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The Visual Properties of Rat and Cat Suprachiasmatic Neurones

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Summary. 1. Responses of single neurones in the suprachiasmatic nuclei (SCN) were recorded in the anaesthetized rat and cat. Visual SCN units in both species were predominantly present in the caudal half of the nucleus. The large majority could be classified as either tonically suppressed or tonically activated according to whether an increase in diffuse adaptation luminance respectively decreased or increased their mean discharge rate.

2. For both the cell types the maintained discharge at different luminance levels was a monotonically decreasing or increasing function over a large range of light intensities. In both species the threshold for luminance-dependent maintained discharge was high (> -1 log cd·m^{-2}). The observation of either cell type was independent of the phase of the circadian cycle but it was not established whether the same held true for the intensity-response relations.

3. A small proportion of suppressed cells in the rat SCN reflected the state of retinal adaptation in their firing rate. After light adaptation these cells attained their steady state dark discharge only very slowly.

4. The receptive fields of cat SCN cells tended to be large ($> 20°$) without a clear antagonistic centre-surround organization. It is proposed that the receptive fields of SCN are the result of the convergence of retinal input from tonic W-cells.

5. It is concluded that their characterization as detectors of diffuse temporal luminance gradients makes visual SCN neurones particularly suitable for their function in the photic entrainment of circadian rhythms. This functional specialization is probably common to both the direct retinofugal projection and the indirect visual projection via the ventral lateral geniculate nucleus to the SCN.

Introduction

Circadian rhythms in various physiological and behavioural processes are a widespread phenomenon in eukaryotic protozoan and metazoan species. Many of these rhythms are endogenous and have the important property of being susceptible to entrainment by 24-h cycles in environmental variables.

In mammals the daily cycle of light and dark is recognized as the foremost entraining agent. However, daily photoperiods as short as a few minutes are equally adequate to entrain circadian rhythms. This and other observations have led Daan (1977) to the conclusion that transitions between light and darkness rather than the tonic effect of a normal photoperiod on the circadian pacemaker are of major importance for synchronization. This notion implies that the photoreceptors involved in entrainment supply the pacemaker with information pertaining to temporal gradients of the overall environmental luminance. For such a non-parametric entrainment mechanism it has been shown that the effects of constant light on the free-running period can be accounted for by assuming that the photoreceptors show adaptation to light (Daan, 1977). Another requirement concerning the properties of the sensory system mediating synchronization underlies both the parametric and non-parametric models of entrainment. From the fact that the free-running period is often a function of light intensity (Aschoff, 1979). follows that the circadian system will show a lumi-

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Abbreviations: LGN_v, ventral lateral geniculate nucleus; *PSTH*, peri-stimulus time histogram; *RF*, receptive field; *SCN*, suprachiasmatic nuclei

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nance dependent response to constant illumination. Moreover, the amplitude of the phase response curve for short light pulses depends on the light intensity (DeCoursey, 1959). In order to study the physiological basis of these macroscopic observations we investigated the functional properties of the pathway for entrainment in the rat and the cat. The recent identification of this pathway in mammals makes such a study possible (Mai, 1978).

By selective ablation of various parts of the visual system it was shown that a direct projection from the retina to the suprachiasmatic nuclei of the mammalian hypothalamus (SCN) is essential for entrainment (Moore, 1978; Zucker et al., 1976; Rusak and Zucker, 1979). The SCN, moreover, are not just terminal nuclei for this retinofugal pathway. Bilateral ablation of the SCN results in complete or partial disruption of a considerable number of circadian rhythms (Rusak and Zucker, 1979). Thus there seems to be a firm experimental basis for the notion that the retino-suprachiasmatic complex is an essential part of the circadian pacemaker in mammals.

Although the importance for entrainment of the direct retinal projection to the SCN relative to more central visual structures in the brain is well documented only few reports on the visual physiology of the SCN are available. Lincoln et al. (1975) were the first to report the presence of visual neurones in the rat SCN. Using stepwise transitions between light and darkness they noted two opposite response types. Some neurones tonically increase their spontaneous firing rate to an increase of retinal illumination, others react with a decrease of their discharge. This finding was subsequently confirmed by others (Groos and Mason, 1978; Kreisel et al., 1978; Nishino et al., 1976; Sawaki, 1979). The activation of SCN cells by either ipsilateral or contralateral photic stimulation is more common than suppression. Furthermore, the responses to electrical stimulation of the optic nerves are consistent with these observations. The present findings elaborate these findings and extend them to the visual neurones of the cat SCN.

Methods

Rat. Experiments were performed on 42 adult albino rats, anaesthetized at various phases of the circadian cycle with urethane (initial dose 1.2 $g \cdot kg^{-1}$ i.p.) or urethane (0.4 $g \cdot kg^{-1}$ initially) and hypnorm (Philips-Duphar, 1 $ml \cdot kg^{-1}$ i.m.) supplemented as necessary. Xylocaine was applied locally to all pressure points and wound margins. The left eye was occluded while the right eye was fixed by a ring with the cornea immersed in physiological saline containing 1% atropine sulphate to maximally dilate the pupil. The entire retina was illuminated with spatially unstructured white light from a glow modulation tube (Sylvania, R1131C).

After craniotomy single unit extracellular action potentials were recorded using glass micropipettes either filled with Wood's metal and platinized at the tip or filled with 3 M KCl.

Cat. Further experiments were carried out on 6 adult cats. For recording cats were maintained on a nitrous oxide/oxygen mixture (72.5% N_2O:27.5% O_2) supplemented with pentobarbitone (Nembutal, Abbott: averaging 1.0 $mg \cdot kg^{-1}\ hr^{-1}$ i.v.). Each experiment lasted approximately 30 h. The cats were artificially ventilated and eyes were immobilised by infusion of gallamine triethiodide (Flaxedil, May & Baker: 20 $mg \cdot ml^{-1}$ in 2.5% dextrose solution at a rate of 1 $ml \cdot h^{-1}$). As for rat experiments, rectal temperature was kept at 37 °C. In addition the EEG, end-tidal CO_2 and heart rate were routinely monitored. The pupils were dilated and nictitating membranes and eyelids retracted by the application of 1% atropine sulphate and 10% phenylephrine hydrochloride eye drops, respectively. The cornea were protected by a pair of neutral contact lenses. Focal correction, using additional lenses, was assessed retinoscopically. Visual stimulation consisted of both flashed white spots or annuli of various diameters onto a tangent screen or of changes in the overall adaptation luminance of the screen. Single units were recorded in the rostral hypothalamus using micropipettes containing 2% pontamine sky blue in 0.5 M NaCl.

Recording Site Identification. All recording tracks were marked by either microiontophoretic deposition of pontamine sky blue or electrolytic marking. Recording sites were reconstructed histologically from cresyl violet or cresyl violet/luxol fast blue stained sections. In addition to histological localisation of recording sites for all visually responsive units an attempt was made to distinguish between a chiasmatic fibre and an SCN cell body recording. The criteria for ascribing the extracellular action potential to an SCN soma were a bi- or triphasic appearance with a small inflection on the first component which could possibly be interpreted as the A potential of the initial segment (Fuortes et al., 1957). If the spike resembled that of the a-type described by Bishop et al. (1962) or in the course of recording showed splitting, the unit was classified as an optic chiasm fibre.

Results

1. The Topographical Distribution of Visual Units

Both in the cat and the rat a considerable proportion of SCN units responded to visual stimulation. In the rat spontaneous activity was recorded from a total of 397 SCN cells mostly contralateral to the stimulated eye.

In the rostral half of the nucleus 16% ($N=19$) of the units could be classified as visual, while in the caudal half 37% ($N=102$) were found to be visually responsive. Although in the rat there was a clear tendency for visual units to be located in the caudal part there appeared to be no preferential distribution along the medio-lateral or dorso-ventral axes of the SCN.

In the cat recordings were obtained from 27 visual SCN neurones. In this sample only cells which proved to be situated well within the boundaries of the SCN were included. The percentage of visually responsive cells in the cat could not be reliably assessed as the

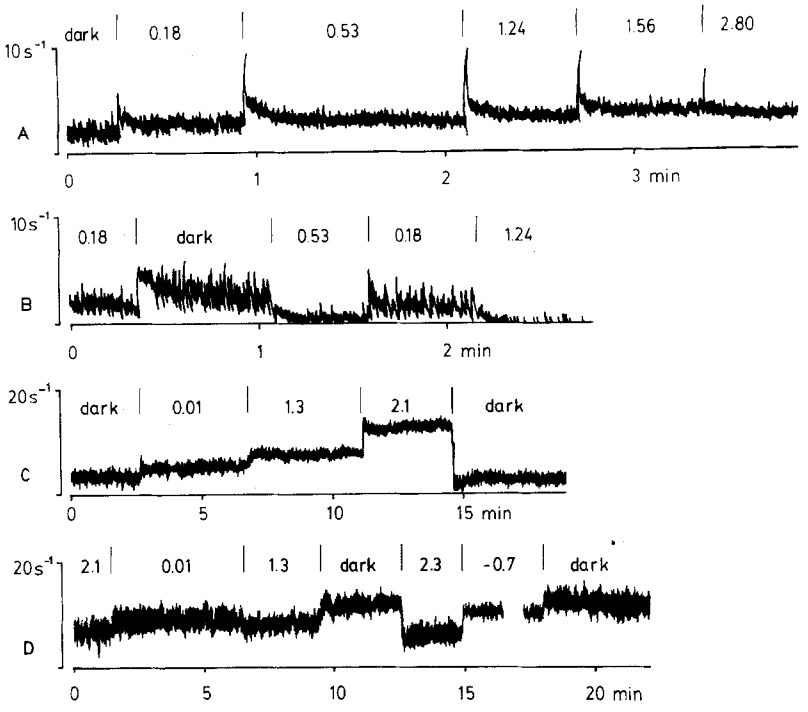

Fig. 1A–D. Discharge rates of SCN neurones at different adaptation levels.
A Light activated cell type of the cat;
C of the rat.
B Suppressed cells of the cat;
D of the rat. Numbers above each recording refer to adaptation luminance in log cd · m^{-2}

lateral extent of the SCN is less well defined than in the rat. However, these units were only encountered in Horsley-Clark planes A 12.5 and A 13.0 suggesting that visual SCN neurones are also predominantly confined to the caudal part of the nucleus as found for the rat. All the visual units in the cat SCN were monocularly driven with the larger proportion (80%) driven through the contralateral eye. The binocular cell type described by Lincoln et al. (1975) in the rat, driven by simultaneous stimulation of both eyes but not by stimulation of each retina separately, was not observed in our cat experiments.

In the rostral hypothalamic areas surrounding the SCN visual units were remarkably scarce. The medial hypothalamus of the cat between Horsley-Clark planes A 15.5 and A 11.5 revealed no visual responses to flashes or tonic diffuse illumination changes in 65 preoptic area and 196 anterior hypothalamic area units. This observation is consistent with the findings of Bremer (1976) who only observed photically suppressed neurones in the preoptic area of decerebrate cats whereas this type of visual cell was absent in animals in which the mesencephalon was not transected. In our rats visually responsive units were absent in a sample of 258 preoptic area and 315 anterior hypothalamic area neurones. Among 47 medial preoptic nucleus units only 2 responded to light but in a way qualitatively different from SCN cells. These observations lend support to the notion that the SCN is a separate anatomical and functional terminal nucleus for visual fibres in the hypothalamus. This point is further amplified by the fact that the properties of visual SCN neurones as described below are in contrast to those of photically driven units in the mediobasal hypothalamus which probably receive their input from the accessory optic system (Kreisel et al., 1978).

2. Tonic Response to Constant Illumination

A characteristic of most visual SCN units that distinguishes them from the majority of retinal ganglion cell fibres was their stable tonic response to steady illumination of the entire retina. The SCN of both the rat and the cat were very similar in this respect. After adaptation to a dark background these cells typically responded to a stepwise transition to some higher luminance level with a sustained increase of their dark discharge.

Following the criteria stated in our earlier report (Groos and Mason, 1978) these cells were classified as light activated or light suppressed, respectively. The occurrence of suppression or activation bore no relation to the extrapolated phase of the lighting regimen to which the animals had been exposed previously. Both types of cells could be recorded within 30 min and within a distance of less than 100 μm. In both species light activated cells were encountered approximately twice as often as light suppressed cells. This ratio is in accordance with that reported earlier for the rat (Groos and Mason, 1978; Nishino et al.,

1976). The response consisted of a transient phase followed, after a variable period, by a steady state discharge (Fig. 1). The transients are commmonly more phasic in the cat as compared to the rat (Fig. 1). Possibly this difference is due to the deeper level of anaesthesia used in our rats. However, although a suppressive effect of urethane on SCN cells can not be ruled out, our findings from both species are essentially similar. The stable discharge at any adaptation level allowed computation of interspike interval distributions for the rat. Examination of the histograms revealed no systematic relation between the standard deviation of the distribution and illumination level. In all cases it proved impossible to fit the interval histograms by a low order Erlang-distribution. In the cat the correlation coefficient between non-zero luminances and the ranges of firing frequency was not significant for light activated units but significant for light suppressed cells ($r = -0.95$; $P < 0.01$).

The SCN neurones respond to increases in environmental luminance with a change in firing rate of visual cells to a level either below or above the baseline discharge in the dark. The dark discharge of a particular cell, however, was commonly not consistent throughout the experiment. Figure 2 shows a typical example of a unit which was consistently activated by light of various intensities after a period of dark adaptation. However, the mean discharge rate at the end of each dark adaptation period was different. Nevertheless, the steady state discharge was commonly dependent on the intensity of the adapting background. This is illustrated in Fig. 3 for non-adapting (see below) light suppressed and light activated cells from both species which were recorded for extended periods of time. From these graphs it is evident that over the intensity range studied there is an essential monotonic luminance-response relationship. Moreover, these graphs illustrate a feature described earlier for the rat (Groos and Mason, 1978) that the threshold for steady state luminance dependent discharge is high relative to the sensitivity of the retina. Only one cell among 23 SCN units in both species the adaptation level responses of which were well documented responded non-monotonically to increasing luminance.

So far we have described the behaviour of those neurones which change their firing rate after a transition from one luminance level to another and subsequently acquire an intensity-dependent steady state discharge. In the cat SCN all visual units fitted this class. In the rat, however, we have observed a small number of units behaving differently. The most common exception were cells which reacted to light with a transitory activation lasting from 0.5 to 2 min whereafter their firing rate reassumed its initial value.

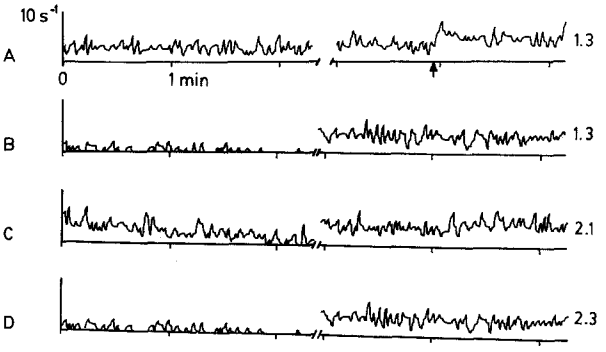

Fig. 2A–D. Variability of dark discharge rate of a light activated SCN unit in the rat. Steady state discharge at the end of a 5 min dark adaptation period on the left. Steady state firing during light adaptation to the right of the time axis interruption in **B, C** and **D**. In **A** luminance increase marked by an arrow. Luminance levels on the right (log cd·m^{-2})

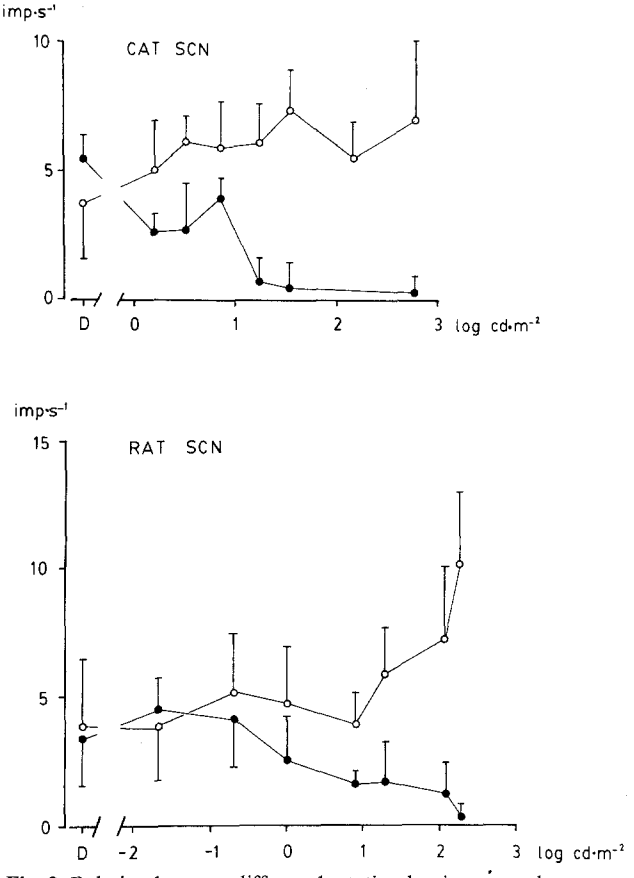

Fig. 3. Relation between diffuse adaptation luminance and average maintained discharge rate for light activated (open circles) and light suppressed neurones (filled circles) in the cat and rat SCN. These curves were determined from extensive recordings from 6 activated and 4 suppressed units in the cat. Curves for the rat determined from 8 units of either type. As there was no significant difference between the maintained discharge after an increase or a decrease to a particular luminance level the corresponding firing rates have been pooled. Vertical bars: one standard error of the mean

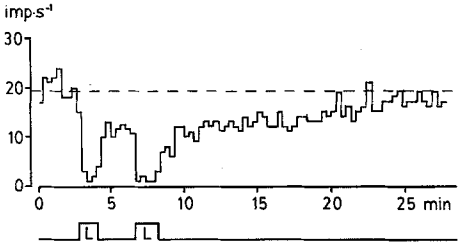

Fig. 4. Dark adaptation in a suppressed SCN unit in the rat. Mean discharge rate after prolonged dark adaptation indicated by the dashed line. After short light adaptation (*L*) the suppressed discharge gradually reassumes the mean rate characteristic of the dark adapted state

In the SCN we did not observe the type of cell described by others (Kreisel et al., 1978; Sawaki, 1979) which responds to diffuse light with a bursting firing pattern. We did, however, encounter an optic fibre dorsomedial in the optic chiasm which behaved similarly. This amplifies the point we raised implicitly in the Methods that every possible effort should be made to distinguish potentials from chiasmatic fibres from those of SCN somata.

In those rat SCN cells which were studied for prolonged periods of time it proved difficult to obtain evidence for adaptation. Only a few light suppressed units were encountered with a time course of their discharge rate in the dark which could be assumed to reflect retinal dark adaptation (Fig. 4). In contrast to the cells illustrated in Figs. 1 and 2 this type of dark adapting cell showed a clear dependence of its firing rate in diffuse illumination on the previous history of retinal illumination.

3. The Transient Response to Light

The tonic change of discharge rate of visual SCN cells after changes in overall retinal illumination is also evident from peri-stimulus time histogram (PSTHs) computed for flashes of short (150–800 ms) duration. Figure 5 (A, B) shows two typical PSTH's for a light activated and a light suppressed rat SCN unit respectively. In this species the majority of visual SCN units responds to flashes illuminating the entire retina with a non-phasic increase or decrease of the ongoing discharge. Tonic activation was apparent at latencies ranging from approximately 84 to 140 ms ($N=27$) while tonic suppressive response latencies were estimated to range between 100–160 ms ($N=9$). After the flash the discharge typically returns to its previous rate in the dark in a non-phasic fashion. Only one activated cell among 52 for which PSTHs were computed in the rat showed a phasic response at a latency of 85 ms (Fig. 5C). Fifteen rat SCN neurones the maintained discharge of which was related to adaptation luminance proved irresponsive to short flashes even after averaging over a hundred sweeps.

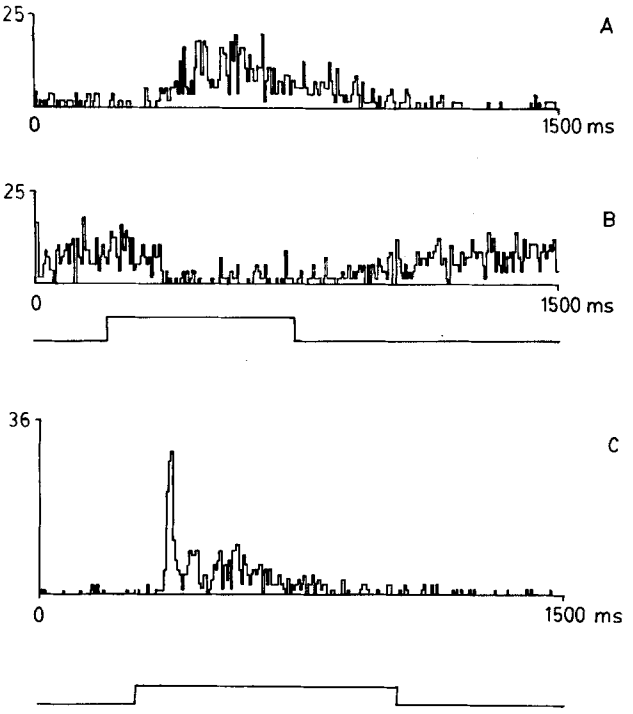

Fig. 5A–C. PSTH computed for a light activated (**A**) and a suppressed cell (**B**) in the rat SCN. **C** A rare example of a phasically excited rat SCN cell

Tonic responses to diffuse light flashes and the absence of phasic on or off discharges was also observed in the cat SCN. In this species the receptive field (RF) properties of each of 17 visual units were fully documented. Fifteen of these responded to a 3° flashing spot with tonic activation or suppression throughout most the visual field. For these cells it proved impossible to determine the RF boundaries as the RFs were commonly very large (> 20° diameter) and not completely confined to the part of the visual field covered by the tangent screen (50° × 35°). The large RFs were characterized by the absence of an antagonistic centre-surround organization, i.e., they exhibited either tonic suppression (see Fig. 6C) or tonic activation to 3° spots throughout the part of the RF studied. This may be compared with the classical centre/surround response of a chiasmatic (retinal) fibre to spot representation in the unit's RF centre (Fig. 6A) and surround (Fig. 6B). No clear spatial sensitivity gradients could be observed within the RF. There was also no evidence of any silent inhibitory-surround component of the RF, i.e., suppression of the response to flashed spots by simultaneous peripheral RF stimulation. In two cells a very weak response to moving gratings of various spatial

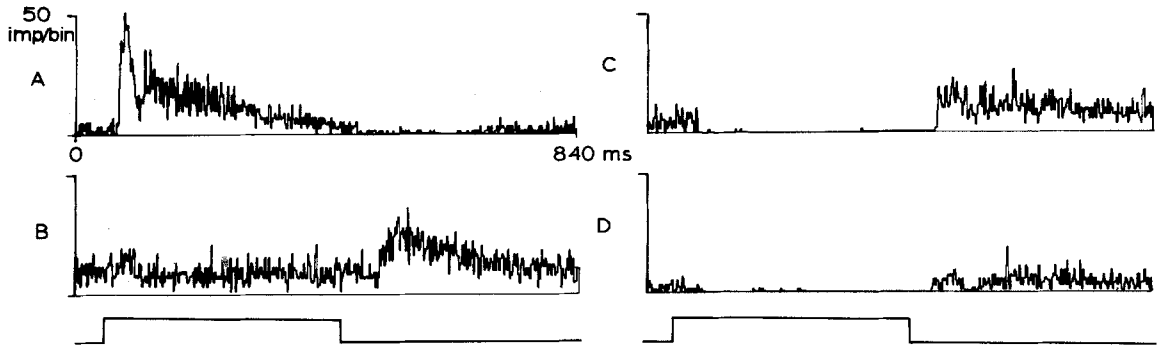

Fig. 6A–D. PSTH computed for an optic fibre (**A, B**) and an SCN cell (**C, D**) in the cat. Stimulation of RF centre (**A**) or surround (**B**) with a 3° flashing spot reveals typical antagonistic centre-surround organization of ganglion cell axons. **C** PSTH for a 3° spot for a suppressed SCN cell. Increasing the spot diameter to 9° does not result in activation of antagonistic surround mechanisms in this cell (**D**)

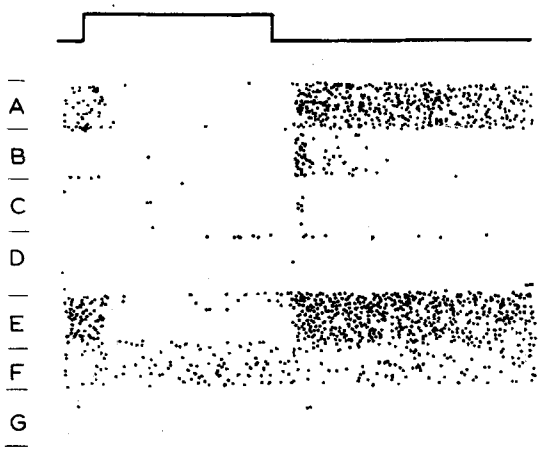

Fig. 7A–G. Dot display of the flash response to a 3° spot of the same SCN unit as in Fig. 6 C, D. In **A** and **E** the spot is flashed against a dark background. In **B, C** and **D** the background luminance is 0.18, 0.53 and 1.24 log cd·m^{-2}, respectively. The latter background luminance was used again in record **G** after a period of dark adaptation (**F**)

frequencies was noted without any preferential direction or velocity.

Figure 7 illustrates a continuous record of unit activity, as a dot-display, for the light suppressed SCN cell shown in Fig. 6C to spot presentations at various background luminances (Fig. 7A to E). It was observed in some cells, as is evident from Fig. 7, that at low luminances the 'off' maintained discharge in the dark (Fig. 7A, E) is replaced by a transient 'off' discharge (Fig. 7B). At higher luminances this transient discharge is weak or absent (Fig. 7C, D).

Discussion

The use of autoradiographic techniques has conclusively demonstrated a direct bilateral projection from the retina to the SCN of the mammalian hypothalamus (Mai, 1978; Moore, 1978; Rusak and Zucker, 1979). This projection has also been visualized by the cobalt precipitation method (Mason et al., 1977). There is a firm experimental basis for the conclusion that this direct pathway is sufficient for the entrainment of circadian rhythms to environmental light-dark cycles (Moore, 1978; Rusak and Zucker, 1979). In addition to the direct retinofugal pathway visual information may be directed to the SCN through two putative indirect pathways, one via the ventral nucleus of the lateral geniculate complex (LGN_v) and another via the midbrain raphe complex.

A recurrent feature of the direct bilateral projection is its predominantly contralateral termination ventrally in the caudal half of the SCN (Mai, 1978). Our description of the topographical distribution of visual SCN units is consistent with these neuroanatomical findings to the extent that in both species the majority of the visual cells tended to be located in the caudal SCN. For the cat, moreover, we could show that the projection is mainly contralateral. Mason et al. (1977) distinguish between a direct projection consisting at least partly of fine ganglion cell axon collaterals to the lateral border of the SCN and a second direct component of large diameter fibres terminating in the ventromedial SCN. In our rat experiments we could find neither a functional nor a topographical correlate for such a dual direct input. We feel that the anatomical distinction put forward by Mason et al. requires further substantiation.

There is substantial neuroanatomical evidence for the existence of a projection from the LGN_v, itself a terminal nucleus for retinal fibres, to the SCN (Hickey and Spear, 1976; Ribak and Peters, 1975). Similarly the midbrain raphe complex receives a retinal input (Foote et al., 1978) and also projects exten-

sively to the SCN (Moore, 1978). Whereas raphe lesions do not significantly affect the circadian system of rodents (Zucker et al., 1976), lesions of the lateral geniculate complex result in delayed re-entrainment of circadian rhythms to a phase shifted illumination cycle (Zucker et al., 1976; Rusak and Zucker, 1979). Consequently the possibility must be recognized that visual SCN cells are not exclusively innervated by fibres of the direct retino-hypothalamic projection but at least also by visual LGN_v efferents. In the present study we did not attempt to discriminate between the properties of direct and indirect visual SCN afferents. Since cells in both the LGN_v and the raphe complex typically respond tonically to illumination changes (Hale and Sefton, 1978; Mosko and Jacobs, 1974; Groos, 1980), it is to be expected that the direct and indirect visual inputs exhibit to a large extent similar properties. Neurones of the LGN_v in particular behave like visual SCN cells in many respects and their RF diameters may be of a comparable order of magnitude (Spear et al., 1977). Sawaki (1979) has shown that interrupting the LGN_v input to the SCN does not alter the visual properties of SCN neurones. These findings lead us to suggest that the direct retinofugal and the geniculate projection to the SCN are largely supplementary.

It is interesting to speculate which retinal subsystem subserves the visual function of the SCN. The tonic response of SCN cells to changing luminance is reminiscent of tonic W-cells found in the cat (Stone and Fukuda, 1974: the sluggish-sustained cells of Cleland and Levick, 1974) which, because of their monotonic intensity-response relation, have been identified with the luminance units described by Barlow and Levick (1969). W-cells have also been observed in the visual system of the rat (Fukuda, 1977; R. Mason, unpublished observations). Moreover, their operational range corresponds quite well with that of our SCN cells (Stone and Fukuda, 1974; Barlow and Levick, 1969). Their RFs, however, have a much smaller diameter than observed for SCN units while they exhibit an antagonistic centre-surround organization (Stone and Fukuda, 1974). Notably a silent inhibitory surround component to their RF is generally absent in this population of retinal ganglion cells (Cleland and Levick, 1974). The long latencies found in visual SCN cells to photic stimulation, when compared with X-, Y- and W-unit responses recorded in the optic chiasm and dorsal lateral geniculate nucleus (R. Mason, unpublished observations), are consistent with an input from the slow conducting W-cell pathway. To reconciliate these observations it can be suggested that a considerable number of retinal tonic W-cells converge onto a single SCN cell in such a way that either activation or suppression dominates. Future studies should be undertaken to provide an experimental basis for this hypothesis.

Their large RFs suggest that visual SCN neurones integrate photic energy from large areas in the visual field. Temporal stimulation patterns are coded tonically in such a way that luminance exceeding a relatively high threshold level is coded by a monotonically increasing or decreasing mean discharge rate. Taken together this visual behaviour is in accordance with the results of entrainment experiments. Non-parametric effects of light (Daan, 1977) require that the SCN is responsive to temporal intensity gradients. This is obviously the case in both species studied, although it remains unclear why the SCN is equipped with two oppositely reacting visual subsystems, the light activated and the light suppressed cell types. The tonic response to light has also been reported by other authors for the rat (Lincoln et al., 1975; Nishino et al., 1976; Kreisel et al., 1978). Luminance detection has been observed in the rat SCN (Groos and Mason, 1978) and is reported here for the cat. The coding of absolute luminance is a property which can be expected on the basis of the parametric effects of light (Aschoff, 1979) although Daan and Pittendrigh (1976) have attempted to reduce the effect of constant light to non-parametric effects by assuming gradual adaptation of the photoreceptors. In our study, however, it proved difficult to find instances of such adaptation as reflected in the discharge of SCN neurones. Those few cases in which adaptation was observed involved light suppressed units only. Their large RF's taken together with the other visual properties of SCN cells described here suggest that the retino-suprachiasmatic system has differentiated towards coding luminance and gross temporal changes of luminance at the expense of spatial and fine temporal resolution. Such a development seems very appropriate in terms of the SCN's function to detect the daily cycle in overall environmental luminance to synchronize endogenous circadian rhythms.

Stable entrainment of circadian rhythms is dependent on a differential sensitivity of the circadian pacemaker to light at different phases of its cycle (Daan, 1977). Consequently, in the study of the visual properties of SCN neurones one should be aware that these may be related to circadian phase. Although we did not attempt long-term recordings from single SCN units, we could establish that the occurrence of activation and suppression was not restriced to particular phases. We cannot, however, exclude the interesting possibility that a unit suppressed by light at certain circadian phases changes its behaviour into that of an activated cell at other phases. On the other hand, it is conceivable that the luminance-discharge relation changes periodically in a less qualitative way.

The circadian rhythm of retinal photic responsiveness as observed for the rabbit (Bobbert et al., 1979) could provide a basis for such differential sensitivity. Studying circadian variations in luminance coding by SCN neurones therefore remains a major objective for future research into the mechanism of photic entrainment.

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