatic, they become increasingly independent of the programming control that inhibitory responses demand, and this is seen in the decreased amount of rhythmical slow activity. Vanderwolf's proposal and the present interpretation suggest that theta rhythm signifies an active state of the hippocampus, in contrast to the views of Douglas (1967) and Grastyán (Grastyán *et al.* 1959).

Among the strongest bits of evidence in this experiment that the hippocampus participates in the anticipatory control or programming of intended acts is the increased theta activity immediately following stimulus presentation on no-go trials, an increase which drops out later in the trial. The immediate appearance of theta on no-go trials, whether or not the monkey's choice turns out to be correct or incorrect, strongly suggests that a fast time calculation of an intention to inhibit the panel press response is made at the very beginning of the trial (Pribram 1971). This calculation has to be properly learned; the difference between go and no-go trials and the anticipatory control of the no-go response does not show up until he has had experience with the task.

The results of the current experiment, therefore, support the assignment of an "intention" rather than an "inhibition", "memory" or "attention" function to the hippocampus. Response inhibition, an explanation so long favored in the literature, has been ruled out by the experimental finding of intact go/no-go alternation performance after hippocampectomy. But what of the

other two possibilities? With regard to memory, Talland (1965, 1968) has argued persuasively that the memory defect seen in men as Korsakoff's syndrome or following bilateral medial temporal lobe removals (amygdala and hippocampus) is due to an inefficient organizing process, a defect in programming—a suggestion also made by Miller *et al.* (1960). The results of the current study would accord with this proposal.

In the light of some recently completed research, the effects of hippocampectomy on attentional processes can also be explained in terms of the current results. In one study the effects of limbic lesions were shown to affect primarily the length of the period of chance performance in learning a discrimination or in making discrimination reversals (Pribram *et al.* 1969). In a subsequent study (Spevack and Pribram, in preparation), with the use of signal detection techniques, this effect was shown to be due to a change in the response bias influencing performance. Response bias can be conceived as a program influencing observing (attentional) as well as instrumental responses, a conception supported by another series of studies of the effect of limbic lesions using an eye camera technique (Bagshaw *et al.* 1970, 1972).

In the context of these results, the data of the current experiment suggest that hippocampal theta reflects a response biasing process which establishes the set point organizing observing and instrumental responding. This suggestion is consonant with the finding that theta rhythm shifts occur as a function of extinction (Gray 1970). Thus response bias influencing memory and attention, not response inhibition or selection *per se*, is the process in which the hippocampus appears to be involved.

SUMMARY

1. Electrical activity from hippocampus and inferotemporal cortex was recorded from monkeys (*Macaca mulatta*) during the learning of two delayed alternation problems: go/no-go alternation and classical spatial alternation.

2. Power spectrum analysis clearly revealed 3–5 c/sec theta rhythm in the electrical activity of the primate hippocampus and the appearance of systematic differentiation in this theta band-

width over the course of learning. Early in learning there were no differences between the trial categories of the go/no-go problem (*i.e.*, go correct, no-go correct, go incorrect, no-go incorrect) or between problems. As criterion was approached, however, theta rhythm became increasingly more prominent on no-go as against go trials. Theta on left-right alternation more closely resembled no-go trial activity. On go trials, theta activity tended to diminish as learning advanced.

3. Theta rhythm on incorrect trials of the go/no-go problem was consistent with the nature of the animal's response. 3–5 c/sec activity was similar on go correct and no-go incorrect trials near and at criterion, and theta on these trial categories was clearly different from no-go correct, go incorrect, and left-right correct and incorrect trial electrical activity.

4. These effects all took place in the period immediately following stimulus onset. Hippocampal electrical activity recorded later in each trial did not show any systematic differences between trial categories or problems.

5. The EEG from inferotemporal cortex differed from hippocampal activity in the greater proportion of fast activity and in the absence of any of the effects observed in the hippocampal leads.

6. The prominent occurrence of theta on no-go trials and the close similarity of the hippocampal power spectra on no-go and left right alternation trials suggests that these responses demand a high degree of modulation or control by an active hippocampus. From the appearance of the theta effects early in each trial, it appears that the hippocampus is involved in the anticipatory programming of intended acts, and the suggestion is that a fast time calculation of an intention to inhibit a response is made at the beginning of the trial. The data of this study suggest that hippocampal theta reflects response bias, conceived as a program organizing observing and instrumental responding.

RESUME

ACTIVITE ELECTRIQUE HIPPOCAMPIQUE DU SINGE AU COURS DE PROBLEMES D'ALTERNANCE RETARDEE

1. L'activité électrique de l'hippocampe et du

cortex inféro-temporal a été enregistrée chez des singes (*Macaca mulatta*) au cours de l'apprentissage de deux problèmes d'alternance retardée, alternance aller/ne pas aller, et alternance spatiale classique.

2. L'analyse de spectre de puissance montre clairement un rythme thêta de 3 à 5 c/sec dans l'activité électrique de l'hippocampe du primate et l'apparition d'une différenciation systématique dans cette bande thêta tout au long de l'apprentissage. A la phase précoce de l'apprentissage, il n'y a pas de différence entre les catégories séquentielles du problème aller/ne pas aller (c'est-à-dire aller correct, ne pas aller correct, aller incorrect, ne pas aller incorrect) ou entre les divers problèmes. Au fur et à mesure que l'on se rapproche du critère d'apprentissage, cependant, le rythme thêta devient progressivement prédominant dans les séquences ne pas aller comparées aux séquences aller. Dans l'alternance droite-gauche, le rythme thêta ressemble davantage à l'activité observée au cours des essais ne pas aller. Au cours des essais aller, l'activité thêta tend à diminuer au fur et à mesure que l'apprentissage avance.

3. Lors d'essais incorrects du problème aller/ne pas aller, le rythme thêta correspond à la nature de la réponse de l'animal. Une activité de 3 à 5 c/sec est similaire dans les essais aller corrects et ne pas aller incorrects lorsqu'on se rapproche ou que l'on atteint le critère d'apprentissage, et au cours de ces catégories d'essais, le rythme thêta est nettement différent de l'activité électrique lors des séquences ne pas aller correct, aller incorrect, et droit-gauche correct et incorrect.

4. Ces effets surviennent tous dans la période immédiatement consécutive au début du stimulus. L'activité électrique hippocampique enregistrée plus tard dans chaque séquence ne montre aucune différence systématique entre les catégories de séquences ou de problèmes.

5. L'EEG du cortex inféro-temporal diffère de l'activité hippocampique du fait d'une proportion plus élevée d'activité rapide et de l'absence de tous les effets observés au niveau des chaînes hippocampiques.

6. La survenue prévalente de thêta dans les séquences ne pas aller et la similarité très proche des spectres de puissance hippocampique dans

les alternances ne pas aller et droite-gauche suggère que les réponses demandent un degré élevé de modulation ou de contrôle par un hippocampe actif. Le fait que les effets thêta apparaissent précocément dans chaque séquence montre que l'hippocampe est impliqué dans la programmation anticipatoire des actes projetés, et on peut supposer que s'il existe une intention d'inhiber une réponse, le calcul rapide en est fait au début de la séquence. Les données de cette étude suggèrent que le thêta hippocampique reflète la tendance de la réponse, conçue comme un programme organisant le mode d'observation et de réponse instrumentale.

REFERENCES

- ADEY, W. R., DUNLOP, C. W. and HENDRIX, C. E. Hippocampal slow waves: distribution and phase relations in the course of approach learning. *Arch. Neurol. (Chic.)*, **1960**, *3*: 74-90.
- BAGSHAW, M. H., MACKWORTH, N. H. and PRIBRAM, K. H. The effect of inferotemporal cortex ablations on eye movement of monkeys during discrimination training. *Int. J. Neuroscience*, **1970**, *1*: 153-158.
- BAGSHAW, M. H., MACKWORTH, N. H. and PRIBRAM, K. H. The effect of resections of the inferotemporal cortex of the amygdala on visual orienting and habituation. *Neuropsychologia*, **1972**, in press.
- BERKHOUT, J., ADEY, W. R. and CAMPEAU, E. Simian EEG activity related to problem solving during simulated space flight. *Brain Res.*, **1969**, *13*: 140-145.
- BLACK, A. H., YOUNG, G. A. and BATENCHUK, C. The avoidance training of hippocampal theta waves in flaxedilized dogs and its relation to skeletal movement. *J. comp. physiol. Psychol.*, **1970**, *70*: 15-24.
- BROWN, T. S. and CHINO, M. *Effects of hippocampal lesions on alternation performance in the monkey*. Paper presented at the Eastern Psychological Association meetings, New York, N.Y., April, **1971**.
- BROWN, T. S., KAUFMAN, P. G. and MARCO, L. A. The hippocampus and response perseveration in the cat. *Brain Res.*, **1969**, *12*: 86-98.
- CAMPEAU, E., ADEY, W. R., DURHAM, R. M., TOLLIVER, J. D., RINGIER, R. and KAMMER, K. M. EEG discriminators of delayed matching to sample performance in *Macaca nemestrina*. *Physiol. Behav.*, **1971**, *6*: 413-418.
- DOUGLAS, R. J. The hippocampus and behavior. *Psychol. Bull.*, **1967**, *67*: 416-442.
- ELAZAR, Z. and ADEY, W. R. Spectral analysis of low frequency components in the electrical activity of the hippocampus during learning. *Electroenceph. clin. Neurophysiol.*, **1967**, *23*: 225-240.
- GRASZYAN, E. The hippocampus and higher nervous activity. In M. A. B. BRAZIER (Ed.), *The central nervous system and behavior*. Josiah Macy, Jr. Foundation, New York, **1959**, pp. 119-205.

- GRASYÁN, E., LISSAK, K., MADARASZ, I. and DONHOFFER, H. Hippocampal electrical activity during the development of conditioned reflexes. *Electroenceph. clin. Neurophysiol.*, **1959**, *11*: 409-430.
- GRAY, J. A. Sodium amobarbital, the hippocampal theta rhythm and the partial reinforcement effect. *Psychol. Rev.*, **1970**, *77*: 465-480.
- GREEN, J. D. The hippocampus. In J. FIELD *et al.* (Eds.), *Handbook of physiology, neurophysiology, II*. American Physiological Society, Washington, D.C., **1960**, pp. 1373-1389.
- ISAACSON, R. L., SCHMALTZ, I. W. and DOUGLAS, R. J. Retention of a successive discrimination problem by hippocampectomized and neocorticate rats. *Psychol. Rep.*, **1966**, *19*: 991-1002.
- MAHUT, H. Spatial and object reversal learning in monkeys with partial temporal lobe ablations. *Neuropsychologia*, **1971**, *9*: 409-424.
- MCFENANEY, K. W. and BUTTER, C. M. Perseveration of responding and nonresponding in monkeys with orbital frontal ablations. *J. comp. physiol. Psychol.*, **1969**, *69*: 558-561.
- MEANS, L. W., WALKER, D. W. and ISAACSON, R. L. Facilitated single alternation go/no-go performance following hippocampectomy in the rat. *J. comp. physiol. Psychol.*, **1970**, *72*: 278-285.
- MILLER, G. A., GALANTER, E. H. and PRIBRAM, K. H. *Plans and the structure of behavior*. Holt, New York, **1960**, 226p.
- MISHKIN, M. Perseveration of central sets after frontal lesions in monkeys. In J. M. WARREN and K. AKERT (Eds.), *Frontal granular cortex and behavior*. McGraw-Hill, New York, **1964**, pp. 219-241.
- MISHKIN, M. and PRIBRAM, K. H. Analysis of the effects of frontal lesions in monkeys: I. Variations of delayed alternations. *J. comp. physiol. Psychol.*, **1955**, *48*: 492-495.
- OLSZEWSKI, J. *The thalamus of the Macaca mulatta. An atlas for use with the stereotaxic instrument*. S. Karger, Basel, **1952**.
- PRIBRAM, K. H. DADTA III: An on-line computerized system for the experimental analysis of behavior. *Percept. Motor Skills*, **1969**, *29*: 599-608.
- PRIBRAM, K. H. *Languages of the brain*. Prentice-Hall, Englewood Cliffs, **1971**, 432 p.
- PRIBRAM, K. H., DOUGLAS, R. J. and PRIBRAM, B. J. The nature of non-limbic learning. *J. comp. physiol. Psychol.*, **1969**, *69*: 765-772.
- PRIBRAM, K. H., LIM, H., POPPEN, R. and BAGSHAW, M. H. Limbic lesions and the temporal structure of redundancy. *J. comp. physiol. Psychol.*, **1966**, *61*: 368-373.
- PRIBRAM, K. H., MISHKIN, M., ROSVOLD, H. E. and KAPLAN, S. J. Effects on delayed-response performance of lesions of dorsolateral and ventromedial frontal cortex of baboons. *J. comp. physiol. Psychol.*, **1952**, *45*: 565-575.
- PRIBRAM, K. H., WILSON JR., W. A. and CONNORS, J. Effects of lesions of the medial forebrain on alternation behavior of rhesus monkeys. *Exp. Neurol.*, **1962**, *6*: 36-47.
- RADULOVAČKI, M. and ADEY, W. R. The hippocampus and the orienting reflex. *Exp. Neurol.*, **1965**, *12*: 68-83.
- TALLAND, G. A. *Deranged memory*. Academic Press, New York, **1965**, 356 p.
- TALLAND, G. A. *Disorders of memory and learning*. Penguin, New York, **1968**, 176 p.
- VANDERWOLF, C. H. Limbic-diencephalic mechanisms of voluntary movement. *Psychol. Rev.*, **1971**, *78*: 83-113.

Reference: CROWNE, D. P., KONOW, A., DRAKE, K. J. and PRIBRAM, K. H. Hippocampal electrical activity in the monkey during delayed alternation problems. *Electroenceph. clin. Neurophysiol.*, **1972**, *33*: 567-577.