Exp. Brain Res. 37, 127–138 (1979)

Experimental Brain Research

Suprachiasmatic Nucleus Neurones: Excitation and Inhibition Mediated by the Direct Retino-hypothalamic Projection in Female Rats

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Summary. The suprachiasmatic nucleus (SCN) of female rats was surveyed with microelectrodes under urethane anaesthesia. In rats with bilateral transection of the optic tracts, repetitive three pulses of 100 Hz applied to the contralateral optic nerve excited 8 and inhibited 11 other of the 86 SCN units examined. Transection of the optic tract did not significantly influence frequency of occurrence of the SCN units that were excited or inhibited by stimulation of the optic nerve. Certain SCN units responded to both of contralateral and ipsilateral stimulations of the optic nerve, indicating that bilateral visual inputs converge on the same single SCN neurones. Oscillatory responses with a period of 100–200 msec were occasionally produced by stimulation of the optic nerve. Flash stimuli with relatively weak intensity, even insufficient for producing wavelets in electroretinograms, produced an excitation and inhibition in SCN units. The mean firing rates were significantly altered by either electrical or flash stimuli repeated 500 times at 0.97 Hz in those units which showed no transitory response. Some of the SCN neurones receiving visual inputs were identified to be the tuberoinfundibular neurone and some other SCN neurones were found to receive converging inputs both from the optic nerve and from the axon collaterals of tuberoinfundibular neurones.

Key words: Suprachiasmatic nucleus neurone – Retino-hypothalamic projection – Electrical stimulation of the optic nerve – Flash stimulation of the retina – Tuberoinfundibular neurone

It is well known that the visual information on environmental light and dark cycles is required for the development and maintenance of circadian rhythms in mammalian species. Accumulating evidence suggests that the suprachiasmatic nucleus (SCN) of the hypothalamus is one of the essential neural structures for the circadian rhythms. Recent morphological studies have shown the existence of the direct retino-hypothalamic projection in rats (Sousa-Pinto and Castro-Correia, 1970; Moore et al., 1971; Hendrickson et al., 1972; Moore and

0014–4819/79/0037/0127/$ 2.40

Lenn, 1972; Mason and Lincoln, 1975, 1976; Colman et al., 1976; Güldner, 1976; Mai and Junger, 1977; Güldner and Wolff, 1978). The previous study (Sawaki, 1977) has demonstrated preliminarily that flash stimulation of the eye and electrical stimulation of the optic nerve evoke either excitation or inhibition in some SCN neurones. However, neurones in the ventral lateral geniculate nucleus (LGNv) have been morphologically shown to project to the SCN in rats (Swanson et al., 1974; Ribak and Peters, 1975). Therefore, the possibility arises that the excitation and inhibition evoked in SCN neurones by the photic and the electrical stimulation might have been mediated indirectly by neurones of the LGNv rather than through the direct retino-hypothalamic pathway.

To test the above possibility, the present experiments were conducted in rats with bilateral transection of the optic tracts and in intact control rats. The experiments were also designed to characterize the responses induced in SCN neurones by electrical stimulation of the optic nerve or photic stimulation of the eye.

Materials and Methods

Forty-three female rats of the Wistar strain, which were kept in an air-conditioned animal room with 14 h of light (05.00 h–19.00 h), were anaesthetized with urethane (1.5 g/kg, s.c.) at about 08.30 h. The preoptic and hypothalamic areas were exposed transpharyngeally according to the technique described previously (Sawaki and Yagi, 1973). For transecting the optic tracts bilaterally a small incision was carefully made in the pia mater by a pair of fine tweezers at the lateral edge of the optic chiasm on each side. An L-shaped fine hook of glass rod was inserted through the incision to lift slightly the optic tract which was then transected by a pair of microscissors. An infra-red lamp (100 W) was used to maintain the rectal temperature of the animal. Rectal temperature and heart rates were continuously monitored throughout the experiment.

For stimulation the optic nerves were cut at a distance of about 5 mm from the anterior end of the optic chiasm and each of them was introduced into a suction electrode of a polyethylene tubing (1 mm o.d.). A negative pulse of 0.2 ms and 0.2 mA was applied by a stimulus isolator (Tektronix, 2620) between a fine silver wire located inside of the tubing and another piece of silver wire attached to the outside of the tubing as the reference electrode for the stimulation. For photic stimulation of the retina the pupil of the right eye was dilated with a cycloplegic mydriatic (Mydrin-P, Santen) and the left eye was masked by a piece of black plastic tape. Single flashes were supplied by a photic stimulator (Sanei-sokki, 2401) equipped with a xenon lamp which was placed at 50 cm from the dark-adapted right eye. A mask with a square hole, 2.9×5.8 cm, was attached to the xenon lamp. Each single flash dissipates 0.64 joule of electric energy. For antidromic activation of tuberoinfundibular neurones the tip of a concentric bipolar stimulating electrode (0.6 mm, o.d.) was placed on the surface of the right half of the median eminence and a negative pulse of 0.2 ms and 0.5 mA was supplied by another stimulus isolator (Tektronix, 2620).

To record spontaneous unit firings a tungsten microelectrode prepared by the technique of Frank and Becker (1964) was introduced into the right SCN at an interval of 100 μm with a help of a micromanipulator (Narishige, SM20). The reference electrode of silver wire for unit recording was placed in a muscle of the jaw. The other recording techniques were previously described (Sawaki and Yagi, 1976). Some SCN units were also tested for stimulation of the median eminence as to whether they could be identified antidromically as tuberoinfundibular neurones. They were identified when the unit spike evoked by stimulation of the surface of the median eminence was of constant latency, followed repetitive stimuli at 100 Hz in a one-to-one fasion, and was cancelled by collision with a spontaneously occurring spike. Post-stimulus time histograms were computed for each SCN units after electrical pulses to the optic nerve or flashes to the eye with a digital computer (Sanei-sokki, 7S06). Unit spikes were compiled in each 5-ms time bin of consecutive 200 bins of the computer. Computations were repeated 500 times at a frequency of 0.97 Hz. Number of spikes

Table 1. Responses of SCN units to electrical stimulation of the optic nerve or photic stimulation of the eye

Stimulation	Number of units excited (%)	inhibited (%)	unresponsive (%)
ELECTRICAL STIMULATION			
Transected optic tracts			
Contra (triple pulses)	8 (9)	11 (13)	67 (78)
Intact optic tracts			
Contra (triple pulses)	12 (9)	13 (10)	109 (81)
Ipsi (single pulses)	1 (1)	2 (3)	68 (96)
Contra (single pulses)	1 (1)	2 (2)	80 (96)
PHOTIC STIMULATION			
Intact optic tracts			
Ipsi (single flashes)	5 (6)	2 (2)	75 (92)

Contra: stimulation of the optic nerve contralateral to the recording site
Ipsi: ipsilateral stimulation

compiled in each time bin was printed on recording paper by a printer (Sanei-sokki, 2201). When the effect of stimuli on mean firing rates was studied, mean number of spikes per bin was calculated from data of 30 bins just prior to the stimulus or identical time bins when stimuli were not applied. Difference in the mean number of spikes per bin thus obtained with or without stimuli in each of the same single units was tested by t-test.

For recording an electroretinogram the tip of a cotton wick electrode which was soaked with Locke's solution was touched to the cornea of the right eye. As a reference electrode for the electroretinogram an Ag-AgCl wire was placed under the skin of the head. Electroretinograms were recorded after flash stimulation applied at 0.97 Hz by the xenon lamp, to which various number of sheets of the neutral density (ND) filter of a factor of 0.5 was attached.

After each experiment a positive current of 100 μA and 30 s was applied between the recording electrode and the reference electrode for recording. The whole brain was fixed with 10% formalin and frontal serial sections of 50 μm in thickness were prepared from the frozen brain. The recording sites and transection of the optic tract were verified histologically by reference to the atlas of König and Klippel (1963).

Results

A total of 456 spontaneously firing units were recorded in the SCN. Responses evoked in the SCN units by electrical stimulation of the optic nerve or photic stimulation are summarized in Table 1.

I. Electrical Stimulation of the Optic Nerve

A. Bilateral Transection of the Optic Tracts

The optic tracts were transected bilaterally in 7 rats. In these rats repetitive three pulses of 100 Hz applied to the contralateral optic nerve either excited or

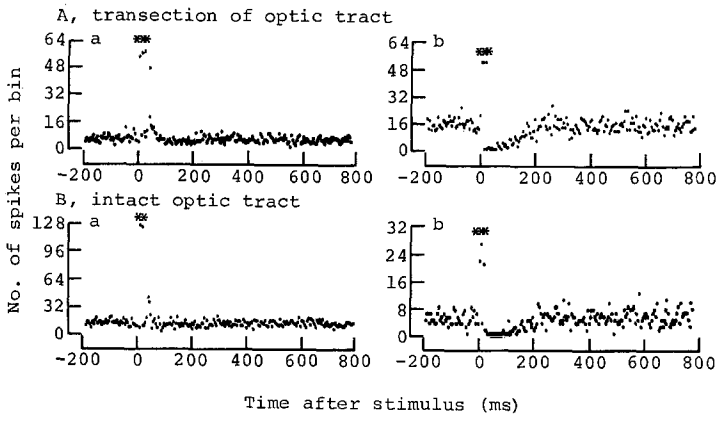

Fig. 1A and B. Excitation and inhibition of suprachiasmatic nucleus (SCN) neurones evoked by stimulation of the optic nerve in rats after bilateral transection of the optic tracts (**A**) and in control intact rats (**B**). Three repetitive pulses of 100 Hz were given at time 0 and a star indicates the stimulus artefact in this and following post-stimulus time histograms. Note a short latency excitation (Aa, Ba) and inhibition (Ab, Bb) produced in SCN units of both rat groups by repetitive three pulses applied to the contralateral optic nerve

inhibited some of the 86 SCN units tested (Fig. 1A and Table 1). Latency of the responses estimated from post-stimulus time histograms with resolution of 5-ms time bin ranged from less than 5 ms to 20 ms.

In 11 control rats with the intact optic tracts the repetitive pulses given to the contralateral optic nerve also excited or inhibited some of the 134 SCN units examined (Fig. 1B and Table 1). Percentages of the units which were excited and inhibited by stimulation of the optic nerve were not significantly different between the rats with transection of the optic tracts and the intact control rats ($P > 0.5$, χ^2-test). Latency of these responses were similar to the responses observed in the rats with the transected optic tract.

B. Converging Inputs from the Contralateral and Ipsilateral Optic Nerves

As shown in Table 1, ipsilateral as well as contralateral stimulation of the optic nerve with single pulses also evoked transitory responses in a few number of the SCN units examined. So, the possibility arises that the same single SCN neurone may receive converging neural inputs both from the contralateral and the ipsilateral optic nerves. Of the 25 SCN units which responded to contralateral stimulation of the optic nerve with triple pulses 7 were also tested for ipsilateral stimulation. Ipsilateral stimulation of the optic nerve with triple pulses excited one of the 2 units which were excited by contralateral stimulation (Fig. 2A). Two of the 5 units which were inhibited by contralateral stimulation were also inhibited by the ipsilateral stimulation (Fig. 2B). The other one of the 5 units was excited by the ipsilateral stimulation. These results clearly indicate that some of the SCN neurones receive visual inputs from both eyes.

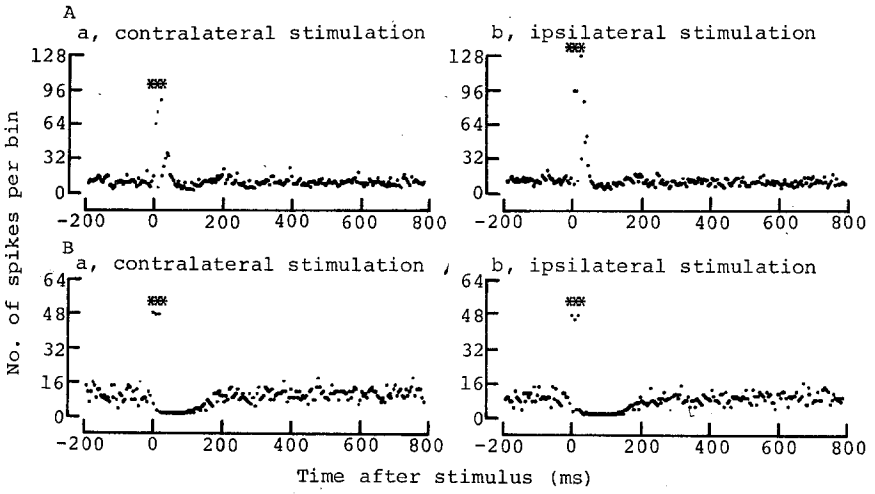

Fig. 2A and B. SCN neurones receiving visual inputs from both of the contralateral and the ipsilateral optic nerve. An example of SCN units which shows an excitation (**A**) and an inhibition (**B**) after each of contralateral and ipsilateral electrical stimulations

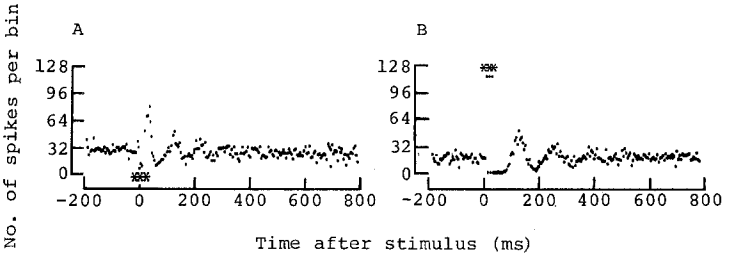

Fig. 3A and B. Oscillatory responses evoked in SCN neurones by electrical stimulation of the contralateral optic nerve. (**A**) an example of the units which showed oscillation of spontaneous unit activity with an initial excitation after the stimulation. (**B**) an oscillatory response with an initial inhibition after the stimulation. This post-stimulus time histogram was obtained in the rat with transection of the optic tracts

C. Effects on Mean Firing Rates

In 62 of the 80 SCN units which showed no transitory response after single pulse stimulation of the ipsilateral optic nerve (Table 1) and in 56 of the 68 units which were unresponsive to contralateral stimulation with single pulses, mean firing rates were estimated with and without stimulation. Mean firing rates were significantly increased in 15 and decreased in 8 of the 62 SCN units tested during the ipsilateral stimulation ($P < 0.01$). The contralateral stimulation also significantly increased the mean firing rates in 9 and decreased in 5 of the 56 SCN units tested ($P < 0.01$).

D. Oscillatory Responses

Oscillatory responses were observed in 8 units after repetitive three pulses applied to the contralateral optic nerve in rats with the intact optic tracts (Figs. 3A and 6Aa). These oscillatory changes of firing rates followed an initial excitation. In rats with the transected optic tracts 2 of the 19 responding units also showed oscillatory responses. One of them showed an initial inhibition (Fig. 3B) and the other one exhibited an initial excitation. Period of the oscillation was from about 100 to 200 ms. These results show that the oscillation of firing rates is mediated by the direct retino-hypothalamic pathway.

II. Flash Stimulation of the Eye

Electroretinograms were recorded in 6 rats. As shown in Fig. 5A, the wavelets superimposed on a large positive b-wave were evoked by the flash when light intensity was stronger than that obtained with the use of 8 or 9 sheets of the ND filter. So, 6 or 7 sheets of the ND filter were used in the following experiments.

A. Evoked Responses

Single flashes applied to the ipsilateral eye in the dark either excited or inhibited some of the SCN units tested as shown in Fig. 4 and Table 1. Latency of the responses estimated from the post-stimulus time histogram with resolution of 5-ms time bin was 50–90 ms for the excitation and 100–105 ms for the inhibition. Duration of these responses ranged from 50 ms to 450 ms.

B. Effects of Stimulus Intensity

The same single SCN units and electroretinograms were tested for flashes of various intensities. The wavelets of electroretinograms (Fig. 5A) were evoked by the flash stimuli with relatively stronger intensity. On the other hand, latency and duration of the response induced in SCN units were remarkably constant in one excited and the other one inhibited units, irrespective of the number of ND filter within the range from 2 to 17 sheets tested (Fig. 5B).

C. Effects on Mean Firing Rates

Effects of the flash stimulation on mean firing rates were investigated in the units which did not show a transitory response to the flash. Single flash stimuli applied to the ipsilateral eye significantly elevated mean firing rates in 3 and depressed in the other 2 of the 19 SCN units examined ($P < 0.01$). The present results show that flash stimuli given to the eye produce transient excitation or inhibition in particular SCN units and an increase or a decrease of mean firing rates in some other SCN units.

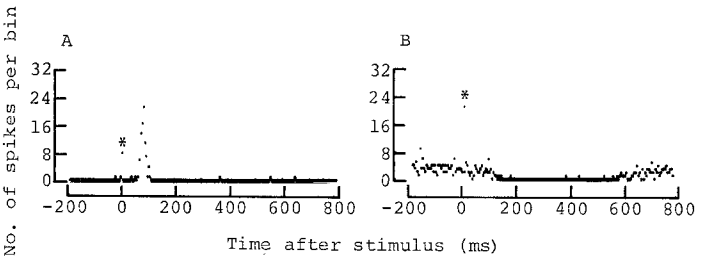

Fig. 4A and B. Excitation and inhibition evoked in SCN neurones by single flashes applied to the ispilateral eye. **(A)** an example of the SCN units which showed an excitation during post-stimulus period. **(B)** an example of the SCN units which showed an inhibition

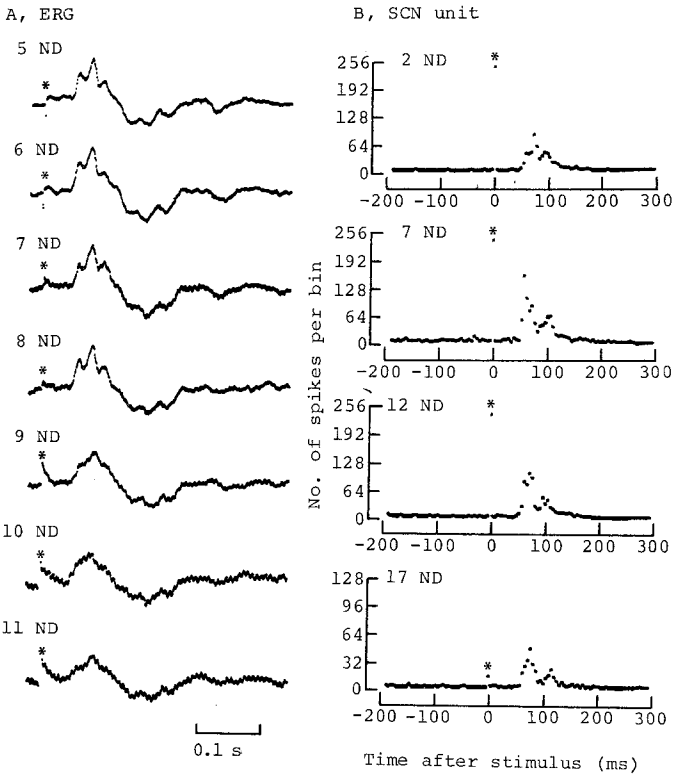

Fig. 5A and B. Effects of intensity of flash stimuli on electroretinogram (ERG, **A**) and spontaneous unit activity of a SCN neurone (**B**). **A** ERG's recorded with various intensity of the flash. The number of sheets of the neutral density (ND) filter of a factor of 0.5 used is indicated above each ERG record. Note that the wavelets superposed on a large positive wave were produced by the flash when 8 or less number of sheets of the ND filter were used. Fifty responses were summated in each ERG record by a digital computer. Selected bandpass was 10 Hz–3 kHz (–3 dB). Upward deflexion indicates positivity in each record. Voltage calibration was not made. **B** post-stimulus time histograms obtained from a same single SCN unit. Latency and duration of transitory excitation evoked by the flash appear to be constant within the range from 2 to 17 sheets of the ND filter. Each post-stimulus time histogram was obtained from 500 computations except for that of 17 ND which shows the result of 250 computations. Data of the initial 100 bins are displayed

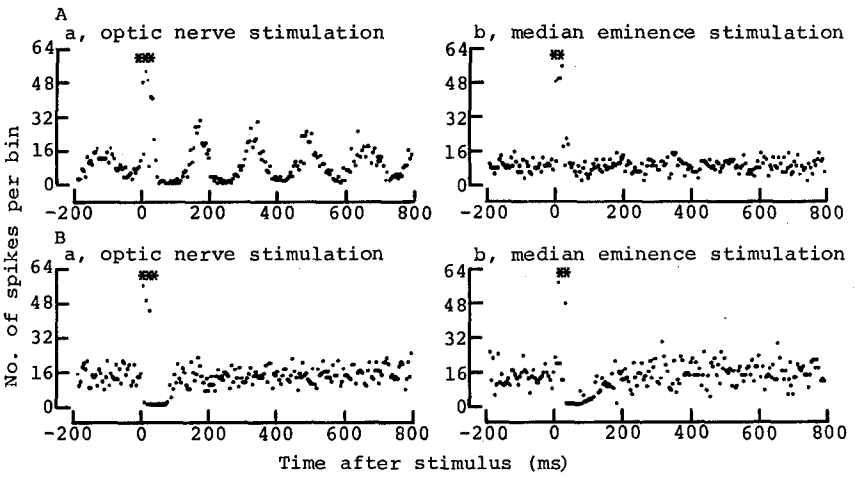

Fig. 6A and B. SCN neurones receiving neural inputs through axon collaterals of tuberoinfundibular neurones as well as the retino-hypothalamic pathway. **A** an example of the units which were excited by stimulations of the contralateral optic nerve and of the median eminence. Both stimulations were made by triple pulses. **B** an example of the units which were inhibited by either of these stimulations

Table 2. Effects of stimulation of the median eminence on spontaneous activity of the SCN units which had been previously tested for stimulation of the contralateral optic nerve with triple pulses

Response to stimulation of the optic nerve	Number of units excited	inhibited	unresponsive
Excitation	1	0	9
Inhibition	2	6	9
No response	6	23	30

III. Electrical Stimulation of the Median Eminence

A. Antidromic Invasion

Fifty-two of the 57 SCN units which showed transitory responses to electrical or photic stimulation and all of the 42 units which significantly changed mean firing rates during the stimulation without a transitory response were also tested for stimulation of the median eminence. Five of the 52 SCN units and 5 of the 42 units were antidromically identified as tuberoinfundibular neurones.

B. Orthodromic Responses

In some of the SCN units which were not activated antidromically by stimulation of the median eminence, post-stimulus time histograms were obtained for

determining whether those units show orthodromic response to the stimulation. Twenty-seven of the 44 units which responded to contralateral stimulation of the optic nerve with triple pulses (Table 1) and 59 of the 176 units which showed no transitory response to the stimulation were examined for triple pulse stimulation of the median eminence. Some of them were excited and some others were inhibited by stimulation of the median eminence (Fig. 6 and Table 2).

Discussion

The direct retino-hypothalamic projection has been shown morphologically to exist in rats by the methods of Nauta and Fink-Heimer (Sousa-Pinto and Castro-Correia, 1970; Moore et al., 1971; Moore and Lenn, 1972; Güldner, 1976), by the radioautographic method (Moore et al., 1971; Hendrickson et al., 1972; Moore and Lenn, 1972; Mai and Junger, 1977), by the iontophoresis-cobalt sulphide precipitation technique (Mason and Lincoln, 1975, 1976) and by the horseradish peroxidase method (Colman et al., 1976; Güldner and Wolff, 1978). In the previous work (Sawaki, 1977) it has been shown that single photic stimulation of the eye and single pulse stimulation of the optic nerve induce transient excitatory or inhibitory responses in certain SCN neurones during post-stimulus period. Lincoln et al. (1975) also have shown that retinal illumination which was applied in the darkness enhances spontaneous activity of certain SCN units in rats with the intact optic tract. Nishino et al. (1976) have demonstrated that photic stimulation of the retina and electrical stimulation of the optic nerve elevate or depress transiently the spontaneous activity level of some SCN neurones in rats with the intact optic tract. These responses, however, might have been mediated by the neural pathway involving the LGNv rather than the direct retino-hypothalamic projection, since radioautographic studies have shown that LGNv neurones project to the SCN (Swanson et al., 1974; Ribak and Peters, 1975). Concerning this possibility the present results clearly demonstrated that electrical stimulation of the optic nerve could evoke excitation and inhibition in SCN neurones even after the optic tracts had been completely transected.

The percentages of the SCN units which were either excited or inhibited by stimulation of the optic nerve were similar in rats with bilateral transection of the optic tracts to those in control rats. So, it seems reasonable to conclude that the direct retino-hypothalamic projection is the main neural pathway mediating excitation and inhibition in SCN neurones. Recently, it has been shown that visual stimuli can produce excitation and inhibition in SCN units even after lesions of the LGNv, though a large part of the responses are abolished by the lesions (Groos and Mason, 1978).

Electrical stimuli applied to the optic nerve evoked an orthodromic excitation and an inhibition with relatively short latency in certain SCN units. It has been demonstrated that optic nerve fibres innervating the SCN terminate with the asymmetrical "Gray-type I" synapses in rats (Moore and Lenn, 1972; Güldner, 1976; Güldner and Wolff, 1978) and in monkeys (Hendrickson et al.,

1972). The asymmetrical synapses of "Gray-type I" have been shown to exist in the lateral geniculate body and to originate from optic nerve fibres (Szentágothai, 1963), and they have been electrophysiologically proved to be excitatory in nature (Singer and Creutzfeldt, 1970). Recently, the symmetrical synapses of "Gray-type II" also have been shown to exist in the SCN (Güldner and Wolff, 1978). The "Gray-type II" synapses have been electrophysiologically demonstrated to be inhibitory in nature in the olfactory bulb (Rall et al., 1966). It is, therefore, highly probably that the primary synaptic inputs from retinal ganglion cells mediate both excitation and inhibition in SCN neurones.

In the present results it was found that photic stimuli with rather weak intensity which were insufficient for evoking the wavelets in electroretinograms, could produce the transitory response in certain SCN neurones. It has been shown that wavelets of electroretinogram as illustrated in Fig. 5A can be evoked in response to high-intensity flashes (Brown, 1969) and that the wavelets are associated with colour vision in man (Babel et al., 1977). Evidence for the two receptor mechanisms, a classical rod and another different mechanism, has been shown in the rat retina (Green, 1971). So it seems likely that the responses induced in SCN neurones by the flashes are attributed to an activation of the scotopic system of the retina.

The present results demonstrated that stimulation of the optic nerve sometimes evokes an oscillatory response of spontaneous activity in certain SCN neurones. Our previous studies (Yagi and Sawaki, 1975; Sawaki and Yagi, 1976) have shown that stimulation of the median eminence evokes the similar oscillatory responses in antidromically identified tuberoinfundibular neurones of the arcuate nucleus of the hypothalamus and a reverberating neural circuit model has been proposed for mediation of the oscillatory response (Yagi and Sawaki, 1978). The period of oscillation observed in SCN neurones is comparable to that reported for tuberoinfundibular neurones. The present results further demonstrated that some of the SCN neurones which receive visual inputs are tuberoinfundibular neurones and some other of them receive neural inputs from neural pathways involving axon collaterals of tuberoinfundibular neurones as well as the optic nerve. It is, therefore, likely that the oscillatory response evoked in the SCN neurones by stimulation of the optic nerve may be due to an activation of a possible reverberating neural circuit which involves both SCN neurones and tuberoinfundibular neurones. Within the other structure of the brain a reverberating neural circuit has been demonstrated to exist between neurones in the nucleus interpositus of the cerebellum and the nucleus reticularis tegmenti pontis (Tsukahara et al., 1973).

Certain SCN neurones which receive visual inputs were antidromically identified as tuberoinfundibular neurones. This result indicates that visual inputs directly modify the outputs of some of the tuberoinfundibular neurones controlling adenohypophysial functions. The present results also demonstrated that certain SCN neurones receive converging neural inputs both from the direct retino-hypothalamic pathway and from the neural pathway involving axon collaterals of tuberoinfundibular neurones. It appears that the converging neural circuits may serve as modification of visual inputs to SCN neurones by tuberoinfundibular neurones.

Acknowledgements. The author thanks Prof. Kinji Yagi for helpful advice and encouragement throughout this work, and Prof. Masao Ito for critical reading of the manuscript. This work was supported by grants 177055 and 977023 from the Ministry of Education, Science and Culture, Japan.

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Received January 31, 1979