

HIPPOCAMPAL THETA FREQUENCY SHIFTS AND OPERANT BEHAVIOUR

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(Accepted for publication: July 3, 1968)

Hippocampal rhythmic activity appears predominantly in the frequency range from 4 to 7 c/sec (review in Green 1964). The activity so characterized is generally known as hippocampal theta rhythm. Shifts in the dominant component of such a rhythm during particular behavioural states have been described (Adey *et al.* 1961; Storm van Leeuwen 1965; Grastyán *et al.* 1966; Storm van Leeuwen *et al.* 1967). Recently Elazar and Adey (1967), in a very detailed study, demonstrated that the hippocampal dominant frequency shifts to 6 c/sec when a cat is approaching a food reward in a learning situation; they interpreted the occurrence of the 6 c/sec burst as being specifically correlated with correct approach behaviour. Experiments conducted by us and reported in the present article show that such a shift in the dominant frequency component occurs also in other behavioural conditions. In our experiments we found a burst at 6 c/sec in the hippocampus whenever a dog received its food reward and withdrew from the pedal in an operant behavioural procedure. An interpretation of this phenomenon is necessary and an attempt in this direction is presented in the discussion.

METHOD AND MATERIAL

a. *Experimental procedure*

Two dogs, German boxers, have been investigated. They will be referred to as K and S. Both dogs were trained to press a pedal when a particular sensory stimulus was presented in order to obtain a food reward. Training took place in a room of about 30 m² in which the animals were able to move freely. On every working day one experimental session was carried out, during which a sensory stimulus was delivered 30 times

with random intervals between presentations. The animals received very little food outside the experimental sessions. The sensory stimulus lasted 2–5 sec, depending on the learning phase and on the animal. In dog K it consisted in a burst of clicks and in dog S in a burst of sine wave modulated light. The experiments were conducted in two phases: the preliminary phase consisted of 4 or 5 experiments in which the animals were habituated to the sensory stimulus and trained to press the pedal; in the second phase conditioning was started and thus the food reward — a piece of meat — was given only when the animal pressed the lever during stimulus presentation. Pressings occurring within the initial 500 msec of the



Fig. 1

Dog carrying telemetering apparatus while pressing the pedal, after the stimulus has been delivered, and expecting the food reward.

stimulus burst were not rewarded, to prevent reinforcement of random pressings. The reward was automatically ejected through a hole in a wall into the experimental room. The dog either picked the food up from the floor, in the neighbourhood of the pedal, or was able to catch it while falling. The experimental set-up is illustrated in Fig. 1. During the experiments the animal's behaviour was monitored by means of closed circuit television and recorded on video tape (Philips video recorder). The experiments here reported were carried out, for each dog, over a period of more than 6 months.

b. Recording

Electrical activities of the hippocampal formation areas were derived from chronically indwelling 100 μ diameter stainless steel wire electrodes insulated to 1 mm from the tip. The electrical activities considered in the present report were derived from the hippocampal formation. The derivations were either bipolar from closely spaced electrodes or against a common reference in the lateral ventricle. In dog K, post mortem histological observation confirmed that the recording was from the fascia dentata (ventral aspect). Dog S has not yet been killed, but both the stereotaxic coordinates and the electrical activities recorded imply that the recording is from the dorsal hippocampus, although it is not yet possible to state from which area. The electrical activities were amplified and transmitted by means of an 8-channel EEG radio-telemetry apparatus (Kamp 1963), recorded on EEG paper (Offner R-type dynograph) and on magnetic tape (EMI multi-channel tape recorder).

A digital time code was recorded simultaneously on EEG paper, instrumentation tape and video tape so that on playback the electrical activities and the behavioural aspects could be precisely related in time (within 0.1 sec). At the same time, signals to mark the occurrence of pressings, the delivery of reward and the presentation of stimuli were recorded.

c. Analysis

The electrical activities were analysed on-line, or from tape, by means of a bank of 20 electronic bandpass filters covering the frequency range 2–32 c/sec. Eleven filters had resonance frequen-

cies from 2 to 12 c/sec and a bandwidth of one cycle; eight others had resonance frequencies from 14 to 28 c/sec, in steps of 2 c/sec, and bandwidth of 2 c/sec; the last one had its resonance frequency at 32 c/sec and 4 c/sec bandwidth (Bekkering *et al.* 1958). The frequency spectrogram was continuously displayed on an oscilloscope screen for visual monitoring. In order to obtain compact, quantitative information about the frequency spectrum two other methods of presentation were employed: (1) The running average of the outputs of the 20 filters (with adjustable integration time constant, usually set at 0.5 or 1 sec), displayed in the form of a histogram on a television screen, was photographed on a continuously moving film once every 250 msec (examples in Fig. 3). (2) The running average of the filter outputs was fed to a Computer of Average Transients (CAT 400b TMC); 20 successive addresses of the computer were used, each corresponding to one filter. The output amplitude of each filter was summed in the respective address. The triggers to the computer could be gated according to the epoch of interest. In this way the frequency spectrum of one epoch was obtained. Furthermore, equivalent epochs of the learning paradigm were summed and any frequency component consistently recurring in a particular epoch was detected (Fig. 4). It should be noted that when the term "peak at 5 or 6 c/sec" appears in this article it is meant that the maximum amplitude in the frequency spectrum was at 5 or 6 c/sec, which does not necessarily imply that a rhythmic component at that exact frequency was present in the original record. To detect frequency shifts the output of only one filter may be insufficient if the shift of frequency occurs within its bandwidth. In our apparatus the response of a filter is 50% of its maximum at a frequency midway between its resonance frequency and the resonance frequency of the next filter. Thus when the ratio of the outputs of two adjacent filters is taken shifts of frequency within the bandwidth of one filter can easily be detected.

RESULTS

a. Hippocampal frequency shifts in the course of operant behaviour

Fig. 2 illustrates the sequence of events oc-

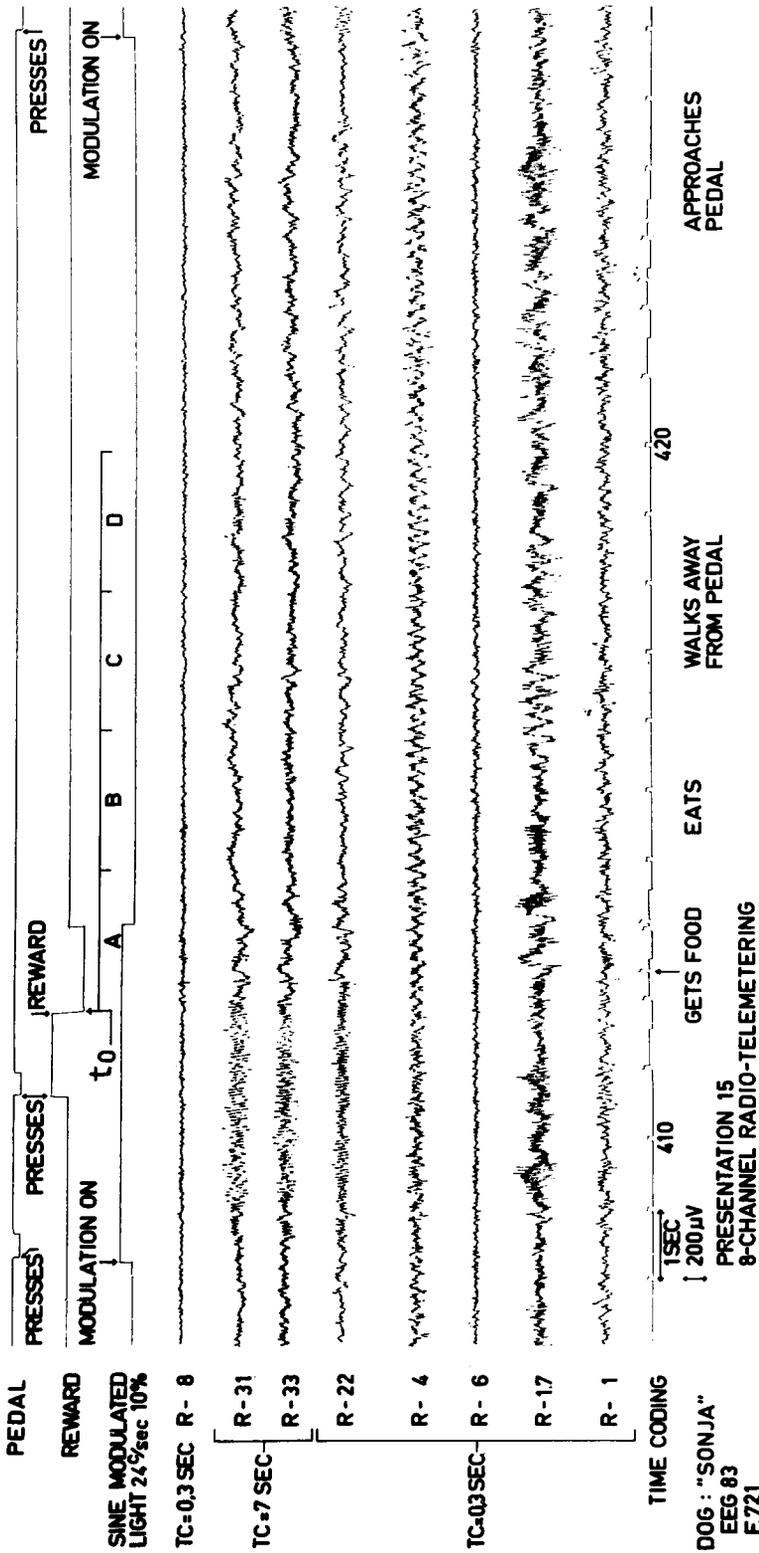


Fig. 2
 Dog S, EEG. At "modulation on" the conditional stimulus (sinusoidally modulated light) is presented. At to the food reward is delivered. Hippocampal activity in R-4. Evoked responses to light in R-31, R-33, R-22 (cortical areas); olfactory bulb activity in R-17; amygdaloid nucleus activity in R-1; caudate nucleus activity in R-8; R-6: outside hippocampus (white matter). The post-reward period is divided in 2 sec epochs, A-D starting from to.

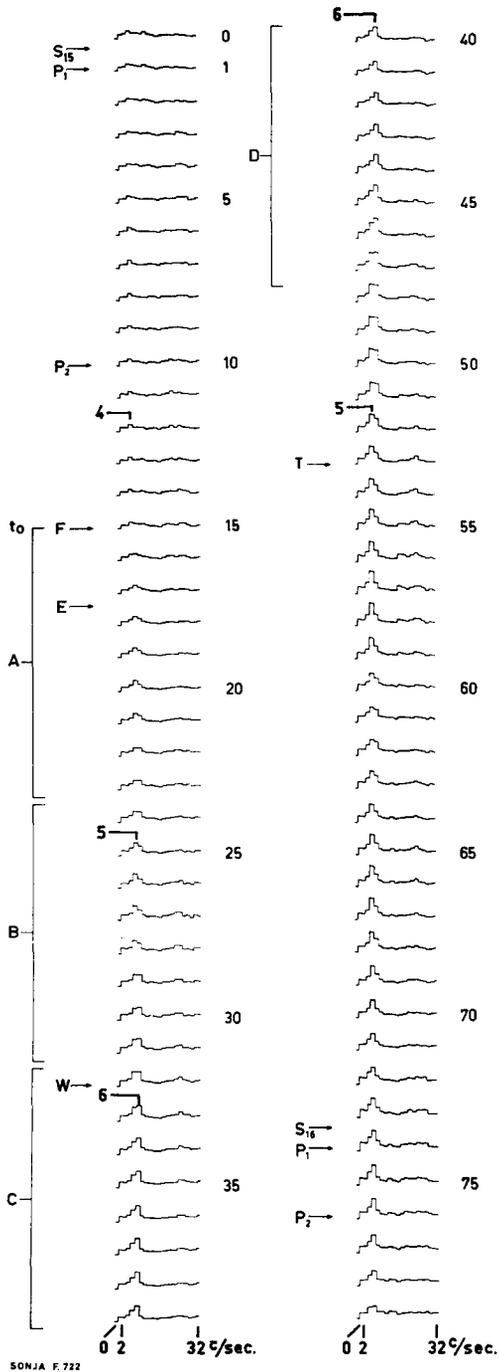


Fig. 3
 Sequential frequency spectra from the trial shown in Fig. 2. Time runs vertically. Interval between two histograms is 0.25 sec. Histograms start with the stimulus. S - start of stimulus; P₁, P₂ - dog presses pedal; F - food delivered; E - eating; W - walks away from pedal; T - turns back. Above some peaks the respective filter resonance fre-

quency is indicated. Filter resonance frequencies are as in Fig. 5. A zero is included, as shown in the last spectrum, to indicate that the first bar of the histogram is a baseline level. Post-reward epochs as in Fig. 2. Note decrease of all amplitudes between S and P. Afterwards a peak appears which is appreciable in spectrum 25 (at 5 c/sec), shifts to 6 c/sec in spectrum 33 and back to 5 c/sec after spectrum 51.

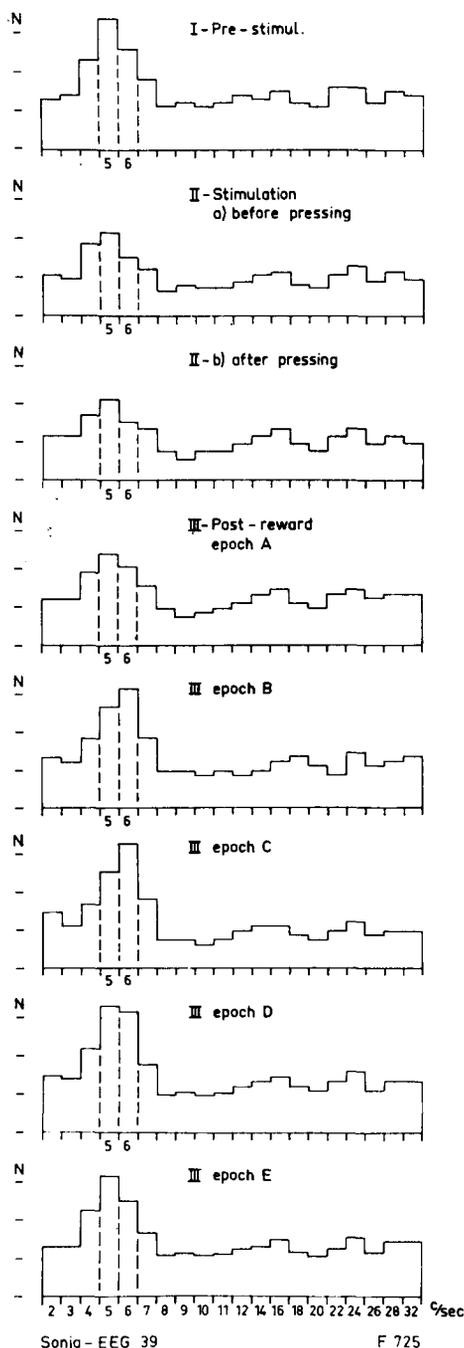


Fig. 4

Frequency spectra integrated over successive epochs from 19th conditioning experiment (dog S, performance level 100%), obtained from all trials in which the dog walked away from the pedal in the post-reward period. Division of epochs as in Fig. 2. Epoch E (from the 8th to the 10th sec post-reward) is included. Note decrease of total histogram area from I to II and peak at 6 c/sec in B and C.

The detailed analysis of the relationships between the electrical activities and the dog's performance in the course of time indicated that the amplitude and duration of the 6 c/sec bursts were dependent on whether dog S walked away after receiving the reward or stood by the pedal. In the rare instances in which dog S did not walk away after having eaten, the occurrence of a peak at 6 c/sec was still observed, but in these cases the duration of the burst was very short and the amplitude of the peak, as seen in the frequency spectrum, was small.

The time of occurrence of the 6 c/sec burst was somewhat variable and related to the time the dog took to start walking away after having eaten. Often it appeared earlier than shown in Fig. 3.

Frequency spectra from individual trials are, of course, less significant than frequency spectra integrated over equivalent epochs of successive trials of one experiment; an example is shown in Fig. 4 (19th conditioning experiment; performance level 100%). Three main aspects emerge from this series of histograms: (a) the dominant frequency was at 6 c/sec in epoch B and especially in epoch C, while the dog was walking away from the pedal; (b) after epoch D 5 c/sec predominated as the dog turned back toward the pedal; (c) the two epochs taken during stimulation showed a general decrease of amplitude in relation to the pre-stimulation period.

Integrated frequency spectra were not computed for all experimental series because the continuous frequency analysis was monitored during the trials and so it was possible to observe the same sequence of hippocampal activities as described above from trial to trial. The only difference that could be distinguished between early experiments (excluding the very early ones which will be reported in section b) and late ones was that the electrical patterns characteristic for each epoch became more stable from trial to trial in the course of conditioning. It is then of interest to show that the difference in dominant frequency between epochs, so clearly seen in Fig. 4 for the 19th conditioning experiment, was already apparent in the 6th. To demonstrate this,

Ordinate: N = number of counts in each computer address (arbitrary scale normalized for all spectra). Abscissa: filter resonance frequencies.

we chose as parameter for statistical analysis the ratio between the amplitudes of the frequency components at 5 c/sec and 6 c/sec, since this gives the relevant information about the shift in dominant frequency in the post-reward period. The mean and standard deviation of the ratio 5 c/sec : 6 c/sec for 9 consecutive trials (all trials of the 6th experiment in which the dog walked away from the pedal) was, for epoch B 1.09 ± 0.17 , epoch C 0.85 ± 0.10 , for epoch D 0.97 ± 0.33 and for epoch E 1.27 ± 0.28 .

To determine whether the difference between group C and the others was significant, Wilcoxon's test was applied (the sample variances being not sufficiently alike, as tested by Snedecor's test, to permit the use of an analysis of variance); the ratio 5 c/sec : 6 c/sec for epoch C differed significantly from that of epoch B ($P < 0.025$) and epoch E ($P < 0.025$). There was no significant difference between epochs C and D. The variance of epoch D was larger than that of epoch C, reflecting that the former was an epoch of transition regarding the shift in dominant frequency. In these trials the mean time interval from the moment the dog received the reward until the moment it returned to the neighbourhood of the pedal was 12 ± 2 sec, which implies that in epoch E (from the 8th to the 10th sec after reward) the dog was either at the pedal or was approaching it.

In dog K the pattern of change in the hippocampal dominant frequency presented some differences in comparison with dog S. Nevertheless, it also presented a peak at 6 c/sec in the post-reward period. An example is shown in Fig. 5 (10th conditioning experiment, performance level = 97%). This Fig. shows that the peak at 6 c/sec was of shorter duration and appeared earlier in relation to the reward delivery than in dog S. Thus, the epochs in which the post-reward period was divided, for dog S, were further subdivided for the analysis of records from dog K so that epoch A of dog S corresponds to epochs A1 + A2 for dog K. Statistical analysis was done as for dog S, taking also as parameter the ratio 5 c/sec : 6 c/sec amplitudes. The mean and standard deviations of this ratio for the same trials as summarized in Fig. 5 were, for epoch A1 1.08 ± 0.20 , for A2 0.76 ± 0.20 and for B 1.13 ± 0.16 . An analysis of variance showed

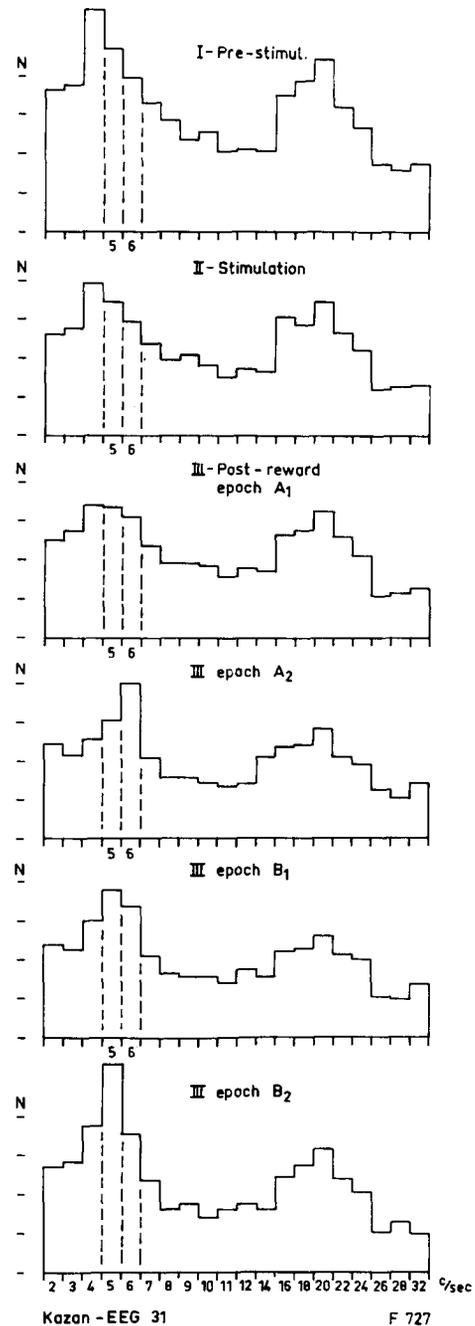


Fig. 5
Frequency spectra integrated over successive epochs for dog K (10th conditioning experiment, performance level = 97%). Reward given immediately after correct pressing. Post-reward epochs are as in Fig. 2 but each is subdivided in 2 epochs 1 sec long (A1, A2), (B1, B2). Note occurrence of peak at 6 c/sec in epoch A2 and at 5 c/sec in epoch B2. Statistics from same experiment in text.

that the difference between the means of epochs A2 and A1 was significant ($F=11.7$, $dF=1/18$, $P<0.005$) as well as that between epochs A2 and B1 ($F=19.2$, $dF=1/18$, $P<0.001$), indicating that the component at 6 c/sec was relatively predominant in epoch A2.

b. *Hippocampal activity in successive learning stages*

To compare different experiments concerning the appearance of the dominant peak at 6 c/sec a quantitative estimate of this frequency component was obtained, as indicated previously. As we did not observe any consistent difference in the time of occurrence of the 6 c/sec burst between early and late experiments, and as in most cases the 6 c/sec peak was most evident in epoch C (dog S), the ratio of 5 c/sec : 6 c/sec amplitude in the frequency spectrum of epoch C was chosen as parameter for comparison. In dog S the group of 6 earliest trials (in which the dog performed correctly and walked away from the pedal) had 1.47 ± 0.15 as mean and standard deviation of the ratio 5 c/sec : 6 c/sec and the group of 14 subsequent trials had 0.90 ± 0.13 . The difference between the two means was statistically significant ($F=68.9$, $dF=1/18$, $P<0.001$).

In dog K an increase in amplitude and consistency of the peak at 6 c/sec in epoch A2 was also found in the course of conditioning. However, the increase was not as clear as in dog S. In the preliminary experiments, in which the dog was still helped to press the pedal and conditioning was not yet initiated, a frequency component at 6 c/sec was more conspicuous in epoch A2 than in other epochs in one quarter of the trials. However, at this stage the general amplitude of the different frequencies in the theta range was relatively small and there was, in the average, as much activity at 4 c/sec as at 5 or 6 c/sec. This picture changed markedly at a later stage, the turning point appearing in the second conditioning experiment. Theta activity became then clearly dominant in the post-reward period and a peak at 6 c/sec in most trials was noted in epoch A2, although in the others the peak was at 5 c/sec. In this experiment the mean and standard deviation of the ratio 5 c/sec : 6 c/sec amplitude in epoch A2 was 0.96 ± 0.21 . In the 5th conditioning experiment (performance level 45%) the corre-

sponding values were 0.76 ± 0.21 , and in the 10th conditioning experiment (performance level 97%) 0.76 ± 0.20 . The difference between the means of the 2nd and 5th experiments was not significant ($F=3$, $dF=1/21$, $P>0.05$) but between the 2nd and the 10th there was a significant difference ($F=5.6$, $dF=1/26$, $P<0.05$).

With the continuation of training no appreciable change was observed in the sequence of events recorded from the hippocampus. The same behavioural pattern and the same sequence of electrical activities were monotonously repeated from trial to trial. However, at very late stages of training the 6 c/sec burst became less conspicuous in dog K, whereas in dog S 6 c/sec persisted even up to the 2500th trial without any appreciable change. It is worth mentioning that a difference in behaviour was also observed between these two animals: dog K gave up pressing out of time, *i.e.*, in the absence of a sensory stimulus, rather early and appeared always calm and exact during the experiments, while dog S, even in late experiments, was invariably eager to get food, did not stop from making occasionally incorrect pressings between stimuli and regularly walked away from the pedal after eating.

c. *Hippocampal activity during conditional stimulation*

All frequency spectra here presented show that during conditional stimulation the activity in all frequency bands decreased. This decrease was slightly more marked for the theta band than for the higher frequencies (above 16 c/sec). This tendency was more evident after a good degree of performance had been reached. However, the difference between early and late experiments in this respect did not attain a level of statistical significance.

In late stages of conditioning, with consistent performance above the 95% level, we observed that in a few cases dog S (but not dog K) did not press the pedal, although it was in its usual position waiting to press, and did not show any outward signs of distraction. In these cases, 6 in all, the hippocampal activity during conditional stimulation presented a high peak at 5 c/sec, very much at variance with the usual pattern. The proportion of activity in the 4–7 c/sec band in these cases was 30.3 ± 1.8 (as a percentage of the total

area of the frequency histogram) whereas in 14 other trials selected at random from the same experiments it was only 24.7 ± 2.6 . The difference between these two means was statistically significant ($F=21$, $dF=1/18$, $P<0.001$), indicating that the inhibition of pressing was correlated with the appearance of a peak in the theta frequency band (mainly at 5 c/sec) during conditional stimulation at a late stage of conditioning.

d. *Observations under free behaviour conditions*

The same animals were also observed outside the conditioning situation while freely moving. In these circumstances a burst at 6 c/sec was occasionally observed in the hippocampus of either dog when it was walking to pick up a piece of food, or a ball, that it had seen thrown at a distance. In these cases the 6 c/sec burst was less sustained than during the learning trials.

DISCUSSION

a. *Hippocampal frequency shifts in the post-reward period*

The experiments here reported demonstrate primarily the existence of a clear time relation between an electrical phenomenon recorded from the dog's hippocampal formation and a well defined behavioural pattern. The basic finding is that the dominant frequency of the dog's hippocampal theta rhythm appears at 6 c/sec in the frequency spectrum during part of the period consecutive to food delivery in an operant behavioural procedure. The shift in frequency is slight and hence is difficult to detect in the primary EEG recording. To put it in evidence the sequential frequency spectra, with the precise time relations to the dog's behaviour, were necessary. The results here presented have been established in two dogs only, but they were observed over a long period of time and in different behavioural conditions. The intensive study of each dog enabled us to obtain confirmation of the correlation in many hundreds of trials. However, differences between the two dogs were observed. Indeed in dog K the 6 c/sec peak occurred earlier after food delivery and was of shorter duration than in dog S. One possibility which could account for this difference is that it reflects the striking dissimilarity of the two dogs in their post-reward behaviour pattern. Dog S nearly

always withdrew from the pedal after eating whereas dog K, in the same period, only adjusted its position near the pedal and rarely walked away. Considering that in dog S the 6 c/sec burst became always more conspicuous and prolonged when this dog presented the typical behaviour of walking away from the pedal, the fact that the 6 c/sec burst was of much shorter duration in dog K may be assumed to reflect its lack of a "walking away" behavioural pattern. However, another possibility is that this difference in the 6 c/sec burst characteristics may stem from the fact that the location of the hippocampal electrodes was probably not the same in both dogs.

b. *Possible neural mechanisms responsible for theta frequency shifts*

Although no definite evidence has been obtained in our experiments, basically, two different neural mechanisms could contribute to such a frequency shift: (a) the phenomenon might be due to real shift in frequency of a rhythmic process in a particular neurone population, or (b) it might be the consequence of a change in the relative contribution to the recorded activity of distinct hippocampal neurone populations having different connections and slightly different frequencies of oscillation. By the first hypothesis we could envisage the shift from 5 to 6 c/sec as depending on a parallel increase of the frequency of burst discharge of septal neurones, probably modulated by increased activation of the mid-brain reticular formation, since Gogolák *et al.* (1967) have shown that there is a clear relationship between the burst discharges of those neurones and theta frequency in the rabbit. Indeed Stumpf (1965) has suggested that the frequency of the hippocampal theta rhythm can be a sensitive index of the degree of reticular excitation. The second possibility finds support in the fact that hippocampal areas are responsive to different inputs and that only unusually may pyramidal cells be driven by both septal and entorhinal stimulation (von Euler and Green 1960). It is also known that entorhinal stimulation influences greatly the granule cells of the fascia dentata (Andersen *et al.* 1966). It is then conceivable that variations in the relative importance of septal or entorhinal inputs might elicit changes in hippocampal theta frequency.

c. *Behavioural correlates of theta rhythm shifts*

In relation to previous studies of hippocampal theta frequency shifts (Storm van Leeuwen 1965; Elazar and Adey 1967; Storm van Leeuwen *et al.* 1967), in which it was shown that a shift to 6 c/sec appeared when a dog or cat approached a goal, our finding of a strong correlation between the frequency shift to 6 c/sec and the dog's withdrawal from the pedal after eating may seem contradictory, if the pedal is assumed as goal. Moreover, we observed that the hippocampal peak frequency clearly shifted back from 6 c/sec to 5 c/sec in our experiments when the dog, after having walked away from the pedal, turned round and approached it.

We also observed bursts at 6 c/sec in the same leads outside the operant behaviour situation when either dog K or S approached a ball or a piece of food that had been thrown to a distance. Thus neither approach nor withdrawal patterns as such can be considered as specific correlates of the 6 c/sec hippocampal shift. It is more likely that significant relations may be found if the whole behavioural situation is considered.

In our experimental situation the dog appeared to be in a tense state while pressing the pedal, *i.e.*, a state of enhanced drive and readiness to act. The moment it got the food the animal underwent a sudden transition from a state of tension, of immobilization and expectancy (presumably also apparent in the cats of Elazar and Adey 1967), to one in which it appeared less tense and moved. It is this sudden transition that appears to be related to the shift of hippocampal frequency towards 6 c/sec. It might also be thought that the change in physiological state elicited by eating food could be correlated with the 6 c/sec shift, but it should be noted that when a dog is eating its normal meal no theta rhythm is usually recorded in the hippocampus, as shown by Storm van Leeuwen *et al.* (1967) and confirmed in our dogs.

The interpretation presented above does not imply that such shifts in theta frequency should occur exclusively in the behavioural condition described. To reinforce the argument it would be of interest to know whether other behavioural situations, such as in avoidance conditioning, in which a clear element of tension reduction exists, are also associated with an increase of theta

frequency to 6 c/sec.

Complementary to the time relation between the 6 c/sec shift and a clearly defined post-reward epoch is that the 6 c/sec bursts become more consistent as conditioning proceeds. This confirms the observation of Elazar and Adey (1967) and reinforces the assumption that the shifts to 6 c/sec in the two series of experiments are related phenomena and should be interpreted considering the general behaviour of the dogs during conditioning. Initially they were continuously tense and even if they occasionally succeeded in pressing the pedal correctly they did not come back to it often enough. It was only when they started to pay attention to the conditional stimulus that they presented a clear increase of tension during stimulation, which alternated with a more relaxed state immediately after receiving the reward. It was then that the behavioural pattern became stable, the hippocampal activity showed a conspicuous theta rhythm in the post-reward period and the 6 c/sec burst appeared clearly.

d. *Hippocampal modes during conditional stimulation*

The observation referred to in section c of Results, that there was a significant difference in hippocampal activity during conditional stimulation between the correct trials and those in which the dog did not press at all, supports the findings of Grastyán *et al.* (1959, 1966) in cats and indicates that a theta activity mode of response of the hippocampus to arousal is not the only one, as initially thought (Green and Arduini 1954). Clearly, in our experiments the "low voltage desynchronized" pattern of activity is elicited by the conditional stimulus and accompanies a state of tension and readiness to act. In contrast the observation of a theta rhythm at 5 c/sec in cases of inhibited pressing indicates that such a pattern is associated with a state of inhibition of a well learned performance. Hence opposite patterns of hippocampal activity reflect two extreme states of behaviourally important functions.

In conclusion it may be envisaged that the shifts in theta frequency seen in our experiments might be the expression of changes in hippocampal functional state associated with decreases and increases in tension or drive. It is not possible, however, to give a precise formulation of the

functional significance of such phenomena. At this stage we can only establish the exact time relations between electrical activities and behaviour patterns.

SUMMARY

1. A shift of hippocampal dominant theta frequency to 6 c/sec has been demonstrated in the post-reward period in two dogs, which occurs consistently related in time to a well defined behavioural pattern in the course of an operant conditioning paradigm.

2. The frequency shift was detected and quantified by means of sequential and integrated frequency displays and was found to be statistically significant.

3. The occurrence of the hippocampal shift to 6 c/sec became more stable, and the burst of larger amplitude and enhanced regularity, as conditioning proceeded. In respect to the predominance of the component at 6 c/sec a significant difference was found between early and late experiments.

4. A regular pattern of "low voltage desynchronized" hippocampal activity was regularly observed during conditional stimulation, at late stages of conditioning, if followed by correct pressing. When the dog did not perform correctly (inhibition of pressing) there was instead a predominance of theta pattern (peak at 5 c/sec) during stimulation. The difference in contributions of theta rhythm to the total frequency spectra between the two conditions was highly significant.

5. Behavioural correlates of the shift to 6 c/sec and the possible neural mechanisms underlying this phenomenon are discussed.

RÉSUMÉ

MODIFICATIONS DE LA FRÉQUENCE THETA HIPPOCAMPIQUE ET COMPORTEMENTS OPÉRATOIRES

1. Un brusque passage de la fréquence hippocampique dominante theta à une fréquence de 6 c/sec a été observé chez deux chiens dans la période consécutive à la gratification, survenant en relation de temps constante avec un pattern de comportement bien défini au cours du paradigme d'un conditionnement opérant.

2. Ce changement de fréquence est dépisté et quantifié au moyen de dispositifs séquentiels

d'intégration de fréquence, et apparaît statistiquement significatif.

3. Le passage à 6 c/sec du rythme hippocampique acquiert plus de stabilité, les bouffées une amplitude plus grande et une régularité accrue au fur et à mesure que le conditionnement se poursuit. Concernant la prédominance de la composante à 6 c/sec, une différence significative s'observe entre les expériences précoces et tardives.

4. Un pattern régulier d'activité hippocampique "de bas voltage désynchronisé" s'observe régulièrement pendant la stimulation conditionnelle au stade tardif du conditionnement si elle est suivie par une pression correcte. Quand le chien ne l'exécute pas correctement (inhibition de la pression) on note au contraire une prédominance du pattern theta (maximum à 5 c/sec) pendant la stimulation. Les différences de contribution du rythme theta au spectre total de fréquence entre ces deux conditions est nettement significative.

5. Les corrélations comportementales du passage à 6 c/sec et les mécanismes neuroniques possibles sous-tendant ce phénomène sont discutés.

We are grateful for the criticisms of Prof. Dr. W. Storm van Leeuwen and Dr. A. van Rotterdam, who checked the statistics, and for the help of the Brain Research Unit staff with the recording.

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