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The influence of constant temperatures upon the circadian rhythm of the Namib Desert Dune Lizard *Aporosaura anchietae* Bocage

by
E. Holm
Desert Ecological Research Unit, C.S.I.R.
(presently: Professional Officer, Agricultural and Technical Services, Pretoria)

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The ecology of *Aporosaura anchietae* Bocage was described by Louw and Holm (1971). In that paper it was *i.a.* pointed out that this lizard is strictly diurnal, ultrapsmmophilous (Koch, 1961) and sand diving, that it is an opportunistic feeder on wind blown grass seeds and small arthropods, and has a large storage capacity for food and water. Its geographic distribution was found to coincide with that of the major dune areas (Koch, 1962) of the Namib Desert of South West Africa.

As it has appeared from field observations that this lizard would utilize the favourable segment of any day for surface activity, resulting in day to day changes in the daily activity cycle, it seemed worthwhile to investigate the nature of the endogenous circadian rhythm of this animal in the laboratory.

The experiments in this paper had to be conducted under highly unnatural conditions, and on their own have no relation to the natural behaviour of the experimental animal. A meaningful deduction can only be made from the results of such unnatural experiments as these below, if the information is translated back to the natural system of the experimental animal. This was attempted by comparative studies in nature (Louw and Holm, 1971) and by comparing first day circadian rhythms in the laboratory on newly captured animals with the natural conditions which prevailed before their capture. The aim of this paper is therefore not primarily to amass data on a relatively unknown desert reptile, but rather to try new ways of interpreting circadian rhythm data.

The upper lethal limit for *Aporosaura* is in the vicinity of 40° C (Louw and Holm, 1971), and the lizard is active between about 20° C and 35° C in the field, with a preference for the higher end of this scale (Louw and Holm, 1971). The dune sand surface may, however, fluctuate from below 10° C to well above 70° C in this area, and the lizard must evade these extremes by sand diving. Staying submerged during favourable surface conditions would constitute a grave disadvantage for any dune living animal in this desert because of the strong competition for food with a high nutritional value and/or moisture content. Emerging in too cold temperature conditions on the other hand, would constitute the disadvantage of rendering the animal sluggish. *Aporosaura* relies on speed in evading enemies (Louw and Holm, 1971).

The day-to-day variation in suitable periods for surface activity poses a definite problem for a stereotyped circadian rhythm, and two possible solutions may be considered. Either the circadian rhythm is poorly developed or degenerated and substituted for an activity cycle based on direct sensory orientation, or the circadian rhythm must be a highly diversified physiological system resulting in a complex of behaviour patterns which will safeguard the lizard under different climatic conditions.

I. PROCEDURE

Five experiments were conducted in the laboratory during May and June 1969 at the Namib Desert Research Station, 100 km SE of Walvis Bay, South West Africa. These experiments consisted of recording surface activity of specimens of *Aporosaura* under constant conditions of 25° C and 35° C, both in constant minimum illumination and with artificial daylight periods.

For the first four experiments, surface temperatures in the field were also recorded for two days preceding the experiments, in order to interpret the initial activity pattern of the lizard after capture.

The apparatus used for providing constant temperatures was a "Lauda" constant temperature water bath (accuracy ± 0,1° C), with three containers 15 cm in diameter and 15 cm high, half filled with sand and submerged in the water of the bath. The water and sand levels were at equal heights and the air in the containers could circulate with the air above the water level inside the bath. This arrangement ensured that both the sand and air space inside the containers were kept close to 100% relative humidity by the circulation of water in a closed chamber. Surface activity of the lizards (one in each container) was measured by photoelectric cells and light sources, a set of which was mounted over every container. These photocell units recorded every interruption of the light beam via a relay system to a 24-hour clock with ink pens and paper charts. The activity of each lizard was traced individually. Illumination was kept at a minimum, since the light-source of the photocell unit was only a 0,25 watt filament at 220 volts. Unfortunately it was impossible to measure light intensity in the cage since it would vary from place to place. The whole apparatus was kept in a dark room, and the lighting was therefore practically constant. For experiment No. 5, 40 watt (white light) electrical light bulbs were inserted into the covers of three containers. These were linked to the current by time switches. The air and surface temperatures of the containers were increased by the heating effect of these lights, so that by late afternoon the surface temperatures in the containers had risen up to 5° C above bath temperatures. The circles and dots preceding the daily curves of diagrams of experiment 5 indicate bath temperatures and these bath temperatures are referred to with "+5° C" behind them in the text and plate to indicate maximum error inside the cages.

II. EXPERIMENTS 1, 2, 3 AND 4: INFLUENCE OF 25° C AND 35° C CONSTANT TEMPERATURES ON THE CIRCADIAN RHYTHM OF *APOROSAURA*

In these four experiments, records were kept of the temperatures *Aporosaura* was subjected to in the field prior to capture for experimental work. The set of curves for surface temperatures in the field for the two days preceding capture were derived from meteorological data of the weather station at Gobabeb (100 km SE of Walvis Bay, S.W.A.) about 3 km from where the lizards were captured, and are based on readings at 0800, 1400 and 2000 hours. The temperatures were taken with a standard mercury thermometer of which the bulb was just covered with sand, on a level surface. This would give a fair average of dune surface temperatures, with a variation of ± 5°C to 7°C for the western and eastern slopes during the morning and afternoon. Although these surface temperatures are, therefore, not a very accurate indication of the surface temperatures that the experimental lizards experienced in the field, they provide a comparative measure of high or low surface temperatures. The shaded parts of the surface temperature curves (above 40° C, ± 5° C) are interpreted as high temperatures for *Aporosaura*, which is an assumption based purely on observation of activity in the field and lethal limits in the laboratory, and not actual body temperatures of the lizards. Refined temperature measurements of the lizard and his environment are not relevant here since the object is only to assess reactions at the higher and lower end of the lizard's natural environmental temperature range.

Results

When the activity diagrams of experiments 1, 2, 3 and 4 are studied, the following observations can be made: —

1. After experiencing relatively **high** surface temperatures in the field, the lizards showed a **bimodal** activity on the first day after capture (A, B, C, J1, K1), and after experiencing **low** surface temperatures in the field, **unimodal** activity was recorded on the first day after capture (D, E, F, G, H).
2. After 3 to 5 days in a **low constant** temperature environment, the initial **bimodal** activity changed to **unimodal,** with emphasis on the afternoon peak (A, B and C) and after one day in a **high constant** temperature environment, the initial **unimodal** cycles changed to **bimodal** cycles (G, H) followed by emphasis on the morning peak, and in one case even becoming unimodally active in the morning only (G). (For increased morning activity under increased temperature, see also M2 and N under experiment 5).
3. **Low** surface temperatures in the field, followed by **low constant** temperatures in the experiment, resulted in a maintained **unimodal** activity cycle, (D, E, F), while **high** surface temperatures in the field, followed by **high constant** temperatures in the experiment, resulted in a maintained **bimodal** cycle (J1, K1, L1).
4. When the **constant high** temperature in experiment 4 was changed to a **constant low** temperature, the noon gap in the activity was reduced, and in two out of the three experimental

animals, **bimodality** was substituted for **unimodality** (J2, K2, L2). When this **constant low** temperature was again substituted for a **constant high temperature**, the modality reversed back to bimodal (J3, L3) and the noon gap in activity was restored (K3).

5. The drift (i.e. the day-to-day shift) in onset of activity in J, K and L tended to earlier onset of activity under **low constant** temperatures, and later onset of activity under **high constant** temperatures.

Conclusions

Four possible circadian rhythms in *Aporosaura* could be discerned, namely **unimodal morning, bimodal, unimodal afternoon** and **unimodal** activity throughout the daylight period.

Furthermore, the circadian activity cycle of *Aporosaura* is influenced by constant low surface (or ambient) temperatures (ca. 25° C) to tend towards unimodality with emphasis on afternoon activity, and by constant high surface (or ambient) temperatures (ca. 35° C) to tend towards bimodality with emphasis on morning activity.

These rhythmic behaviour patterns are endogenous, since they were persistent under constant conditions. (Temperatures were constant, and all other factors were constant to the limits generally agreed upon for testing endogenuous rhythms in animals. Marler and Hamilton, 1966.)

Temperature also influences the rate or direction of drift of at least afternoon activity.

III. EXPERIMENT 5: INFLUENCE OF LIGHT AND TEMPERATURE ON THE CIRCADIAN RHYTHM OF *APOROSAURA*

Experiment 5 was started under the same conditions as experiment 4 for the first 5 days (O1, M1, and N1). Thereafter lizard "O" was subjected to a 12-hour light and 12-hour semi-dark cycle (O2, still at 35° C, but with surface temperatures rising to 40° C during the "daylight" part of the cycle, as discussed above). Lizards M and N were subjected to 4 days of increasing "daylight" length, by adding an hour to the beginning and the end of every consecutive "daylight" period (M2, N2). Thereafter the "daylight" cycle was reduced to a constant 10 hours "daylight" followed by 14 hours semi-darkness (M3, M4, N3, N4). After 4 days, temperature was reduced from 35° C (+ 5° C) to 25° C (+ 5° C) (M4, N4).

Results

Results of experiment 5 are less conclusive than those of the first experiments, but the following phenomena could be observed: —

1. All lizards tended to synchronize their activity with the "daylight" period (viz. O2, M2, N2), but the tendency to lengthen the noon gap in response to high temperatures, was overriding this synchronization (viz. O2, M3, N3).
2. When temperatures were reduced to 25° C (+ 5° C), the noon gap was reduced and synchronization of activity and "daylight" period was fair. Light period was therefore only effective in controlling the drift under appropriate temperature conditions. Unimodal activity cycles were not induced in this experiment by bath temperatures of 25° C since surface and air temperatures rose to ± 30° C.

Conclusions

Light may have a timing effect on the circadian rhythm of *Aporosaura*, very similar to that found in other animals (viz. De Coursey, 1961, on flying squirrels). However, since the temperature of the environment rose under the experimental lighting conditions in the experiment described above, the possibility that the lizards were reacting to this temperature curve cannot be excluded.

Although a regular light period eliminated regular drift, the effect of temperature overruled its effect on initiation and cessation of activity.

IV. GENERAL DISCUSSION

The effect of different temperatures on the circadian rhythm of *Aporosaura* can be seen as a series of responses in circadian activity triggered by these temperatures. All individuals fitted into the following hypothetical gradient of activity patterns: —

Very high temperatures — morning activity only.
High temperatures — bimodal activity.
Moderate temperatures — unimodal activity, whole day.
Low temperatures — afternoon activity only.

There was some individual variation in reaction to specific temperatures, in the sense that one specimen might have interpreted 35° C as a high temperature, while another specimen might have reacted to 35° C as a very high temperature. Every individual would, however, comply with the abovementioned arrangement in so far as it would switch to the appropriate next activity pattern on the scale if temperature was raised or lowered.

The above mentioned four modes of activity were furthermore not clearly separated, since intermediate modes of activity are also evident, viz. a short noon gap in activity, a reduced morning activity or a reduced evening activity.

It is interesting to note that Hoesch (1966) found that *Aporosaura* taken from the desert to the inland, switched from bimodal activity to evening activity only. Unfortunately no temperature data were obtained.

Constant temperatures and modality

The phenomenon that constant temperatures induced different modalities of circadian activity, similar to the modalities of activity in the field with temperature curves (Louw and Holm, 1971), may be explained in two ways. Either *Aporosaura* may react to an average daily temperature, or it may become more sensitive to temperature at a certain phase in the circadian rhythm. The latter is the more likely hypothesis since it was demonstrated that cockroaches, deer mice and flying squirrels become sensitive to light during a particular phase of their circadian activity cycle (De Coursey 1964, Harker 1964). It seems likely that temperatures are "measured" by *Aporosaura* in the early morning, since it was found by the author that the lizards spent the night just submerged (two to four cm deep) and could respond to temperatures in the early morning at that level quite appropriately with the above mentioned modes of activity. There is, however, no reliable evidence for this hypothesis, and further experimentation with temperature curves is needed.

The effect of light

The fact that some synchronization of activity with light occurs, poses the problem that *Aporosaura* must be able to use either sunrise or sunset only during very hot or cold spells to synchronize their activity with the light period (G1, J2).

No further work has been done on the timing effect of temperature curves but it is very likely that temperature is also the main timing factor for synchronization of activity with the daylight period, as indeed such instances are known (viz. Roberts 1960, Aschoff 1963), with light as a secondary factor.

Drift and scatter in activity

The modification of the direction and/or degree of drift of the afternoon activity period of *Aporosaura* by temperature seems to have the following advantages: —

1. The utilization of as much of the warm noon time of the day for activity under cool conditions by forward drift in afternoon activity (i.e. the tendency to emerge sooner), and/or a tendency to merge bimodal activity peaks over the noon period.

2. The avoidance of excessively hot noon periods, by the tendency to commence later with afternoon activity (i.e. a backward drift in the afternoon peak) and/or a noon gap in activity resulting in the bimodal activity pattern.

The "afternoon only" and "morning only" modes of activity are the logical extremes of these two tendencies respectively. The drift pattern continues in the afternoon activity, even if the morning activity is stopped altogether, and is, therefore, ordinary drift and not connected with gradual changes from one mode of activity to another (J2, L2). Furthermore, this drift is reversible by reversing the temperature conditions (K, J, L). In *Aporosaura* drift is therefore modified by changes in temperature, and appears to be functional. It could very well be a search pattern to predict suitable temperature conditions, evolved to the specific ecological situation of the animal, and it would be interesting to know whether any parallel phenomenon is found in the drift patterns of other animals' circadian rhythms.

The circadian rhythm of *Aporosaura*, therefore, is apparently built up of a series of possible behaviour patterns rather than one stereotyped pattern, triggered selectively by prevailing temperature conditions, and serving the purpose of activating the animal during suitable segments of different days.

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Figure 1. Horizontal lines represent consecutive days, (starting at 0 hours and ending at 24 hours), with vertical lines at 4-hour intervals. Traces on the horizontal lines represent activity of *Aporosaura* as registered by photo-electric event recorder.

Every set of traces marked with the same letter represents the activity of a single specimen of *Aporosaura,* while numbers after these letters (N1, N2, etc.) refer to changes made in the environment, as explained below.

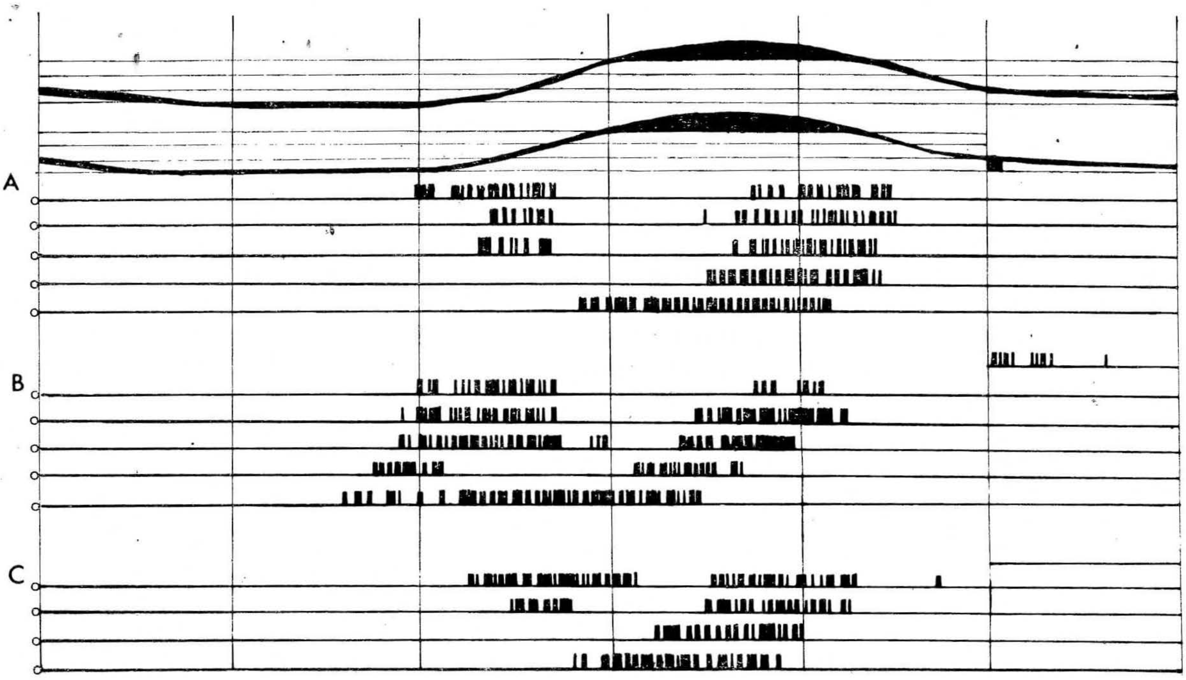
The two bars of horizontal lines directly below the captions of experiments 1, 2, 3 and 4 respectively, indicate field surface temperatures for two days preceding that experiment, i.e. the surface temperatures *Aporosaura* A, B and C were subjected to for the two days preceding experiment 1, are indicated directly below the caption "EXPERIMENT I". The horizontal lines are at 10° C intervals, with the lowest line at 10° C and the highest at 40° C. Shaded parts of temperature curves indicate temperatures above 40° C.

Constant temperatures of 35° C (± 1° C) are indicated by black dots preceding a daily activity diagram while circles are used to indicate constant temperatures of 25° C (± 1° C).

Heavy bars below daily activity diagrams in experiment 5 indicate periods of artificial daylight, while all other times are semi dark. The +5° C in front of those activity diagrams with a light period indicates that surface temperatures in the containers rose by 5° C during the light cycle.

(Actual dates of the experiment appear behind every line of activity diagrams. Animals were introduced from the field with less than one hour delay at the point where any lettered activity diagram starts, after being captured by hand.)

EXPERIMENT 1



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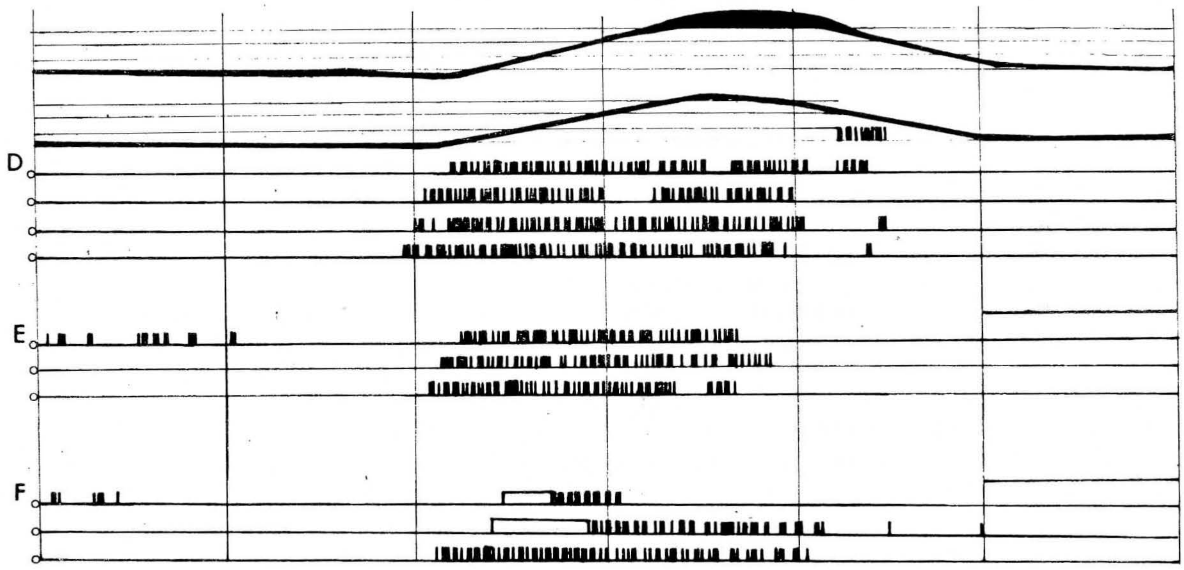

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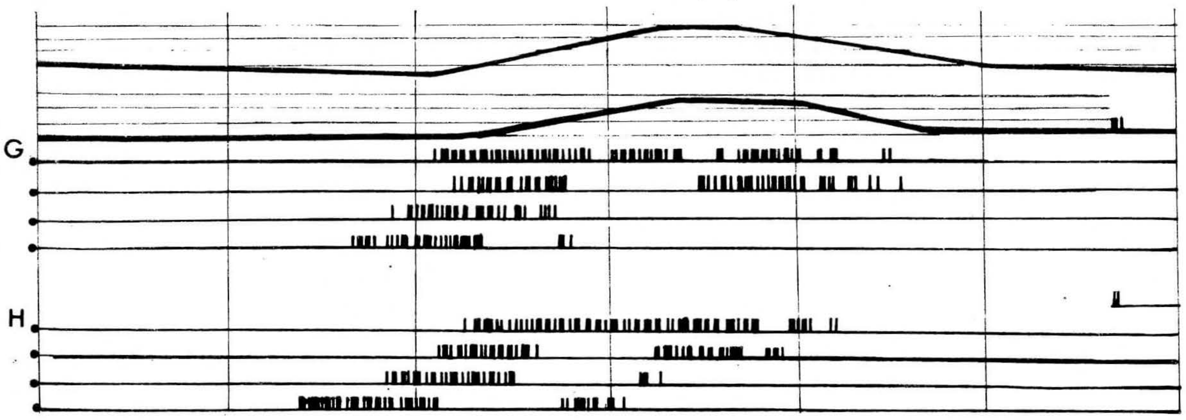

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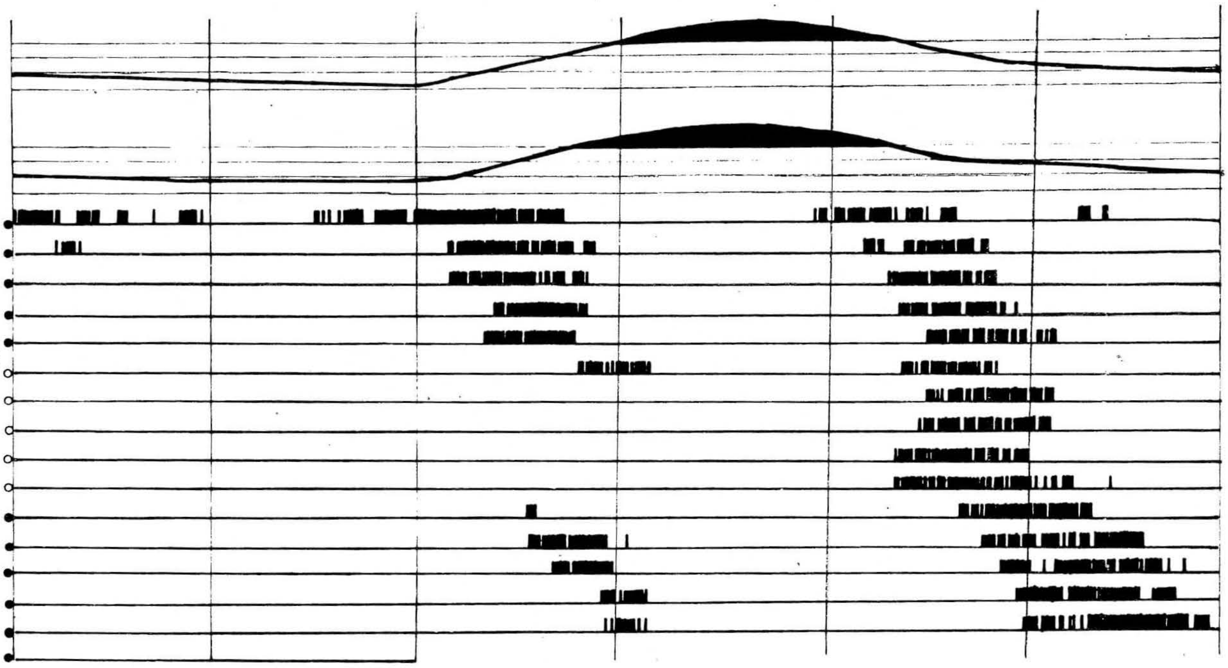

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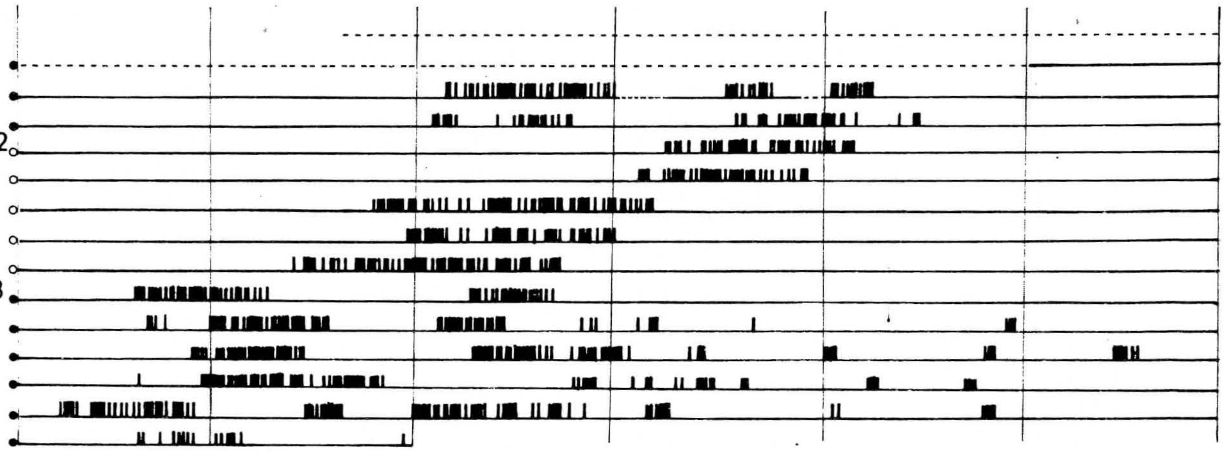

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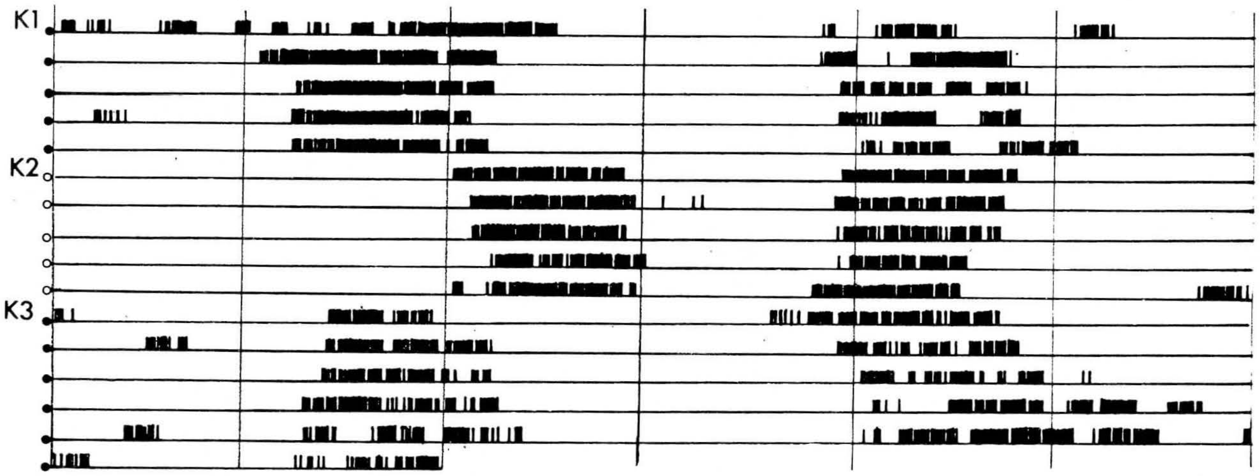
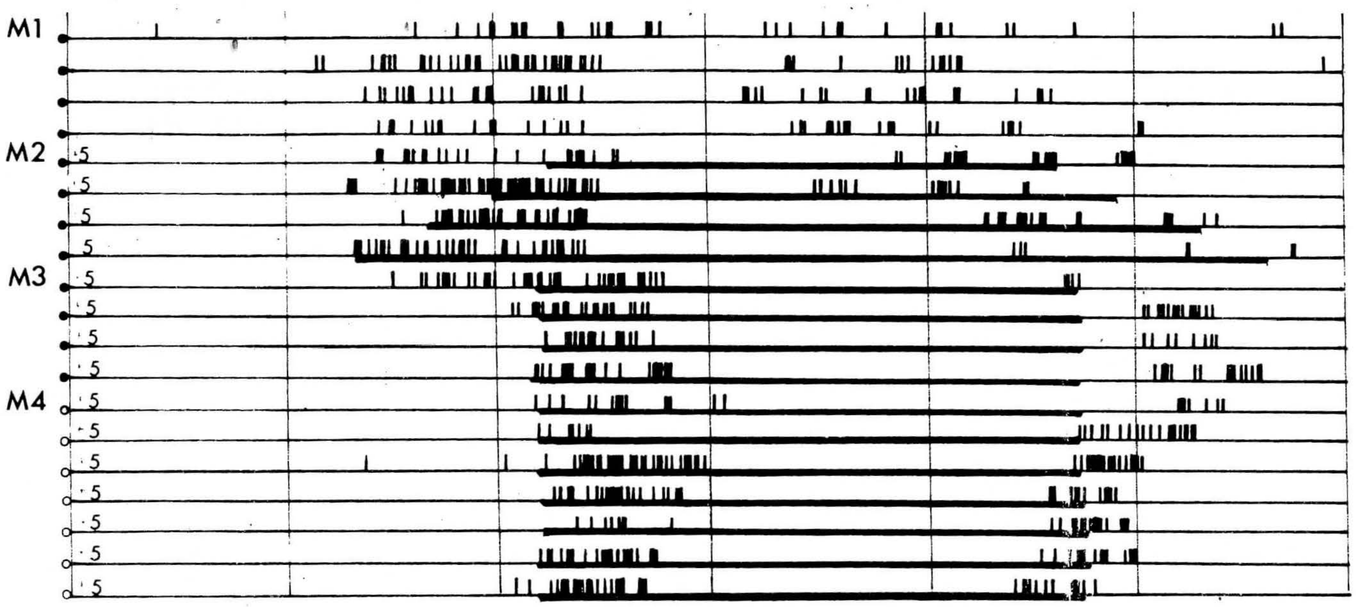


EXPERIMENT 5



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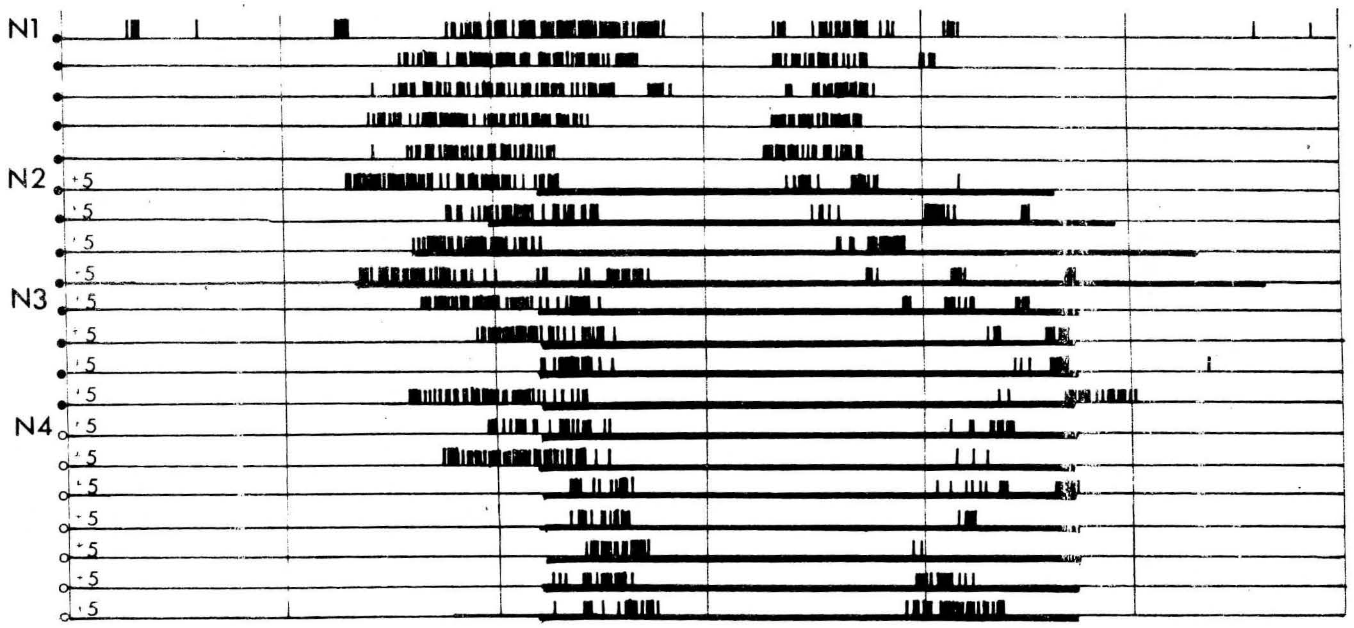

EXPERIMENT 5 (cont.)