

HIPPOCAMPAL EEG AND BEHAVIOUR IN DOG. III. HIPPOCAMPAL EEG CORRELATES OF STIMULUS-RESPONSE TASKS AND OF SEXUAL BEHAVIOUR¹

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(Accepted for publication September 14, 1978)

In previous papers (Arnolds 1978; Arnolds et al. 1979a, b) we have presented arguments which support the hypothesis that the RSA spectral component of the hippocampal EEG of dogs reflects the degree of motor activity of the animal in a predictable but non-specific way. This rhythmic slow activity (RSA) is the typical hippocampal rhythmic field potential which, in various species including the dog, is confined to the theta band, but in other species such as the rat can reach up to 12 c/sec. Our hypothesis is that the peak frequency, the amplitude and the rhythmicity of the hippocampal EEG increase as the animal's motor activity increases, irrespective of the motivational circumstances under which such changes in motor activity occur. Arguments may also be found in support of the idea that unhabituated sensory stimuli are also reflected in the hippocampal EEG (Arnolds et al. 1979a). The literature, however, contains many reports on the hippocampal EEG correlated with the performance in various stimulus-response tasks. From such studies it has been concluded that RSA is a correlate of learning (Landfield et al. 1972; Landfield 1976), information processing (Klemm and

Douglass 1974), frustration (Gray and Ball 1970), arousal and attention (Kemp and Kaada 1975). Clearly variables such as learning, frustration and attention cannot be measured directly, therefore in such experiments the motor behaviour in the stimulus-response task is taken to indicate that these 'internal processes' have taken place.

Whether the EEG phenomena observed during the execution of the task may be related to the directly observable motor behaviour mediating the performance of the task is commonly not investigated. In this way, the animal's performance, described in terms of 'correct' and 'incorrect' responses is used to relate hippocampal EEG to 'internal processes'.

In this paper experimental data will be presented to show that it is necessary to take into account the overt motor behaviour in experiments, designed to investigate such 'internal processes'. Our experiments were designed to test, on the one hand, whether the correlation between the spectral properties of the hippocampal EEG and motor behaviour holds during the performance of stimulus-response tasks. On the other hand, we investigated whether differences could be demonstrated between the EEG correlated with 'correct' and 'incorrect' performance, which would *not* be related to differences in motor behaviour. To this end we investigated the hippocampal EEG correlates and the motor behaviour related to the performance of a sound and a spatial discrimination task.

¹ The investigations were supported (in part) by the Foundation for Medical Research FUNGO, which is subsidized by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.)

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We chose a two-way discrimination task since several reports in the literature relating changes in hippocampal EEG to learning make use of this type of task. Usually these are visual discrimination tasks (Moise and Costin (1974) in monkeys and Elazar and Adey (1967) in cats). Since dogs appear to be more dependent on sound and smell than on sight, an auditory cue appeared to be more appropriate for this experimental animal. Moreover, the execution of the task employed by us would necessarily involve strong orienting behaviour. This would allow comparison of our results with those of Grastyán (Grastyán et al. 1959, Grastyán and Vereczkey 1974), who reported RSA to be related to the orientation reflex exhibited by cats in a sound discrimination task. The type of place-learning task employed by us involved 'frustrative non-reward' which, by Gray and Ball (1970), is claimed to be associated with a higher RSA frequency than normally rewarded trials in a runway task in rats. Moreover, this task was chosen because it gave rise to a sufficient number of incorrect responses to allow a statistical comparison of the EEG and behavioural measurements made during 'correct' and 'incorrect' responses.

Furthermore, we investigated whether the motor behaviour during social interaction was correlated with the hippocampal EEG in the same way as stated above. We therefore studied the EEG correlates of some motor acts involved in copulatory behaviour.

An intensive longitudinal study of 2 dogs gave rise to the data upon which this paper is based. The histology of both animals is shown in Fig. 1 of Arnolds et al. 1979b. Placement A gave rise to the signals used for Figs. 2, 3 and 4, placement B to those used for Fig. 5 in this paper.

Material and methods

These were the same as described previously (Arnolds and Lopes da Silva 1977; Arnolds et al. 1979a). The experimental procedures em-

ployed are described in the paragraphs preceding the results of each separate experiment (see Results).

Data acquisition and computer processing

The procedures were the same as described previously (Arnolds et al. 1979a). In all analyses EMG refers to the rectified smoothed EMG of a forepaw muscle, ACCB and ACCH to the output of a movement transducer on the dog's back and head. I_{PF} is the index of the peak frequency in the theta band. I_{AM} indicates the amplitude in the theta band. I_R is an indicator of the apparent rhythmicity (i.e. bandwidth). \blacktriangle indicates arbitrary units. The arrow indicates the trigger event. The bar through each data point indicates the standard error of the mean. N is the number of averaged events, \bar{D} the average duration of a number of periods that have been averaged. Where a curve is thickened there exists a statistically significant difference between that part of the curve and the value indicated by an asterisk, chosen as a reference (sign test). The thicker the line, the higher the significance of the statistics ($P < 0.05$ in any case). The greatest thickness indicates $P < 0.001$. The series of histograms at the bottom of the analysis represents the spectral analyses of the EEG of a number of 200 msec time bins around the trigger event. The placement of the spectra corresponds to the time scale of the curves.

Results

(1) Left-right sound discrimination

Procedures. The animal was placed in the treadmill in an isolated experimental room as described previously (Arnolds et al. 1979a). To the left and right of the food dish in symmetrical positions 2 loudspeakers were placed. In front of each loudspeaker there was a pedal (Fig. 1). A single trial comprised the following elements.

The dog was required to stand quietly near the food dish. Then either of the 2 speakers

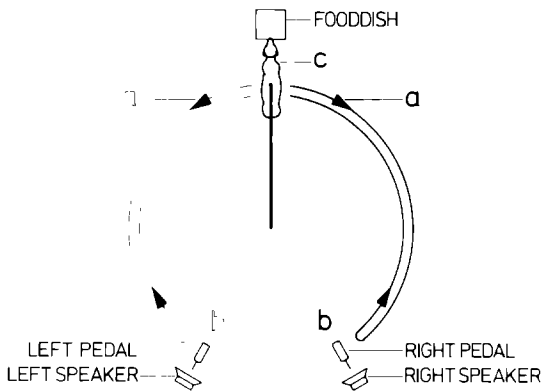


Fig. 1 Scheme of the experiment used to study the behaviour during the performance of a left-right sound discrimination task. For explanation see text.

produced white noise for a period of 7 sec maximum. The dog was required to walk towards this speaker and press the pedal in front of it. If it pressed the correct pedal it was rewarded at the food dish with a number of food pellets from a noisy food dispenser. At the same moment that either of the 2 pedals was pressed the sound stopped. Each experimental session lasted till the dog had emptied the food dispenser, which contained its complete daily food allowance, or till it had lasted 3000 sec, whichever came first.

Results and discussion. Shaping was used to teach the dog to perform this task. When it succeeded it reached a performance of about 100% very rapidly. Only in the experiment during which the dog could do without help for the first time, 4 faulty trials occurred.

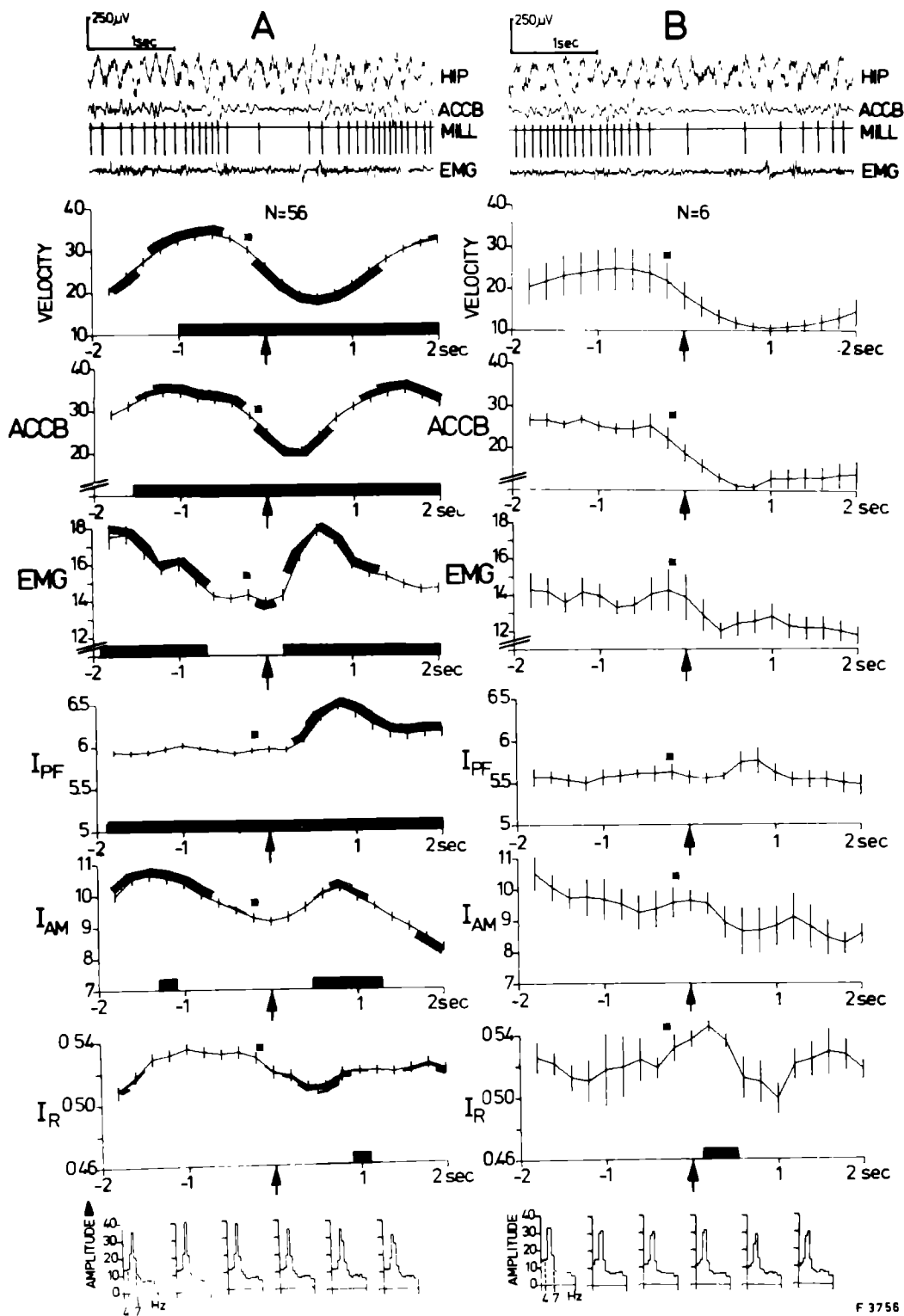
This was not enough material for an extensive statistical analysis of the differences between 'correct' and 'incorrect' responses as regards EEG and behavioural parameters. Yet it could be established that in the 1st, 2nd and 3rd seconds after conditioned stimulus (CS) presentation, the average values of I_{PF} , I_{AM} and I_R did not differ significantly between correct and incorrect trials (Wilcoxon, $P > 0.05$). At the same time neither the outputs of the movement transducers on head and back nor the output of the displac-

ment transducer on the treadmill differed in a significant way on correct and incorrect trials in the 3 sec following the onset of the CS (Wilcoxon, $P > 0.05$).

In stimulus-response tasks another type of 'incorrect response' frequently occurs, often called 'pressings in between', i.e., the animal performs the behavioural sequence normally elicited by the presentation of the CS in the absence of a CS. In order to increase the number of 'pressings in between' we gradually lowered the intensity of the sound serving as CS. Any daily experiment was run, however, with a CS at a fixed sound level. This procedure resulted in an increased occurrence of 'pressings in between', such that a comparative analysis of a sufficiently large number of correct responses and 'pressings in between' was made possible.

Spectral and movement parameters were analysed as a function of time with the pressing of the correct pedal as trigger point (Fig. 2A). The fact that the dog slows down to a stop in order to press the pedal is indicated by a decrease in the output of the movement transducer on the back of the animal and of the output of the displacement transducer on the treadmill. The amplitude of the EMG decreases as well. When the correct pedal press was rewarded the dog responded with a vigorous head movement and a turn of the body in response to the click of the food dispenser. These features were reflected in the movement parameters. At the same time there occurred significant modulations in the spectral parameters in correlation with this motor behaviour. I_{AM} appeared to follow the modulations in EMG output rather closely while I_{PF} showed a transient increase in relation to the presentation of reward and the motor behaviour contingent upon reward. In relation to this increase in I_{PF} a transient decrease in I_R could be observed.

The same behavioural and EEG parameters have been analysed in relation to 'pressings in between' (Fig. 3B). Again modulations in these parameters could be observed which



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Fig. 2 Each graph represents the average values of a movement or a spectral parameter as a function of time in relation to the moment the dog presses the pedal. In column A the trigger point is a correct pedal press, in column B a 'pressing in between'. A statistical comparison of the corresponding graphs in columns A and B has also been performed. A significant difference between the values at comparable abscissae is indicated by a thickening of the x-axis in the figure showing the larger values ($P < 0.05$, Wilcoxon). Note the correlation between spectral and movement parameters and the fact that where spectral parameters differ between A and B, so do movement parameters.

appear to be related to the overt behaviour, which was more hesitant than in the case of correct presses. Due to the small number of examples these modulations could not be shown to be statistically significant, however.

Finally, the average time course of behavioural and spectral parameters in relation to correct responses was statistically compared to the analysis of 'pressings in between' (Fig. 2). It was found that the movement parameters in relation to correct responses were generally higher than in relation to 'pressings in between'. Similarly, the spectral parameters were in general found to be higher on correct responses than on 'pressings in between'. I_R was higher, however, during the second following a 'pressing in between'. In general these differences may be explained on the basis of the hypothesis that more vigorous motor behaviour is correlated with higher values of the hippocampal EEG parameters. This is also apparent from the analysis of 'correct' pressings as such.

(2) Place learning

Procedures. The discrimination task used in experiment I was transformed into a place learning task as follows.

The 2 speakers were replaced by a single speaker opposite the food dish. Both pedals remained in place. On presentation of the CS the animal had to walk to one of the 2 pedals and press it. Pressing of the other pedal was in no case rewarded. When the animal had pressed the correct pedal in 10 successive trials the paradigm was switched between 2 trials so that pressing the previously rewarded pedal became ineffective while pressing the other pedal resulted in reward. The dog did not notice this reversal until the next trial which was considered to be the 'learning trial'. In the following trials the dog had to learn to press the pedal on the other side for reward.

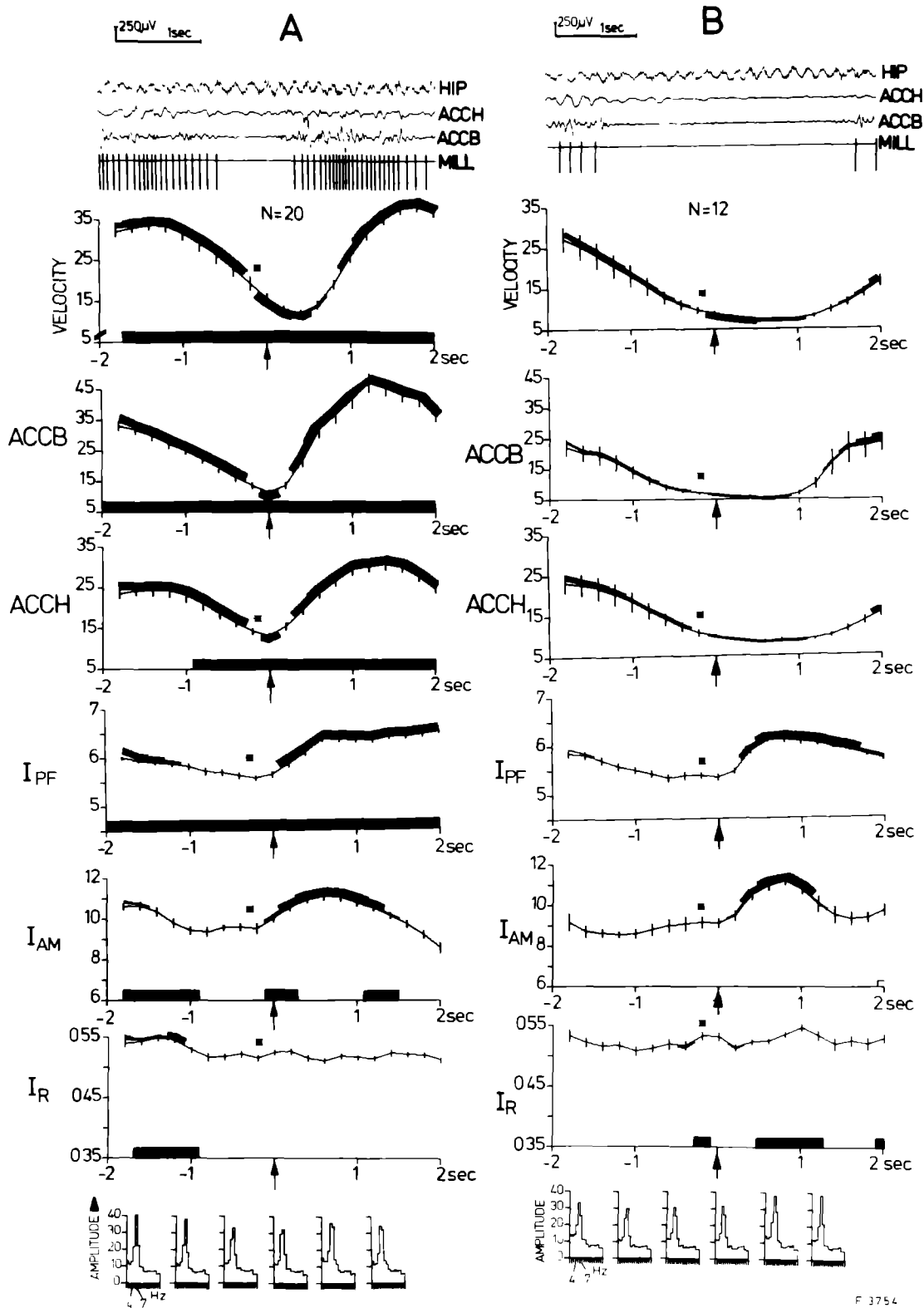
Results and discussion. After the learning trial the dog kept pressing the wrong (previously correct) pedal on a number of trials, then came a period during which both correct

and incorrect responses occurred. Finally the habit was reversed completely, and the animal performed correctly in more than 10 trials in the reversed situation.

The total number of wrong responses following the learning trial up till the first series of 10 correct responses decreased gradually from about 15 at the first experiment to 3 when this series of experiments was stopped after 8 sessions. During the period in which the dog made mistakes some of the wrong responses were followed by a period of about 200 sec during which it was lying down, often with alpha rhythm present in the neocortex.

Fig. 3 shows an analysis of spectral and movement parameters related to correct and incorrect pedal pressings on the right side. This analysis is analogous to the one described under experiment I. Again the correlation between the modulation in spectral and behavioural parameters is evident in the analyses of correct pedal presses (Fig. 3A). In part B of this figure it appears that I_{PF} and I_{AM} increase immediately after the incorrect pedal press while the increase in movement parameters lags by 1 sec. It must be noted, however, that in case of an incorrect pedal pressing the sensory cue (click of the food dispenser) signalling the animal to return to the food dish is lacking. The transition from 'standing' to 'walking' may therefore in this case be comparable to the spontaneous transition from 'standing and eating' to 'walking' investigated previously (Arnolds et al. 1979a). In that case also an increase in amplitude was observed preceding the behavioural transition. For further discussion of this point see below.

Statistical comparison of the average time course of behavioural and spectral parameters related to correct responses and to incorrect pressings again revealed that significant differences exist between correct and incorrect trials with respect to both spectral and movement parameters. These differences are due to the fact that in incorrect trials the animal approached the pedal in a more hesitant manner than in correct ones. It slowed down appreciably as it approached the pedal and



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Fig. 3 Changes in EEG- and movement-related parameters related to (A) correct responses on the right hand pedal during a place learning task and (B) faulty responses on the same pedal. Note the correlation between spectral parameters and movement indicators in column A and the increase in I_{AM} and I_{PF} preceding the increase in movement parameters by about 1 sec in column B. Note also that where spectral parameters differ between A and B, so do movement parameters.

sometimes waited for 1 or 2 sec with its paw hovering above the pedal before actually pressing it. After a faulty response the return to the food dish was slower than in correct trials, while the brisk head movement usually

displayed upon the click of the food dispenser was also lacking.

Differences were found between correct and incorrect trials regarding spectral and movement parameters in relation to the onset of the CS. The first hippocampal EEG wave following the onset of the CS was of a shorter duration (i.e. the frequency was higher) in incorrect than in correct trials. The amplitude of the first and the second EEG wave after the onset of CS was greater in incorrect than in correct trials. These differences appeared to be related to the fact that in incorrect trials the dog reacted to the onset of the CS with a shorter latency than in correct trials (Fig. 4).

Moreover, the outputs of the movement transducers on back and head were found to be significantly higher on unrewarded trials in the 200 msec period during which the CS came on and during the next 200 msec (Wilcoxon, $P < 0.05$). Thus one could say that the initial behavioural transition accompanying 'incorrect' responses was more vigorous than the transition related to 'correct' responses. In accordance with this behavioural difference, the frequency and amplitude of the RSA were higher in faulty than in correct trials, immediately following the onset of the CS.

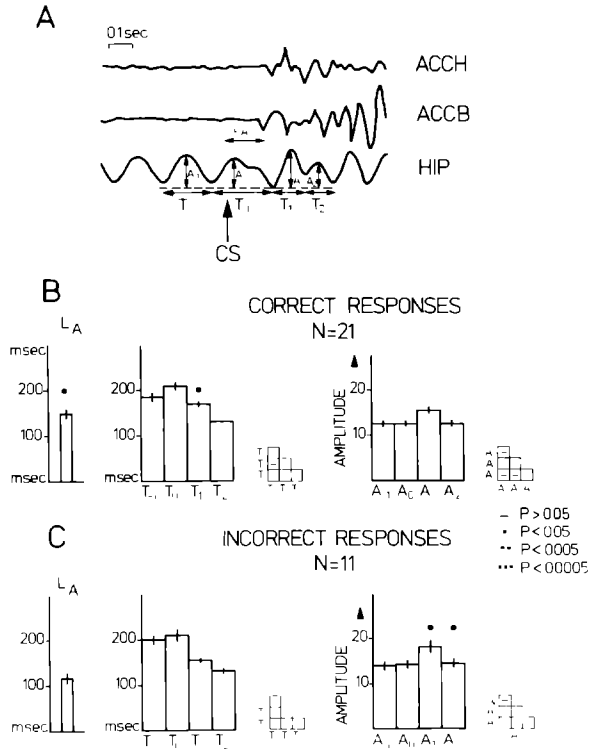


Fig. 4 A single typical record for the correct response to the presentation of the CS in a place learning task (hippocampal EEG bandpass filtered between 4 and 8 Hz) B shows, for correct responses (1), the average latency between the onset of the CS and the response in the movement transducer on either head or back (whichever came first), (2) the average duration of the EEG wave during which the CS was presented (T_0) and that of the wave preceding (T_{-1}) and the two waves following T_0 (T_1 and T_2) The amplitudes of these waves are indicated as well (A_{-1} , A_0 , A_1 , A_2) C shows the same information for incorrect responses The degree to which the values in one bar diagram differ statistically is shown in the table on the right of each diagram (sign test). Statistically significant differences between correct responses and incorrect ones are indicated by means of dots above the values which are significantly larger. Note that the response latency is significantly smaller for faulty than for correct responses, correspondingly T_1 is smaller and A_1 and A_2 are larger during faulty than during correct responses.

(3) Sexual behaviour copulation

Procedures In these experiments the male dog from which we recorded was left in the experimental room together with a sterilized bitch which was kept in heat artificially by means of the i.m. injection daily of 1 mg Dimenformon®. Apart from the recording of the usual behavioural parameters, the behaviour was recorded on videotape Also, in order to obtain 2 reference values of the EEG correlate to well-known behavioural situations (Arnolds et al. 1979b), some records were made of walking on a conveyor belt at 1.8 m/sec and walking around in the treadmill at approximately 1.5 m/sec.

It was our aim in this experiment to select behavioural states within the social setting which were different only with regard to the

intensity of the motor behaviour. We intended to compare the EEG correlated with these behavioural states to see whether the results would support our general hypothesis outlined in the Introduction.

Results and discussion. The dogs showed vivid interaction as soon as they were put together. It was difficult, however, to find behavioural states which on the one hand were identical regarding the circumstances under which the behaviour took place, and on the other hand showed clear-cut differences in motor behaviour that could be measured reliably by means of the few transducers at our disposal.

Two suitable behavioural states could nevertheless be found. After copulation had taken place the 2 dogs remained attached to each other for some minutes. During this period they stood either quietly or made clumsy movements seemingly intended as efforts to

walk away, which was not possible.

Fig. 5 (D/E) shows spectra of the hippocampal EEG during these 2 behavioural states. Statistical analysis shows that I_{PF} , I_{AM} and I_R are lower during 'standing still' (Fig. 5E) than during 'movement' (Fig. 5D) periods. The same applies to the output of the movement transducers. It may still be noted that during copulation, which in Vanderwolfs' theory would be labelled an automatic behaviour, there exists nevertheless a clear-cut RSA component in the hippocampus (Fig. 5C). It must be stressed that the statistical comparison of the behavioural variables ACCB and ACCH in Fig. 5 is for a number of cases difficult to interpret since the measurements come from behaviours with very different morphology, of which only 2 limited aspects are measured by means of the movement transducers on back and head. In principle the comparison of such variables is valid only if the behavioural

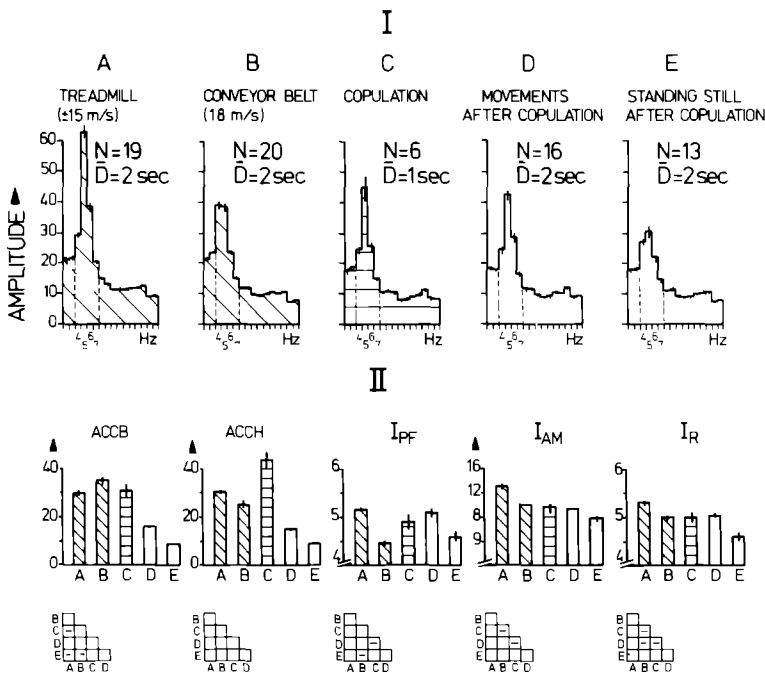


Fig 5. I: each histogram (A through E) represents the amplitude spectrum of the hippocampus while the dog is in the behavioural state indicated II each bar diagram shows the average value of a movement or a spectral parameter during these same periods of behaviour A through E The statistical comparisons of the 5 values comprising each bar diagram are shown in a way similar to Fig 4 Behaviours of similar morphology have been indicated by means of similar shading of the corresponding spectra and bars.

states which are compared can be considered to be homologous with respect to their morphology while the experimental circumstances under which these behaviours occur should be comparable as well.

General discussion

Our results show that different hippocampal EEG correlates can be found with different (correct or incorrect) responses to operant conditioning tasks. Also 2 behavioural states that can be recognized during copulatory behaviour were shown to have different EEG correlates. On quantitative consideration of the actual motor behaviour, these differences in EEG properties appear to be correlated with differences in motor behaviour as well. The findings generally support the hypothesis that motor behaviour is reflected in a non-specific way in the hippocampal EEG. They show that an interpretation of the differences in EEG correlates in terms of 'internal processes' is tenable only if it can be shown that the overt behaviour remains constant while only the 'internal process' can be assumed to vary. Moise and Costin (1974), for example, found different hippocampal EEG correlates between correct responses and 'pressings in between' in monkeys performing a visual discrimination. They conclude that 'since the motor movements in the discriminative response and the spontaneous presses are the same, the EEG prior to a discriminative response reflects at least some extra-motor activity that may be related to arousal, anticipation of the response outcome or information processing'.

The results of experiment I make such a conclusion doubtful as long as detailed comparative measurements have not shown both motor behaviours to be indeed identical. At least in our experiments this appeared not to be the case. In an absolute sense the RSA frequency in experiment II was lower in incorrect than in correct trials. This is contrary to the findings of Gray and Ball (1970) in rats.

Possibly rats show an increase in motor activity in reaction to 'frustrative non-reward'. If so this would explain the noted contradiction. Since measurements of the actual behaviour are not shown, however, in the study of Gray and Ball, the possible correctness of this assumption cannot be verified. The behaviour of the dog in the operant tasks of our experiments contained orientation reactions both to the CS and to the click of the food dispenser. In accordance with the findings of Grastyán et al. (1959) in cats, RSA was correlated with these orientation reactions. However, RSA is also correlated, e.g., with pelvic thrusting or walking on a conveyor belt. Both of these behaviours do not contain clear orientation aspects. We therefore hold the position that the RSA correlation with orientation reactions is a special case of the more general correlation that exists between RSA and sensori-motor events (Arnolds et al. 1979a).

As to the comparison between correct and incorrect responses in the place learning experiment (II) the following should be remarked. A correct response (pedal press) is followed immediately by the click of the food dispenser to which the dog promptly reacts with a transition from standing to walking. Coinciding in time with this cued behavioural transition an increase in I_{AM} and I_{PF} occurs. Incorrect responses are not followed by sensory cues. About 1 sec after the incorrect pedal press follows a spontaneous transition from standing to walking. An increase in I_{PF} and I_{AM} precedes this uncued behavioural transition by about 1 sec. Furthermore, it is remarkable that on statistical comparison of correct and incorrect responses the I_R immediately following an incorrect response appears to be significantly higher than following a correct pedal press (this is also the case in experiment I). Neither of these effects appears from our measurements to be related with a clear-cut motor or sensory event. Thus the possibility cannot be excluded that these effects reflect some internal process related to the fact that the response was incorrect or uncued.

As for the increase in I_{AM} and I_{PF} , it should be noted that similar changes in the hippocampal EEG preceding behavioural transitions have been reported in relation to other uncued behavioural transitions, in experimental situations in which 'learning' was not involved (Vanderwolf 1969, Arnolds et al. 1979a). One might therefore think of this phenomenon as an archicortical correlate of the 'Bereitschaftspotential', reflecting an increase in activity in the brain stem preceding the execution of a motor act (Kornhuber and Deecke 1965).

Furthermore it must be stressed that the present results concern mostly analyses of behaviour that is very complex, not only from the point of view of the employed stimulus-response tasks but also with respect to the motor activity of which it consists. Upon analysis of the digitally scored behaviour one finds, for example, that a correct response to a sound from the right in the sound discrimination task comprises, on average, the following elements: standing with head neutral; left or right; presentation of CS; walking — head right; walking — head neutral; standing — head neutral; pressing pedal; reward (click of food dispenser); standing — head right; turning — head right; walking — head right; walking — head neutral; standing — eating. This entire sequence was habitually performed in 6–8 sec.

Every vigorous head movement (of which there are several in this behavioural sequence) is on its own related to a change in RSA peak frequency in the order of magnitude of 0.5 Hz (Arnolds et al. 1979a). Furthermore, the hippocampus shows a ringing RSA response which takes something like 1 or 2 sec to die away. At the same time we do not as yet know precisely the process by which such ringing responses related to subsequent phasic events interact. Therefore it is at present not possible to relate the hippocampal RSA in detail to behavioural sequences as complex as those studied in the present experiments. It is indeed surprising that, with the relatively crude movement transducers we employed, such consistent results could be obtained. We

believe, on the basis of this study as well as of the preceding ones (Arnolds et al. 1979a,b), that it is necessary in studying the hippocampal EEG correlates of behaviour to quantify precisely the patterns of overt behaviour which are performed.

Summary

A dog was trained to perform a spatial sound discrimination. The hippocampal EEG correlates and the movement correlates of correct trials were compared with those of incorrect trials and of 'pressings in between'.

Correct and wrong responses on a place learning task were compared both with respect to the hippocampal EEG correlates and to the motor behaviour. Where significant differences in EEG correlates were found, the motor behaviour differed significantly as well. The same was found for 2 behavioural states with different motor behavioural qualities which occurred during copulation.

The data support the hypothesis that the spectral properties of the hippocampal EEG reflect in a predictable but non-specific way the intensity of motor behaviour. They question the postulated correlations between hippocampal EEG and 'internal processes', on the ground that unambiguous experimental verification of such hypothesis appears to be very difficult.

Résumé

EEG hippocampique et comportement chez le chien. III. Corrélations avec des tâches de type 'stimulus-réponse' et le comportement sexuel

Un chien a été entraîné à effectuer une discrimination spatiale entre stimulus sonores. Les paramètres spectraux de l'EEG hippocampique et les mesures des mouvements accompagnant l'exécution correcte de la tâche ont été comparés avec celles accompagnant des

réponses incorrectes et des réponses entre essais ('pressings in between').

L'EEG hippocampique et les mesures de mouvement étaient comparés tant pour les réponses correctes, qu'incorrectes, ceci dans une tâche dans laquelle le chien devait apprendre le lieu où il devait presser une pédale pour obtenir une récompense alimentaire. Lorsque des différences significatives ont pu être démontrées entre les données d'EEG, les évaluations comportementales différaient également. Tel fut aussi le cas pour la comparaison entre 2 états comportementaux, différents par leurs manifestations motrices, et qui se produisent pendant la copulation.

Ces données expérimentales appuient l'hypothèse que les qualités spectrales de l'EEG hippocampique reflètent d'une façon prévisible mais non-spécifique l'intensité de l'activité motrice. Ils mettent en doute les corrélations que l'on a postulées, entre l'EEG hippocampique et des 'processus internes', une vérification non-ambiguë de telles hypothèses étant en fait très difficile.

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