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Effects of Pinealectomy on Circadian Locomotor Activity Rhythms in European Starlings, *Sturnus vulgaris*

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Summary. Removal of the pineal organ from starlings had drastic effects on their freerunning circadian activity rhythms; in birds kept in continuous darkness the period (τ) shortened and the activity time (α) lengthened. Concomitantly both τ and α became relatively unstable and the separation between activity and rest time was obscured. In a few birds activity became continuous and apparently arrhythmic. The activity rhythms of the birds were entrainable to a 12:12 h light-dark cycle.

These results differ from those obtained previously by Menaker and his co-workers on the house sparrow, in which pinealectomy always resulted in arrhythmia. Nevertheless, it is suggested that the differences between these two species are only quantitative in nature rather than an expression of a qualitative difference in the organization of the circadian system. The results are consistent with the following modification of the model developed for the house sparrow: The avian pineal is the seat of a self-sustaining circadian pacemaker that acts on a population of secondary self-sustaining oscillators. These secondary oscillators, located outside the pineal, are only weakly coupled to each other but strongly dependent on the pineal driver. Their net circadian period is shorter than that of the pineal driver but, like the pineal driver, they can be synchronized by light. – It is proposed that this model fits both the starling and the sparrow data and clarifies some previously unexplained results.

1. Introduction

Recent investigations of Menaker and his coworkers have shown that the pineal organ plays an important role in the control of circadian rhythms in the house sparrow (*Passer domesticus*). If sparrows that are held in constant darkness are pinealectomized, their free-running rhythms of locomotor activity and body temperature are abolished. Rhythmicity is restored, however, when the pineal of another sparrow is transplanted into the anterior chamber of the eye; the induced rhythm emerges with the phase of the donor. These and several other observations have led to the hypothesis that the pineal is the seat of a circadian master oscillator controlling overt rhythms, and that the information about circadian time is chemically transmitted from the pineal to the subordinate system (Gaston and Menaker, 1968; Gaston, 1971; Binkley et al., 1971, 1972; Zimmerman and Menaker, 1975; Menaker and Zimmerman, 1976; Zimmerman, 1976).

Although pinealectomy has been reported to have similar effects on free-running activity rhythms in two other species of fringillid birds (Gaston, 1971; McMillan, 1972), recent preliminary investigations on the starling have yielded results that are inconsistent therewith. Surgical removal of the pineal in this species did not (Rutledge and Angle, 1977) or only occasionally (Gwinner, 1977) lead to arrhythmicity in constant darkness. However, whereas Gwinner observed significant changes in the pattern of locomotor activity after pinealectomy, Rutledge and Angle concluded from their results from 10 starlings that pinealectomy has no effects at all on circadian locomotor activity rhythms. In view of these discrepancies between results obtained from sparrows and starlings on the one hand, and from two independent studies of the starling on the other, it seemed desirable to reinvestigate the effects of pinealectomy in starlings in more detail. This communication reports results that, indeed, indicate differences in pineal involvement in the control of circadian activity rhythms in sparrows and starlings. However, it is proposed that these differences are only quantitative in nature, rather than the result of fundamental qualitative differences in the organization of the circadian system.

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2. Methods

European starlings were captured in winter near Mannheim, Germany, and subsequently kept in large outdoor aviaries for at least 1 month. During the experiments the birds were individually housed in registration cages inside soundproof and temperature regulated chambers. They were provided with food (chick starter mash) and water ad libitum. The perch-hopping activity of each bird was recorded by microswitches mounted under one of the two perches. The impulses were stored on magnetic tape. From these, computer plots of the daily distribution of activity were made (for details see Daan, 1976). For quantitative evaluation of the data an estimate of the circadian period (τ) and the circadian activity time (α) was made for all successive 4-week intervals. τ was determined to the nearest tenth of an hour by eye-fitting a straight line through the onset of activity for each 4-week segment. Similarly, α was estimated to the nearest half hour by measuring the interval between an eye-fitted line connecting the onsets and another one connecting the ends of activity. Especially in the pinealectomized birds, the estimation of α was difficult and the values given must be considered as rough estimates. If activity was continuous, α was given the value of 24 h. If no circadian rhythmicity was detectable by visual inspection, the activity pattern was designated "arrhythmic". It should be mentioned, however, that in some of these records a residual rhythmicity might have been detectable by power spectral analysis.

Pinealectomy was performed in the following manner: After the bird had been anesthesized with Ketanest its head was fixed in a stereotactic head holder. The skin on the dorsal surface of the head was cut sagittally in the occipital region and pulled to both sides. A piece of skull above the pineal was removed and three cuts were made into the meninges, one over each hemisphere and one over the cerebellum. Then the sagittal and transverse sinuses were cut and the pineal was carefully removed with a pair of fine mouse toothed forceps. The skull piece was then replaced and the skin sutured (Sham-operations were done in the same manner including the cutting of at least one sinus, but the pineal was left in its position). During surgical procedures the birds were exposed to bright light for about 1 h.

In most pinealectomies the chorioid plexus was still attached to the pineal stalk when the organ was removed. When it was suspected that parts of the stalk might not have been removed the birds were not used for the experiment. Some of the pineals were fixed in Bouin's solution and later stained with Carmine red. At the end of the experiment the birds were sacrificed. Their brains were fixed in Bouin's solution, and subsequently prepared for histological examination (10 µm, sagittal sections, hematoxylin and eosin stain). In most preparations, no traces of pineal tissue could be detected. Only in a few instances parenchymal proliferations were found for which a possible pineal origin could not be excluded with certainty. However, because the results obtained from these birds were not different from those of the others, they were included in the present analysis.

3 experiments were conducted. In *Experiment 1,* 24 female starlings were used. The birds were moved to one of two experimental chambers on May 21, 1975 and exposed to a 12:12 h light-dark cycle (LD 12:12, 200:0.05 Lux) where they were visually isolated from each other. To reduce mutual acoustical interactions a background noise of about 70 dB, produced by a noise generator, was played into the chambers. On June 12, the light-dark cycle was discontinued and the birds were subsequently kept in complete darkness (DD) until October 2. Between July 10 and 12, 16 birds were pinealectomized and 8 sham-operated.

A laparotomy was performed before the transfer to DD. It indicated that the ovaries had regressed in most birds. By that time the majority of birds had begun to molt. Bill coloration was in the process of changing from yellow to black; it remained black throughout the experiment suggesting that the ovaries were in an inactive state (Witschi and Miller, 1938; Gwinner, 1975a).

In *Experiment 2,* 10 female birds were moved on May 5, 1976 into the same chambers as the birds in experiment 1, and exposed to an 8:16 h light-dark cycle (LD 8:16, 200:0.05 lux). Conditions were as in experiment 1 except that no background noise was played into the chambers. From May 21 to the end of September the birds were exposed to DD. On July 1 and 2, 5 birds were pinealectomized and 5 sham-operated. A laparotomy was simultaneously performed which indicated slightly enlarged ovaries with largest oocytes ranging from 1.0 to 2.7 mm in diameter.

The birds were later exposed for 16 days to a 12:12h light-dark cycle (LD 12:12, 200:0.05 lux) with interposed dawn and dusk periods of 25 min. Their locomotor activity patterns under these conditions were compared with those obtained during the preceding and subsequent DD exposure.

In *Experiment 3,* 5 male birds were maintained completely isolated from each other in individual soundproof and temperature controlled boxes. For two of these birds the experiment started on October 13, 1975. They were exposed for two days to constant bright light and subsequently for 17 weeks to DD. They were castrated on October 26, and pinealectomized on December 10. – For the other three birds the experiment began on July 2, 1976. They were maintained for 5 days in constant light and subsequently for 32 weeks in DD. These birds were pinealectomized on November 26. At the beginning of the experiment all three birds were molting. The testes of these 3 birds remained inactive throughout the experiment as judged from bill coloration.

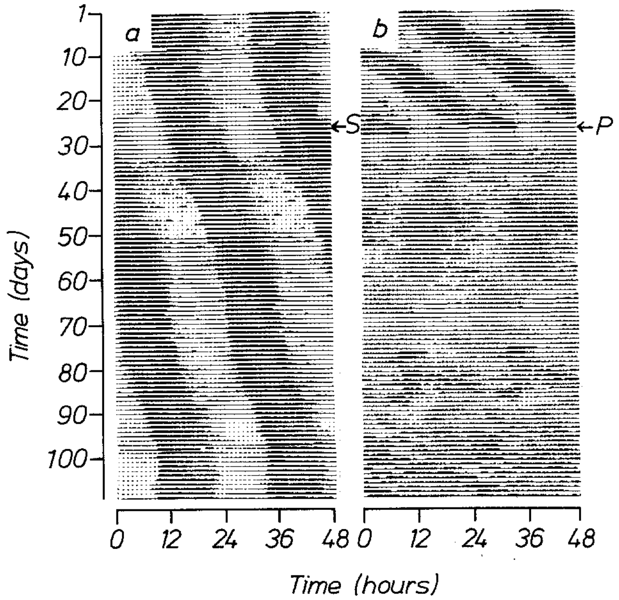

Fig. 1a and b. Activity recordings of 2 starlings from experiment 1 kept in DD. Each horizontal line from hour 0 to 24 represents the activity record of one day. Records of successive days are mounted underneath each other. To facilitate inspection of the data the records have been double-plotted on a 48-h time scale. Vertical marks indicate activity within any 1 min time interval. During times of intense activity the marks fuse into a black block. **a** Record of a bird that was sham operated (*S*). **b** Record of a bird that was pinealectomized (*P*) on the day indicated by the arrow

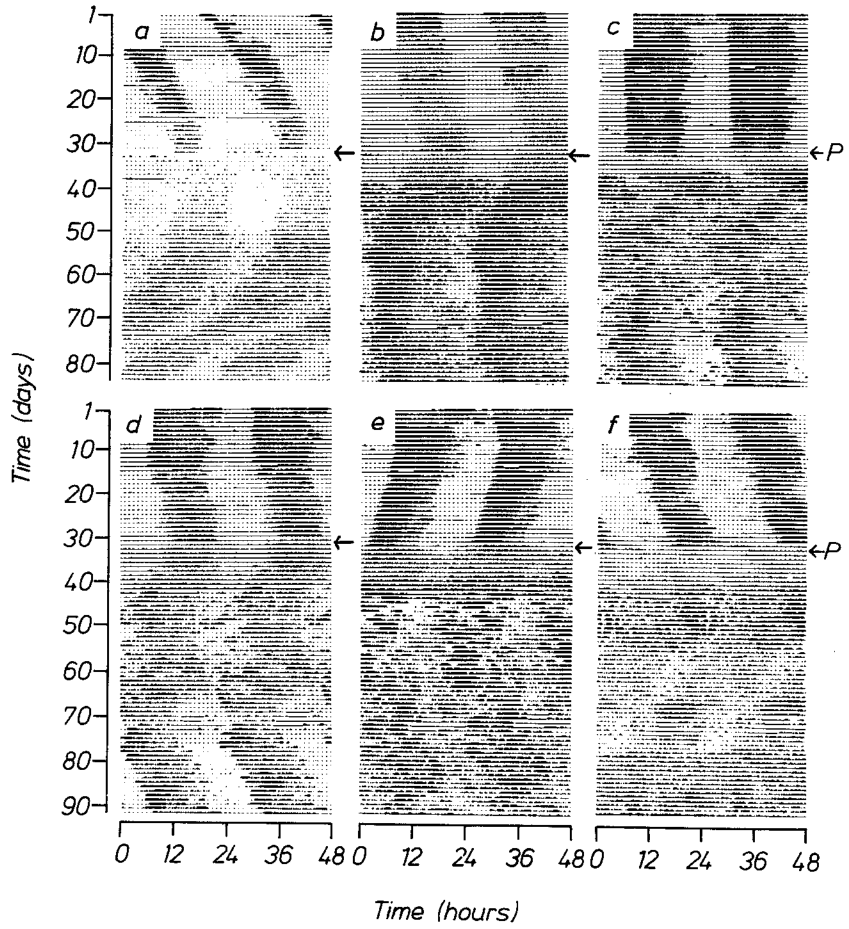

Fig. 2a–f. Activity recordings of 6 starlings from experiments 1 (**b–f**) and 3 (**a**) maintained in DD. The birds have been pinealectomized (P) on the days indicated. For further explanations see Figure 1

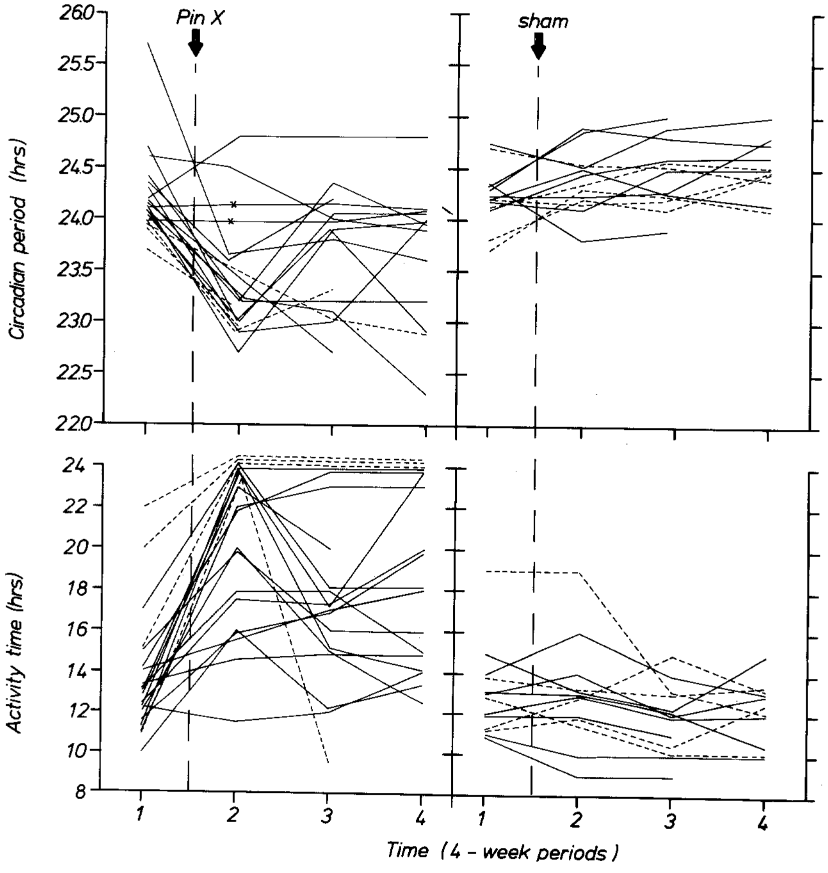

Fig. 3. Changes in τ (upper two diagrams) and α (lower two diagrams) of the pinealectomized (left) and sham operated (right) birds of experiments 1 and 2. Each curve connects the 4-weekly estimates of τ and α for the individual birds that did not become permanently arrhythmic in experiment 1 (solid lines) and 2 (dashed lines). X indicate that no τ value could be estimated during that interval because the bird's activity was apparently arrhythmic

3. Results

A. Effects of Sham Operations in DD

The activity recording of a control starling is shown in Figure 1a. It can be seen that the sham operation had no major effects on the free-running circadian activity rhythm. Activity time and rest time are clearly separated from each other and the rhythm persisted with high precision and with a period τ slightly longer than 24 h throughout the experiment. This recording is typical for all sham-operated birds. Figure 3 (right) summarizes the temporal course of both τ and α of all individual sham-operated birds in Experiments 1 and 2. Apart from a slight tendency for τ to increase in the course of the experiment (which is typical for starlings under such conditions; Gwinner, 1975b), no systematic changes of either τ or α could be observed. The comparison of values from the 4 week interval before (τ_1) and after (τ_2) the operation reveals that τ_2 was longer than τ_1 in 7 birds and shorter in 5 birds (with no change occurring in 1 bird). A corresponding comparison of α_1 and α_2 indicated longer α_1 values in 5 birds and shorter ones in 5 other birds (with no change in α in 3 birds). This confirms the impression from Figure 1 that sham operations have no effects on these two parameters of the circadian activity rhythm.

B. Effects of Pinealectomy in DD

Of the 26 pinealectomized birds, only 3 (2 in Experiment 1, 1 in Experiment 2) became permanently arrhythmic. In 6 others arrhythmicity was observed in at least one 4-week interval (3 in Experiment 1, 2 in Experiment 2, 1 in Experiment 3). Examples of possible, temporarily arrhythmic activity patterns are shown in Figure 2e, f.

In all the other pinealectomized birds rhythmicity persisted throughout the experiment. However, the activity rhythms of these birds were clearly affected by pinealectomy in at least 4 respects:

(1) In most pinealectomized birds, τ became shorter after pinealectomy. This can be seen in Figures 1b and 2a, b, c, d, f, as well as in the summary diagram of Figure 3 (left) for all birds of Experiments 1 and 2. Comparison of τ for individual birds 4 weeks before (τ_1) and after (τ_2) pinealectomy revealed that τ_2 was shorter than τ_1 in 14 birds and longer in 1 bird ($p<0.001$, Wilcoxon test for pair differences; experiment 3: τ_2 shorter than τ_1 in 3 birds, longer in 1 bird). Even though in several birds τ became longer again later in the experiment, it remained on the average shorter than before. Compared with the sham-operated birds, the τ_s of the pinealectomized birds were significantly shorter at each of the three 4-week intervals following pinealectomy ($p<0.01$, Mann Whitney's U test).

(2) In most pinealectomized birds α became longer after pinealectomy. This is apparent from all recordings in Figures 1 and 2, and from the summary diagram, Figure 3 (left) for all the birds of experiments 1 and 2; α_2 was longer than α_1 in 20 birds and shorter in 1 bird ($p<0.001$; experiment 3: α_2 longer than α_1 in all 5 birds). Compared with the sham-operated controls, the α_s of the pinealectomized birds were significantly longer at each of the three 4-week intervals following pinealectomy ($p<0.01$).

(3) After pinealectomy, both τ and α were often subject to rather sudden changes (e.g., Fig. 2b, d). This lead to the very irregular picture in the summary-

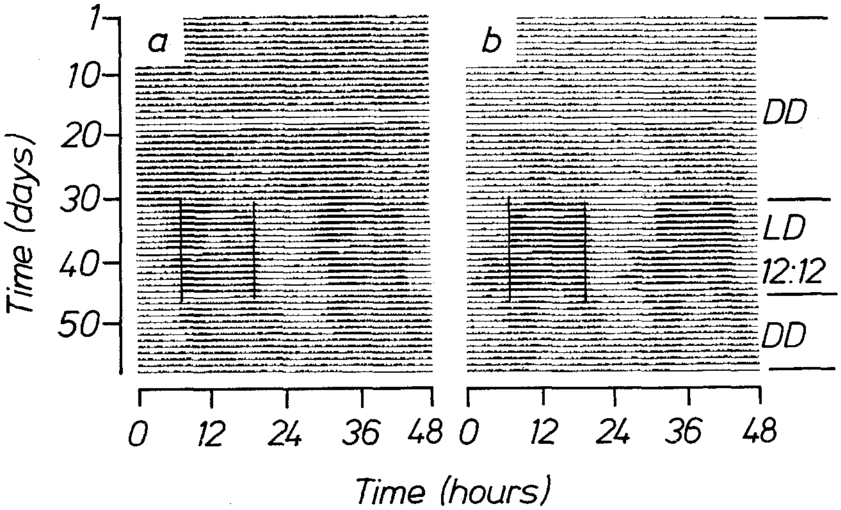

Fig. 4. Activity recordings of two pinealectomized starlings from experiment 2 kept in DD from day 1 to 31 and from day 47 to 58, and exposed to an LD 12:12 h light-dark cycle from day 31–46. The daily times of lights on (7 AM) and lights off (7 PM) are connected by vertical lines in the left-hand part of the records. For further explanation see Figure 1

diagram of Figure 3. Since these changes in τ and α were rather dramatic in both directions, the overall range of τ and α of the pinealectomized birds was considerably larger than in the controls.

(4) In most birds the separation between activity and rest time became less clear after the pineal had been removed. This was due mainly to continuous activity at a low level during "rest-time". Moreover, it seems that there was more day-to-day variability in the successive onsets and ends of the main activity period (Fig. 1, 2).

C. Pinealectomized Birds in LD 12:12

The pinealectomized birds – like the controls – entrained to the 12:12 h light-dark cycle. This was true even for birds whose activity was continuous and only residually rhythmic during the previous DD treatment (Fig. 4). Striking differences in the behavior of the control and experimental birds were not apparent. However, in view of the limited number of birds tested under these conditions, this negative statement should be taken with reservation.

4. Discussion

The results presented here are consistent with those from previous investigations on the starling in that they indicate that a circadian rhythmicity of locomotor activity persists in most pinealectomized birds maintained under constant environmental conditions (Gwinner, 1977; Rugledge and Angle, 1977). This was true for birds of both sexes, for birds with active and inactive gonads, and for castrated birds. Moreover, a continuing circadian rhythmicity was observed in starlings kept together in the experimental chambers as well as in birds completely isolated from each other.

However, while a circadian rhythmicity persisted in most pinealectomized starlings, its pattern was drastically affected. The most obvious effect was that of a general loss of stability and an increased "sloppiness" of the rhythm. This became aparent in (a) the tendency of both the circadian period (τ) and the circadian activity time (α) to undergo sudden and spontaneous changes; (b) the increase in the total range of τ_s and α_s; (c) the loss of a clear separation between activity and rest time; and (d) the increased scatter in onset and end of the main activity period. In addition τ was shortened and α lengthened after pinealectomy. That Rutledge and Angle (1977), apparently, did not see these effects and, hence, concluded "that pinealectomy does not alter circadian perchhopping activity rhythms to any significant extent in this species" is not surprising. In their experiment neither the behavior of control birds nor the activity rhythms of pinealectomized birds compared with their own pre-operative performance were investigated.

In contrast to the starling, the circadian activity rhythm of the house sparrow in DD was abolished after pinealectomy (Gaston and Menaker, 1968). The same was true for two other species of passerine birds (Gaston, 1971; McMillan, 1972). The question arises then whether these differential effects of pinealectomy reflect fundamental differences in the organization of the circadian system in these species. To answer this question, some of the results obtained from house sparrows and the model derived from them (Menaker and Zimmerman, 1976) must be briefly discussed. Three sets of findings are of significance:

(1) When a pineal gland is implanted into the anterior chamber of the eye of a pinealectomized, arrhythmic sparrow, the circadian rhythmicity is resumed (Zimmerman and Menaker, 1975). The phase of the reestablished rhythm closely corresponds to the phase of the rhythm of the donor birds (Zimmerman, 1976). This indicates that the pineal is the seat of a self-sustaining oscillator ("D" in Fig. 5a). It is likely that this pineal driver transmits its circadian information chemically to the subordinate system ("C" in Fig. 5a). (2) Even in the pinealectomized house sparrow a residual rhythmicity is retained. This is demonstrated, for instance, by the observation that pinealectomized sparrows still entrain to a light-dark cycle with activity onsets preceding lights on. If such birds are then transferred to DD they do not immediately become arrhythmic; rather it takes some cycles before the rhythms have faded away (Gaston and Menaker, 1968). These findings have been taken to suggest that the pineal driver acts on a damped oscillator ("d" in Fig. 5a) by which locomotor activity is directly controlled. (3) Locomotor activity of intact and pinealectomized sparrows entrains to 24-h light dark cycles with different phase angles. This suggests that both the driving and the driven oscillator can be separately affected by light (Gaston, 1971).

While the model of Figure 5a accommodates the empirical data obtained from house sparrows – and, indeed, is almost certainly correct as far as the assumptions about "D" are concerned – it obviously does not accommodate the results obtained from starlings which show that after pinealectomy a rhythmicity is retained. This might indicate that, in contrast to the house sparrow, the starlings's pineal does not contain a circadian pacemaker but rather affects the circadian system in a more unspecific way. This seems possible in view of the fact that the pineal has many

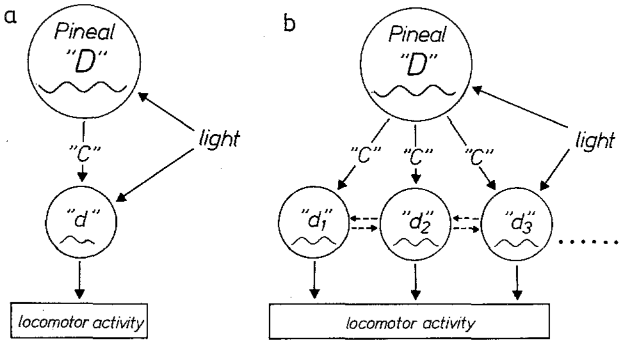

Fig. 5. a The Menaker-Zimmerman model of the circadian system controlling the locomotor activity rhythm in the house sparrow. The self sustaining circadian oscillator "D" in the pineal drives a damped oscillator "d" located outside the pineal by its rhythmic output "C"; "d" in turn controls locomotor activity. Both "D" and "d" have access to light. **b** Modification of this model to explain both the results obtained from house sparrows and starlings. In this version "D" drives a whole population of "d" oscillators, which are all self-sustaining and weakly coupled to each other. "D" and at least one of the "d" oscillators have access to light

different functions in various groups of vertebrates (e.g. Wurtman et al., 1968) and is most probably not a central circadian pacemaker in the rat (Richter, 1967). Nevertheless, it seems more likely that the differences in the behavior of pinealectomized sparrows and starlings are not due to such qualitative differences in the location and/or organization of the pacemaker but rather to quantitative differences in the organization of the driven system. I propose to modify the Menaker-Zimmerman model in the manner shown in Figure 5b. This modified model differs from its original version in that the driven system controlling activity, does not consist of one oscillator which is damped, but rather of two or more oscillators which are all self-sustaining. They are weakly coupled to each other but strongly dependent on the pineal driver. They can, as a whole, be synchronized by light. As long as they are synchronized with each other their net natural period τ_{nd} is shorter than that of the pineal driver (τ_{nD}) and their mutual phase relationship is such that α is longer than in the intact bird. If the pineal driver is removed one of two things can happen:

(1) Coupling among the "d" oscillators is too weak to keep them synchronized with each other. As a result each oscillator will freerun with its own natural frequency resulting eventually in a damping of the overt function.

(2) Coupling among the "d"-oscillators is sufficiently strong to keep them synchronized with each other. Because the net natural period τ_{nd} of the mutually entrained oscillators is shorter than the natural period τ_{nD} of the pineal driver, the system will freerun with a period shorter than that of the intact bird. Moreover, because of the weakness in mutual coupling such a system can be expected to be unstable and subject to external disturbances.

This modified model has the advantage that it rationalizes the data from both the house sparrow and the starling. The first alternative accounts for the behavior of all pinealectomized house sparrows and of those pinealectomized starlings that became arrhythmic after pinealectomy. The second alternative accounts for the behavior of those starlings in which pinealectomy did not result in permanent arrhythmia. Hence, if this model applies the differences found between the behavior of pinealectomized starlings and sparrows would be due only to quantitative differences in the coupling strength between the "d" oscillators.

Additional observations support this modified hypothesis. For instance, there is now good evidence that more than one circadian oscillator is involved in the control of locomotor activity rhythms in birds. This is strongly suggested by the phenomenon of "splitting" which has been observed in mammals as well as in birds (Pittendrigh, 1960; Hoffmann, 1971; Gwinner, 1974). Moreover entrained circadian activity rhythms behave in many respects like systems of at least two oscillators one of which being coupled to dawn, the other one to dusk (Pittendrigh and Daan, 1976).

More direct support for the above hypothesis comes from the behavior of activity rhythms of pinealectomized birds. Gaston (1971) observed that in sparrows entrained to a 24 h light-dark cycle, α became longer and the phase-angle difference between the locomotor activity rhythm and the light-dark cycle became more positive after pinealectomy. Since the latter would be expected when the natural period shortens (Aschoff, 1965) the behavior is consistent with the prediction that τ_{nd} is shorter than τ_{nD} which determines the period of the overt rhythm in the intact bird.

Finally, recent results on the effects of melatonin on circadian activity rhythms of house sparrows must be considered in the present context. Turek et al. (1976) found that continuous administration of melatonin via intraperitoneally implanted silastic capsules either shortened τ or induced continuous and apparently arrhythmic activity. Hence these melatonin treated sparrows behaved like the pinealectomized starlings in the present experiments. Melatonin is one of the leading candidates for the postulated transmitter of circadian information from the pineal to the subordinate system; its synthesis and secretion from the pineal is known to follow a pronounced circadian pattern (e.g. Pelham, 1975; Binkley, 1976). If one assumes that administration of melatonin by silastic implants (probably resulting in continuous and high melatonin levels) obscures or suppresses the endogenous melatonin rhythm, such birds should indeed behave like birds whose pineal has been removed.

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References

Aschoff, J.: The phase-angle difference in circadian periodicity. In: Circadian clocks (ed. J. Aschoff), pp. 262–276. Amsterdam: North Holland Publ. Co. 1965

Binkley, S.: Comparative biochemistry of the pineal glands of birds and mammals. Amer. Zool. **16**, 57–65 (1976)

Binkley, S., Kluth, E., Menaker, M.: Pineal function in sparrows: circadian rhythms and body temperature. Science **174**, 311–314 (1971)

Binkley, S., Kluth, E., Menaker, M.: Pineal and locomotor activity: levels and arrhythmia in sparrows. J. comp. Physiol. **77**, 163–169 (1972)

Daan, S.: Light intensity and the timing of daily activity of finches (Fringillidae). Ibis **118**, 223–236 (1976)

Gaston, S.: The influence of the pineal organ on the circadian activity rhythm in birds. In: Biochronometry (ed. M. Menaker), pp. 541–549. Washington, D.C.: Nat. Acad. Sci. 1971

Gaston, S., Menaker, M.: Pineal function: the biological clock in the sparrow? Science **160**, 1125–1127 (1968)

Gwinner, E.: Testosterone induces "splitting" of circadian locomotor activity rhythms in birds. Science **185**, 72–74 (1974)

Gwinner, E.: Die circannuale Periodik der Fortpflanzungsaktivität beim Star (*Sturnus vulgaris*) unter dem Einfluß gleich- und andersgeschlechtiger Artgenossen. Z. Tierpsychol. **38**, 34–43 (1975a)

Gwinner, E.: Effects of season and external testosterone on the freerunning circadian activity rhythm of European starlings (*Sturnus vulgaris*). J. comp. Physiol. **103**, 315–328 (1975b)

Gwinner, E.: Role of the pineal in the control of circadian and circannual rhythms in European starlings. Proceedings of the First International Symposium on Avian Endocrinology (ed. B.K. Follett), pp. 28–29. Bangor: University College of North Wales 1977

Hoffmann, K.: Splitting of the circadian rhythm as a function of light intensity. In: Biochronometry (ed. M. Menaker) pp. 134–148. Washington, D.C.: Nat. Acad. Sci. 1971

Menaker, M., Zimmerman, N.: Role of the pineal in the circadian system of birds. Amer. Zool. **16**, 45–55 (1976)

McMillan, J.: Pinealectomy abolishes the circadian rhythm of migratory restlessness. J. comp. Physiol. **79**, 105–112 (1972)

Pelham, R.W.: A serum melatonin rhythm in chickens and its abolition by pinealectomy. Endocrinology **96**, 543–546 (1975)

Pittendrigh, C.S.: Circadian rhythms and the circadian organization of living system. Cold Spr. Harb. Symp. quant. Biol. **25**, 159–184 (1960)

Pittendrigh, C.S., Daan, S.: A functional analysis of circadian pacemakers in nocturnal rodents. V. Pacemaker structure. A clock for all seasons. J. comp. Physiol. **106**, 333–355 (1976)

Richter, C.P.: Sleep and activity: their relation to the 24-h clock. Proc. Assoc. Res. Nerv. Ment. Dis. **45**, 8–29 (1967)

Rutledge, J.T., Angle, M.J.: Persistence of circadian activity rhythms in pinealectomized European starlings (*Sturnus vulgaris*). J. exp. Zool. **202**, 333–338 (1977)

Turek, F.W., McMillan, J.P., Menaker, M.: Melatonin: effects on the circadian locomotor rhythm of sparrows. Science **194**, 1441–1443 (1976)

Witschi, E., Miller, R.A.: Ambisexuality in the female starling. J. exp. Zool. **79**, 475–486 (1938)

Wurtman, R.J., Axelrod, J., Kelly, D.E.: The pineal. New York: Academic 1968

Zimmerman, N.: Organization within the circadian system of the house sparrow: hormonal coupling and the location of a circadian oscillator. Ph. D. Thesis, University of Texas, Texas 1976

Zimmerman, N., Menaker, M.: Neural connections of sparrow pineal: role in circadian control of activity. Science **190**, 477–479 (1975)