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MAINTAINED ACTIVITY OF LATERAL GENICULATE NEURONES IN DARKNESS

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Spontaneous activity is a striking feature of the sensory side of the nervous system. Long after specific stimuli have been excluded, or at least minimized, neurones in the various afferent centres continue to discharge impulses. For a review of the earlier literature in this field see Granit (1955). In the mammalian visual system most investigators who have examined the evoked activity of single units have also commented on the background firing, though usually only briefly (Kuffler, 1953; Jung, 1953; Tasaki, Polley & Orrego, 1954; Lennox, 1958; Bornschein, 1958*a*, *b*; De Valois, 1960; Erulkar & Fillenz, 1960; Hubel, 1960; Grüsser-Cornehls & Grüsser, 1961; Fuster, 1961; Hubel & Wiesel, 1961; Negishi & Verzeano, 1961; Arden & Söderberg, 1961; Bishop, Burke & Davis, 1962*a*; Arduini & Pinneo, 1962; De Valois, Jacobs & Jones, 1962; Horn, 1962; Lömo & Mollica, 1962; Negishi, Lu & Verzeano, 1962; Burns, Heron & Pritchard, 1962). The most detailed specific study is that of Kuffler, FitzHugh & Barlow (1957), who examined some of the statistical properties of the maintained discharges of retinal ganglion cells. It is not easy to find an appropriate descriptive term for this firing. The use of the adjective 'spontaneous' has its difficulties, but since the term is widely current and the difficulties are generally appreciated its use seems preferable to that of others such as 'background', 'maintained' or 'on-going'.

The mean firing rate of spontaneously active single units is easy to record, and although it is the simplest of the statistical measures it is an essential preliminary to the application of the more involved methods of analysis such as the interval histogram and the joint interval histogram (Gerstein, 1960; Gerstein & Kiang, 1960; Grossman & Viernstein, 1961; Levick, Bishop, Williams & Lampard, 1961; Levick, 1962; Rodieck, Kiang & Gerstein, 1962). The application of these methods requires that the process investigated should be stationary or at least non-stationary

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in a known way. Briefly, a stationary process is one in which the statistical properties are invariant with time. One attribute of a stationary process is that its mean rate should be steady. Mean rate recordings can therefore be used both to define the time interval over which a given pulse train is potentially stationary and to detect portions of the record which are obviously non-stationary.

The present paper is concerned with the mean rate of firing of single neurones in the lateral geniculate nucleus (LGN) during total darkness. A remarkable variety of patterns of behaviour has been revealed in different units and in the same unit at different times. A preliminary account has been published (Bishop, Levick, Kozak & Williams, 1961). Selected dark discharges of these single units will be subjected to more elaborate statistical analyses in subsequent papers.

METHODS

Experiments were conducted on twenty-five adult cats (2·2–5·5 kg). Only healthy cats were selected and these were given daily intramuscular injections of penicillin 100,000 u. for 2 days before use. Atropine sulphate ointment (1 %) was applied to the eyes on the day before experiment. For premedication, atropine sulphate (0·5 mg/kg) together with pethidine hydrochloride (3·3 mg/kg) was administered intraperitoneally, and after 15 min anaesthesia was induced with sodium pentobarbitone (28 mg/kg) intraperitoneally. Since experiments were usually carried into the third day the risk of infection was reduced by keeping sites of incision surgically clean. The head was firmly clamped in a stereotaxic instrument, Horsley-Clarke (H.-C.) planes of reference being used. In most of the experiments only a small craniotomy opening was made at H.-C. anterior 7·0 mm, left lateral 8·5 mm over the central part of the LGN (Bishop, Kozak, Levick & Vakkur, 1962). The opening was sealed with bone wax through which the micro-electrode was subsequently inserted. Plastic contact lenses were fitted to prevent drying of the corneae. Supplementary applications of atropine eye drops (1 %) were usually necessary to maintain the pupils at full dilatation. A catheter was routinely placed in the bladder to avoid disturbing effects from over-distension. The volume, specific gravity and pH of the urine gave some indication of the animal's condition. In some experiments the femoral arterial pressure was monitored by means of a mercury manometer. At the commencement of the experiment proper the animal was paralysed by a single intravenous injection of gallamine triethiodide 80 mg. Paralysis was maintained by continuous infusion (see later). The lungs were ventilated with 100 % oxygen via a tracheal cannula by means of a respiratory pump. The stroke volume was set to 13 ml./kg and the pump made 19 strokes/min. Respiratory exchange was assisted by suspending the body of the animal clear of ventral support with a spinal clamp. At regular intervals during the course of the experiment tracheal aspiration was performed, the lungs being subsequently inflated with several 100 ml. strokes from the pump. Facilities were not available for monitoring the end-tidal P_{CO_2}.

It is not generally appreciated how far the state of respiratory exchange of an animal, anaesthetized with barbiturate, may depart from normal. In a series of eight cats lightly anaesthetized with pentobarbitone the average ventilation minute volume was found to be 165 ml./kg. The value for the normal animal, i.e. 240 ml./kg, was estimated from the alignment chart in Spector (1956).

Maintenance. Since stability of conditions was a prime requirement, the estimated needs of water and electrolytes were supplied in the form of a solution of composition (g/100 ml.):

NaCl 0·18, KCl 0·23, glucose 3, by constant intravenous infusion at 6 ml./hr. The solution also contained gallamine triethiodide (8 mg/hr) and the maintenance requirement of sodium pentobarbitone for constant light anaesthesia (1·4 mg/kg.hr). The dose of sodium pentobarbitone was determined in a separate series of experiments in which various anaesthetics (chloralose, urethane, thiopentone sodium, sodium pentobarbitone) were tested by infusion at a constant rate without paralysis. Although chloralose and urethane did not depress respiration, only sodium pentobarbitone yielded a steady level of anaesthesia (assessed by the response to painful stimulus) without discernible cumulative effect or development of tolerance over 2–3 days. Constant infusion undoubtedly yields better stability than intermittent dosage. Bickford (1950) used the electroencephalogram both as a monitor of the level of anaesthesia and as the source of a signal to control the rate of administration of anaesthetic. However, this technique was considered to be inappropriate for the study of spontaneous activity, since it would be illogical to alter the rate of administration to keep a particular spontaneous neural signal at a constant level in a feed-back loop. The temperature of the cat, monitored by a mercury thermometer and a thermistor placed deeply between the scapula and rib-cage, was maintained by a feedback-controlled electric heating blanket at $38 \pm 0{\cdot}2°$ C in most experiments. Intramuscular penicillin 100,000 u. and sulphacetamide eye drops (10 %) were administered daily during the experiment.

Micro-electrodes and recording. In early experiments glass micropipettes filled with either 4 M-NaCl, 3 M-KCl or saturated potassium ferricyanide were used in conjunction with a pressure-tight chamber sealed around the craniotomy opening. However, most of the experiments were carried out with specially varnished (3 coats of 'Insl-X E-33-N', 1 coat of 'B.A.L.M. V-668 stoving enamel') tungsten micro-electrodes (Hubel, 1957). Potentials were led via a cathode follower to conventional amplifiers and cathode-ray tube displays. One time base was used free-running at slow speed to give an over-all view of the train of impulses. The fast sweep of another time base was triggered at an early instant on each wave form and allowed detailed inspection of shape. Action potentials of single units were converted into standard pulses by using a Schmitt trigger with variable threshold and a 20 μsec monostable, the output of which was applied to the recording head (saturation recording) of a conventional magnetic tape deck running at $3\frac{3}{4}$ in. (95 mm)/sec. This output was also applied to the second beam of the cathode-ray tube displaying the spike wave form, thus enabling detailed examination of the conversion from spike to standard pulse; only complete reliability was accepted for these experiments, this point being rigidly assured by continuous observation. In this way some 275 hr of unit activity were preserved for detailed study.

Mean rate recorder. The mean rate of the discharges was measured by a device in which a parallel RC network was charged to a standard voltage with each input pulse; analysis showed that the average voltage across the network should be approximately proportional to the mean rate of input pulse trains having a variety of interval distributions. This behaviour was checked experimentally with periodic, Poisson, Gaussian and stable geniculate-unit sources. The output of the circuit was displayed with a pen recorder and the over-all error was less than ± 5 %. In the averaging part of the circuit two time constants were found useful, 0·5 and 10 sec.

Dark room. Most experiments were carried out in a specially blacked-out room. Unsuccessful attempts were made to obtain an objective measurement of the level of the residual illumination. It was less than the threshold (0·0001 μlm) of a Photovolt Corporation multiplier photometer, type 520-M. Two different observers were consistently unable to detect any source of light in the room under conditions of optimal light detection described by Pirenne (1948).

Verification of recording sites. Except in the pilot experiments the cat was always perfused and the brain examined. The recording site was verified in the LGN by examination of serial histological sections. With ferricyanide electrodes the recording site was marked

electrophoretically. With tungsten electrodes needle tracks could be followed into the LGN. Wave forms indicated cell body recording (Bishop, Burke & Davis, 1962*a*). There did not appear to be any obvious correlation between recording site, position of receptive field and pattern of spontaneous activity.

Retinal blockade. Raising the intraocular pressure sufficiently above arterial pressure blocks transmission of impulses from the retina (Bornschein, 1958*a*, *b*). In early experiments this was achieved by the injection of a special fluid (Merriel, Fleming & Girard, 1960) under 300 mm Hg pressure through a needle inserted into the anterior chamber; this proved to be unsatisfactory since the eye showed signs of damage after a few hours (opacity of cornea, tight constriction of pupil) and there was no certainty that the retina was normal for the remainder of the experiment. In subsequent experiments block was achieved by manual pressure applied to the eyeball for periods of 1–2 min through the contact lens protecting the cornea; no obvious signs of ocular damage appeared after many cycles of this treatment extending over more than a day. There is little doubt that this method is just as effective, since a complete block of visual function could be produced in the experimenters' own eyes in less than 1 min by substantially less pressure than was used on preparations. Furthermore, similar results were obtained using either the injection or the manual method.

Cerveau isolé preparations. A technique similar to that of Iwama & Jasper (1957) was used. Two large (7 cm × 1 mm) needles, insulated except for 2 mm at the tips, were held parallel about 2 mm apart with the tips separated by about 8 mm longitudinally. Two gross lesions were placed on each side at the intercollicular level (H.-C. anterior 1 mm, lateral 1–3 mm, vertical −1 mm and +4 mm) by the passage of RF current for 5–10 sec; this was of sufficient strength to coagulate egg white almost instantaneously. Subsequent histological examination in each case showed gross destruction of the mid-brain at the level of the lesion. These animals were maintained during the experiment in exactly the same way as those with intact brains.

RESULTS

In these experiments the behaviour of 322 single units in the LGN and the optic radiation above it was examined. Identification in relation to pre- or post-synaptic, cell body or axon was based on the scheme of Bishop, Burke & Davis (1962*a*). The present study was confined to the activity of post-synaptic elements in the nucleus itself or in the optic radiation and units obviously affected by damage (wave form break-up, injury discharge) were disregarded. The possibility that the results were influenced by minor degrees of irritation from the electrode was much harder to exclude. When cell spikes were first encountered during the advance of the electrode, it was sometimes observed that the firing rate was initially fast and rapidly settled to a lower value. As far as could be judged by the subsequent behaviour of the unit, this initial disturbance was probably of little consequence. A direct test of electrode influence was attempted by advancing the needle in steps of 12·5 μ and waiting 1–2 min between steps. Up to the point at which obvious damage occurred it was possible to produce large changes in amplitude or shape of the wave form without inducing anything more than occasional increases in the mean rate lasting only a few seconds. In some cases it was then possible

to retract the electrode, the reverse sequence of wave forms being observed without change in mean rate. However, retraction of tungsten electrodes not uncommonly led to immediate injury. With the electrode held in a fixed position, the usual experience was to find only minor changes in wave form over hours of study, the longest continually monitored unit response being recorded for a period of 14 hr. Significant irritation from the electrode was unlikely in such circumstances. The behaviour of radiation axons did not seem to differ from that of geniculate cell bodies.

Dark firing

The most characteristic feature of the behaviour of geniculate units in darkness was the great variety of mean rate patterns. Even in the same unit the type of firing often changed markedly with time. This is illustrated in Fig. 1*A*, where the sequence of patterns was: (i) stable mean rate, 21 min; (ii) irregular transient excitations, next 25 min; (iii) stable mean rate, next 8 min; (iv) fairly regular 'bi-stable' behaviour, next 27 min; (v) irregular transient excitations, last 29 min. This shows that it is more appropriate to classify *patterns* of activity than to classify types of units.

To simplify description the following arbitrary grouping of mean rate patterns was adopted: (*a*) stable; (*b*) irregularly unstable; (*c*) regularly unstable. Patterns were distributed roughly equally between the groups.

Stable mean rate. Examples of patterns described as stable are illustrated in Fig. 1*B–E*. The traces are ragged owing to the usual local irregularity of the spontaneous activity. Since the same time constant (10 sec) was used in all recordings it might be thought that the varying degrees of raggedness would be accounted for by the different mean rates of firing: the number of impulses averaged increases with increasing mean rate; thus the relative raggedness of the trace would become less. However, this is a minor effect, as is shown by Fig. 1*F* and *G*, which illustrates the mean rate recordings of two random pulse trains derived from the disintegrations in a radioactive source. The slower pulse train has a relatively more ragged mean rate trace. But the effect is insufficient to account for the relative raggedness of the trace in Fig. 1*E*. In this case the degree of local irregularity of the spontaneous activity is of major importance.

Many units showed a stable mean rate for short periods (5–10 min) but it was uncommon for it to be maintained for longer than 30 min (maximum 80 min). There is considerable interest in the frequency with which the various stable mean rates were encountered. The estimate of the stable mean rate of each unit was made by eye from the mean rate trace. Where a unit displayed several stable states, the earliest in time was used. The

frequency distribution of mean rates is shown in Fig. 2. Two-thirds of the stable discharges had mean rates below 10/sec. The commonest observations were 4–6/sec.

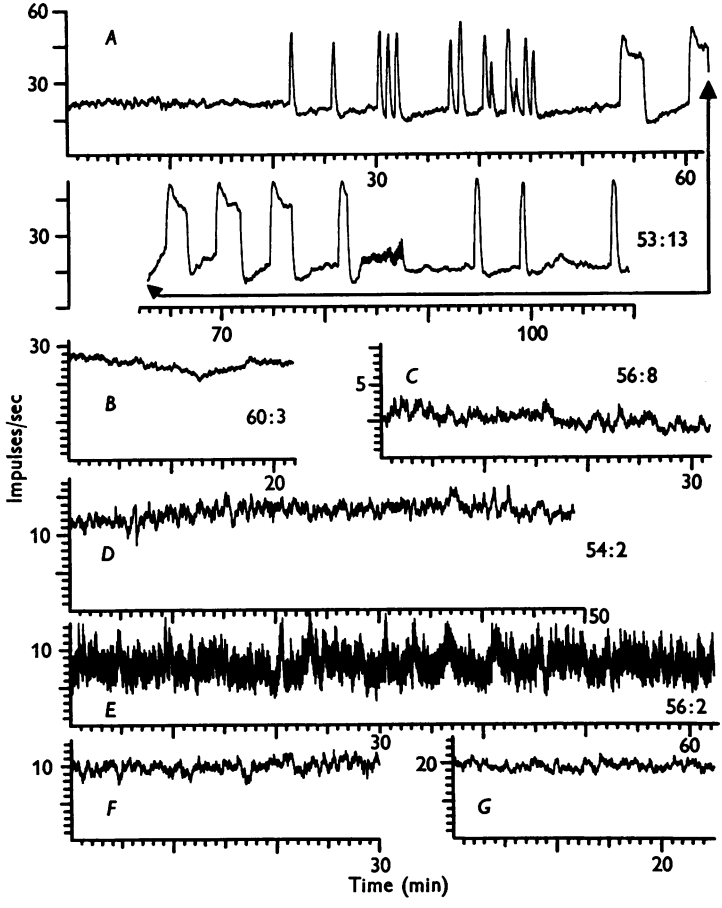

Fig. 1. Dark firing. *A*, Unit displaying several different patterns of mean rate at different times. *B–E*, Several examples of stable mean rates. *F*, *G*, Mean rate graphs of Poisson pulse trains (radioactive source) for comparison of stability and degree of fluctuation at two different mean rates. All the graphs were obtained with 10 sec time constant in the averaging circuit. The numerals '53:13', etc. in all figures indicate the cat and the unit respectively which yielded the information.

Irregularly unstable. Examples of this group are shown in Fig. 3 *A* and *B*. The displacements of the trace are more sustained (minutes rather than seconds), more variable and larger in magnitude than with the most ragged of the stable mean rates.

Regularly unstable. In this group the mean rate varied in a fairly

orderly cyclic manner. Only four of the many examples are shown in Fig. 3 *C–E*, and Fig. 4. It is reasonable to define the period or cycle for most of such patterns as the time interval between successive transitions of the graph in the same direction. Although successive periods in some discharges progressively shortened (Fig. 3 *C*) or lengthened, many were strikingly constant (Fig. 3 *D* and *E*). In those with long periods, the detailed behaviour during each cycle was often closely repeated (Fig.

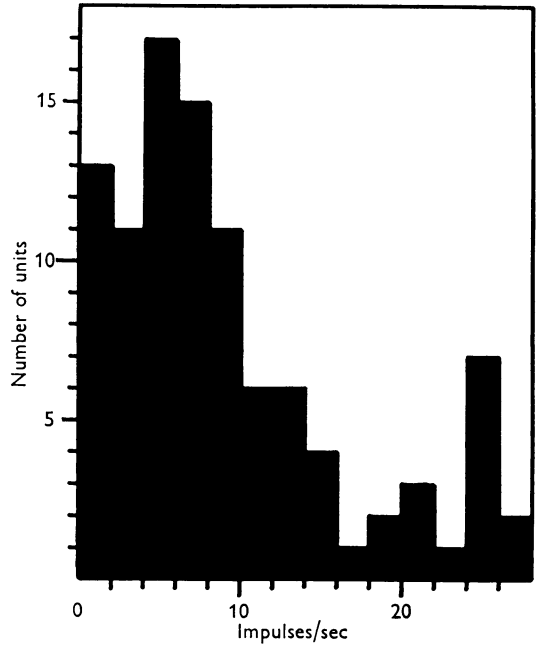

Fig. 2. Frequency distribution histogram of stable mean rates; 99 observations.

3 *C*). In some cases there was evidence of superposition of two separate cyclic processes (Fig. 3 *D*; indicated by dots and bars, respectively).

The longest period or cycle observed was 50 min; the most persistent pattern continued for 270 min during which time 7 cycles were completed. The shortest period was approximately 0·3 sec; in the example illustrated (Fig. 4 *B*) the pattern was almost beyond the resolution of the mean rate circuit (short time constant setting, 0·5 sec) but could easily be detected with the loudspeaker monitor as the sound of running footsteps. The effect was produced by the bunching of impulses into two or three groups in each second (Fig. 4 *D*); each group consisted either of the high frequency 'burst' typical of post-synaptic elements (Bishop, Jeremy & McLeod, 1953; Hubel & Wiesel, 1961; Negishi *et al.* 1962; Widén & Ajmone

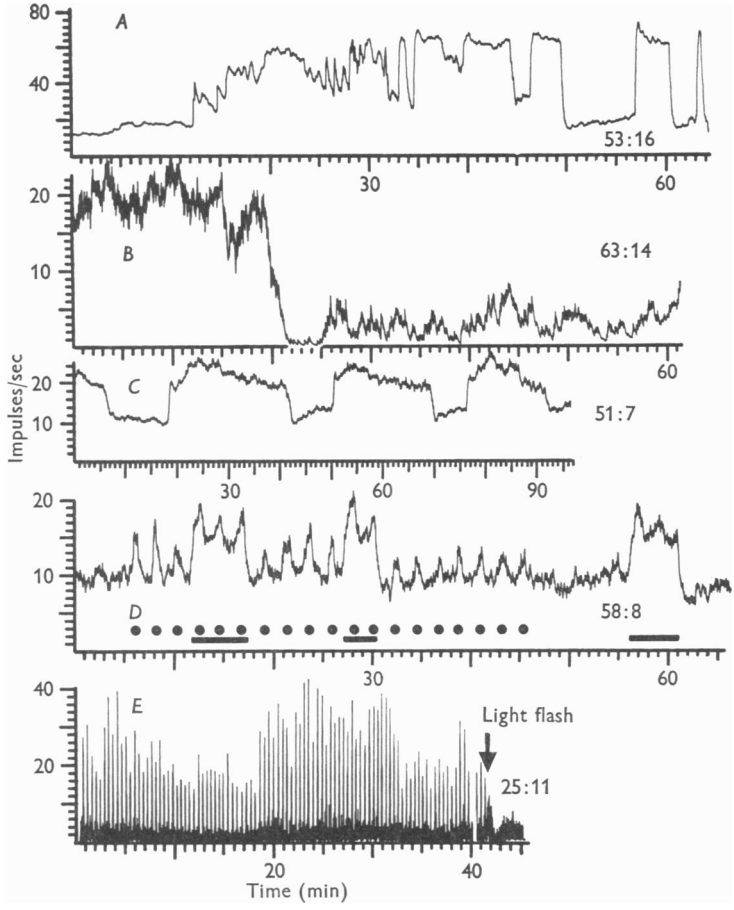

Fig. 3. Dark firing. *A* and *B*, Examples of irregularly unstable types of mean rate graph. *C–E*, Examples of regularly unstable firing rates; *C*, slow cyclic firing; *D*, superimposition of two different cyclic firing patterns (marked by dots and bars); *E*, fast cyclic firing, abolished by a light flash. The graphs, except for *E*, were obtained with 10 sec time constant in the averaging circuit. The 0·5 sec time constant was used in *E* to highlight the 'surges' of impulses.

Marsan, 1960) or more widely spaced single impulses, or both. Usually this pattern was maintained for only a few minutes but recurred at infrequent intervals, the intervening firing being relatively undistinguished and of lower mean rate. Thus the mean rate trace revealed the periods of cyclic firing as a temporary elevation of the graph (Fig. 4*A*).

Since this fast cyclic firing had a repetition frequency very close to the cat's heart rate, it is important to consider the evidence against an artificial cause (e.g. the cell body being thrust on to the micro-electrode by arterial pulsation): (i) when the electrocardiogram appeared with the spikes in photographs of the discharge, no obvious relation could be

found (one experiment); (ii) the onset of the activity was not accompanied by alterations in spike shape or amplitude; (iii) synaptic potentials (when present) still preceded the 'bursts' just as when activity was not cyclic; (iv) the activity was abolished by a flash of light in all cases tested; (v) it was also abolished by raising the intraocular pressure of the appropriate eye in all cases tested; (vi) many separate phases of the activity were observed over a considerable time interval; (vii) it was possible to produce large changes in wave form by advance of the micro-electrode, without influencing the pattern of activity; (viii) background units more remote from the electrode showed the same behaviour (Fig. 4 *C*); (ix) the activity was observed in radiation axons as well as geniculate cells. Similar evidence was found for the physiological nature of the other types of cyclic firing.

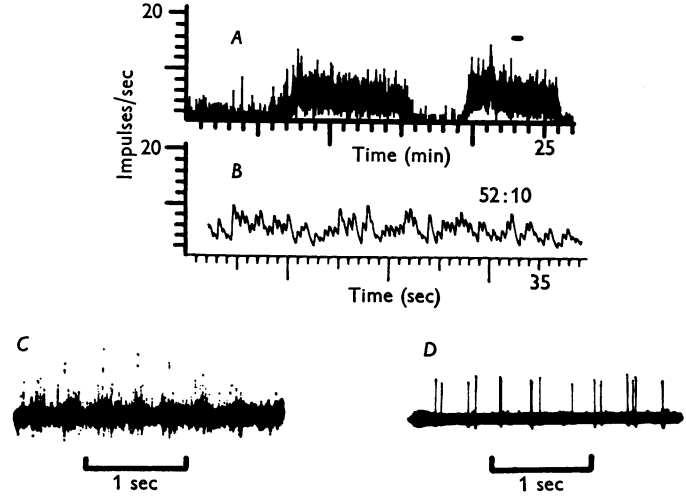

Fig. 4. Very fast cyclic firing. *A*, Mean rate graph (0·5 sec time constant) showing increase of mean rate during the phase of cyclic firing. *B*, Fast time base; the individual groups of impulses cause separate humps in the mean rate graph; there are about 2 humps/sec. *C*, Micropipette recording; the base line is rhythmically thickened by small background units firing cyclically in synchrony. *D*, Micropipette recording; negative cell spikes are grouped, with about 2–3 groups/sec.

TABLE 1. Analysis of cyclic firing

Type	Period	No. of observations	Relative frequency (%)
1. Very short period	0·3–0·5 sec	19	41
2. Short period	1 sec–1 min	4	9
3. Medium length period	1–20 min	18	39
4. Long period	> 20 min	5	11

An examination of 46 examples suggested a convenient grouping of cyclic patterns into 4 classes. The relative frequencies of occurrence are shown in Table 1. The paucity of long-period types was strongly influenced by the relatively short times for which many units were studied.

The role of the retina

Almost all geniculate neurones were affected by raising the intraocular pressure of the appropriate eye. Figure 5 illustrates a frequent type of response. The main spike is the A, B potential complex, and the lower amplitude wave the synaptic potential (Bishop, Burke & Davis, 1962*b*). The main features are: (i) depression of the A, B spike rate and of the synaptic potential rate a few seconds after application of raised pressure; (ii) return of both rates near to the original level; (iii) secondary slight depression and recovery of A, B spike rate; (iv) abrupt cessation of both A, B spikes and synaptic potentials. Except for the isolated burst 12 sec later there was no further firing until 22 sec after relief of the elevated pressure (2 min duration).

Fig. 5. Effect of pressure block of the retina. Tungsten recording of geniculate cell and synaptic potential. To left of arrow is normal dark firing (time markers 5 sec). Manual pressure applied to ipsilateral eyeball commencing at arrow and continuing throughout (time markers 0·5 sec).

Complete cessation of firing during and shortly after application of pressure to the appropriate eye was produced in 14 (61 %) out of 23 units studied sufficiently. Of the remaining 9, 4 were strongly depressed but continued to fire at a very slow rate until recovery after removal of pressure. The other 5 were either not affected or showed transient excitatory or inhibitory effects. In these 9 cases pressure block of the opposite eye had no effect.

Cerveau isolé preparations

In *cerveau isolé* preparations (anaesthetized and paralysed as usual) the dark firing patterns displayed the same variability and general characteristics as in animals with intact brains. Cyclic firing was still observed. No new effects were noted. The only difference encountered was in connexion with the effects of retinal pressure block: it was now found that 33 out of 39 units were completely blocked by eliminating the input from the appropriate eye with the standard procedure. The difference in behaviour, judged by an exact treatment of the fourfold table, was just significant ($P = 0{\cdot}037$).

Other factors

A series of experiments was carried out to test whether the unstable behaviour of units was correlated with residual fluctuations of the experimental variables.

Body temperature. Slow change of temperature over the range 35–41° C (heating by electric blanket; cooling by circulation of iced saline through the stomach) was usually without obvious effect, and any apparent influence was never reproducible. Consistent effects were obtained only with sudden brief cooling (intravenous injection of about 10–25 ml. of iced 5 % glucose solution; maximum temperature fall 1° C) which often caused a transient depression of firing rate.

Over-ventilation. This was produced by doubling or occasionally trebling the stroke volume of the respiratory pump. Some unit discharges were not affected by up to 60 min of this treatment. Although others appeared to be affected in various ways, the only consistently observed effects were transient changes of the mean rate within a few minutes of the onset or cessation of over-ventilation. Cyclic firing was observed to persist during over-ventilation.

Hypercapnia. A gas mixture consisting of 5 % CO_2 and 95 % O_2 was substituted for oxygen. The only consistently observed effect was an initial transient depression of mean rate lasting a few minutes. Cyclic firing was again observed to continue during hypercapnia.

Drugs. Test doses of all drugs used were given by rapid injection into a forelimb vein. The minimum dose of pentobarbitone producing a change in mean rate varied from 0·3 to 6·0 mg with different units. Fluctuations in the rate of injection of pentobarbitone by the infusion pump during the course of a typical experiment corresponded to doses much smaller than 0·3 mg. Gallamine, penicillin and sulphacetamide had no effect. Although pethidine and atropine had definite effects on unit firing rate, these would have subsided long before observations were commenced in the main series of experiments.

The above control experiments showed that variability of unit activity was not the result of residual fluctuations of body temperature, ventilation and rate of infusion of anaesthetic and relaxant occurring as part of the normal routine of the main series of experiments. However, since the addition of doses of pentobarbitone (0·3–6 mg), small compared with the initial dose (28 mg/kg), did cause significant changes in the mean firing rate, it is clear that the level of this drug is likely to be an important factor influencing the results.

DISCUSSION

To our knowledge the work reported here is the first detailed survey of the spontaneous firing patterns of units of the LGN in total darkness under constant conditions. While undoubtedly the monitoring of the mean firing rate is an essential preliminary for the selection of potentially

stationary patterns of discharge, it is also an important routine procedure since many of the cyclic patterns of spontaneous activity may easily be overlooked by other approaches.

The behaviour of geniculate units in darkness provided much new information. Of the stable discharge patterns, most had mean rates less than 10/sec. The corresponding analysis has not been made for retinal ganglion cells but judging from the work of Kuffler *et al.* (1957) and others (Kozak, Bishop & Levick, unpublished), the mean rates of stable dark discharges are predominantly greater than 10/sec. These results suggest the possibilities (i) that some retinal inputs to geniculate neurones are inhibitory, (ii) that considerable spatial and/or temporal summation is required for excitation of geniculate neurones. The first possibility has already been suggested in the case of the rabbit (Arden & Söderberg, 1961) on the basis of the effects of retinal pressure block.

Of the unstable patterns, the cyclic firing group is of particular interest. The study of regular rhythms in the diencephalon is an old one. As long ago as 1936 Gerard, Marshall & Saul made a survey of multineuronal slow potentials and often observed '. . . a regular rhythm of from 2 to 4 a second found throughout the optic structures'. The cyclic firing of very short period frequently encountered in this study is evidently the manifestation of this rhythm at the level of the single neurone. Gerard *et al.* (1936) also described the occurrence of two independent rhythms. The present experiments show further that it is possible for two rhythms to occupy a single neurone at the same time (Fig. 3 *D*). Others have reported the occurrence of fast cyclic activity in the neurones of the LGN (Hubel, 1960; Arden & Söderberg, 1961). However, the rhythmic bursts described by Bishop & Davis (1960) and Bishop, Burke & Davis (1962*a*) probably have a different origin, since they were related to the slow waves of the LGN (Bishop & Davis, 1960) and occurred in the absence of retinal activity. By contrast, the type of fast cyclic firing described in this investigation was stopped during acute retinal blockade.

Arden & Söderberg (1961) observed rhythmic fluctuations of activity which fit into our short-period (1 sec to 1 min) group. However, cyclic firing with longer periods does not appear to have been previously described. With these slow patterns the reproduction of the detailed course of activity throughout successive cycles (Fig. 3 *C*) is just as striking as the duration of the cycles (up to 50 min). The significance of the observations is not clear. The patterns may provide the neurophysiological basis of the 'intrinsic light of the retina', an evolving structured hallucination which is experienced in total darkness (Duke-Elder, 1932).

Dependence of geniculate activity on the retina

Experiments showed that acute interruption of the dark firing emanating from the retina completely stopped (61 %) or powerfully suppressed the dark discharge of geniculate units. The proportion which still retained some activity compares closely with the percentages found by Bishop, Burke & Davis (1962*a*) to be spontaneously active after permanent destruction of both retinae (37 % of cells of the LGN; 36 % of post-synaptic axons). This is in strong contrast with the findings in the rabbit (Arden & Söderberg, 1959, 1961; Söderberg & Arden, 1961). Species differences are probably responsible but the alternative experimental circumstances may also be significant. Light barbiturate anaesthesia was used in the present experiments, whereas local anaesthesia and the *encéphale isolé* preparation were used for the rabbit.

The behaviour of several geniculate neurones soon after the onset of raised intraocular pressure differed considerably from that of optic nerve fibres described by Bornschein (1958*b*). For instance, the unit of Fig. 5 progressed through phases of depression–excitation–depression–excitation before firing stopped, whereas most optic nerve fibres displayed a single phase of depression which developed at different times with different units. Our results can be explained by the hypothesis that (i) there are two or more optic nerve fibres forming synapses on a geniculate cell, and (ii) at least one fibre has an inhibitory effect.

The origin of the residual geniculate discharge after retinal blockade is of considerable interest in view of the accumulating evidence for an ascending pathway from the reticular formation to geniculate neurones (Hubel, 1960; Fuster, 1961; Söderberg & Arden, 1961; Suzuki & Taira, 1961; Ogawa, 1963). The finding that a larger proportion of geniculate units is completely stopped by appropriate retinal blockade in *cerveau isolé* preparations constitutes further evidence for the pathway. However, the *cerveau isolé* lesion did not have any obvious influence on the geniculate dark discharge. This finding contrasts strongly with the result from the rabbit, in which geniculate neurones have little resting discharge in the *cerveau isolé* condition (Arden & Söderberg, 1961).

SUMMARY

1. The activity of single lateral geniculate neurones in darkness was studied under constant conditions for long periods of time in lightly anaesthetized cats. A survey was made of the patterns of behaviour revealed by monitoring the mean rate of firing.

2. The outstanding feature of dark firing was the great variety of

patterns exhibited, not only by different units but also by the same unit at different times.

3. The patterns were classified into 3 groups, (*a*) stable; (*b*) irregularly unstable; (*c*) regularly unstable (cyclic). The most frequently observed stable mean rates were 4–6/sec. With the cyclic patterns, the 'period' (defined as the time between successive transitions of the mean rate graph in the same direction) ranged from a fraction of a second up to almost an hour.

4. The variability of unit activity was not the result of residual fluctuations of body temperature, ventilation and rate of infusion of anaesthetic and relaxant.

5. Lateral geniculate dark firing was critically dependent on a functional retina. Residual discharge after retinal blockade was probably supported by activity arising at or passing through the intercollicular level of the brain stem. However, massive lesions at this level had no obvious effect on normal dark firing.

6. The behaviour of lateral geniculate neurones during the onset of retinal blockade appeared to differ significantly from the behaviour reported for optic nerve fibres.

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