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Gonadotropic and Photosensitive Abilities of the *Lobus paraolfactorius*: Electrophysiological Study in Quail[1]

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Abstract. Spontaneous and flash-altered multiunit activity MUA was recorded from the *lobus paraolfactorius* of young male quail reared in either long or short daily photoperiods. The birds were subjected to testosterone administration, castration, optic nerve section or retroparaolfactory disconnection and compared to intact controls. In all experimental and intact quail, iterative flashes led to decreased paraolfactory MUA. Spontaneous firing rates were found to be significantly higher during the light than during the dark part of the photoperiods, indicating some direct effect of environmental lighting on the paraolfactory neuronal populations. However, blinded as well as paraolfactory disconnected animals failed to exhibit any difference in firing rates according to the daily short and long photoperiods as seen in controls, suggesting that the light regime might also indirectly influence the paraolfactory activity.

Extraretinal photoreceptors for photoinduced testicular response were demonstrated in the avian rhinencephalon. Shedding light directly on the rhinencephalon of ducks through a quartz rod strongly stimulated the gonads [6]. Implantation of solid radioluminous material (spheres of 0.8 mm in diameter) in the olfactory bulbs of quail induced testicular growth in more than 50% of the birds [13]. Placement of small discs of radioluminous material, bilaterally [27] or unilaterally [31], in the paraolfactory lobe of quail held in short daily periods led to significant increases in testicular weight and plasma testosterone level. However, retroparaolfactory disconnection prevented such a gonadal response to be elicited by local photic stimulation of the *lobus paraolfactorius* [27].

On the other hand, horseradish peroxidase injection in the gonadotropic region of the infundibular complex demonstrated neural afferents to this area, originating from the paraolfactory lobe [25].

It is known [for review: see ref. 24] that, in avian species, the light-induced gonadal growth may involve both superficial (retina) and deep (brain) receptors. Retinal information can be conveyed to the gonadotropic hypothalamus via optic fibers, preoptic-anterior hypothalamic and/or rostral dorsal thalamic relays and finally through neural projections to the infundibular complex. As to the mechanisms by which deep photoreception occurs, they are completely unknown. In an attempt to obtain some functional data about deep photoreceptors for gonadostimulation, we decided to investigate electrophysiologically the paraolfactory neuronal populations whose photostimulation resulted in increased gonadotropic activity.

Spontaneous and flash-altered multiple unit activity (MUA) was recorded from the *lobus paraolfactorius* in various environmental lighting conditions (daily photoperiods and phases in the photoperiod). The hypothetical influences of retinal information and of neural afferents from brain formations were studied by means of bilateral optic nerve section and retroparaolfactory disconnection, respectively. On the other hand, photoperiodic regimes markedly affect the gonadotropic axis, resulting in either resting or active testicular functioning. In turn, plasma testosterone levels could modify some functional characteristics of deep infundibular photoreceptors [19]. This eventuality was tested at the paraolfactory level after combination of testosterone administration and castration with short and long daily photoperiods.

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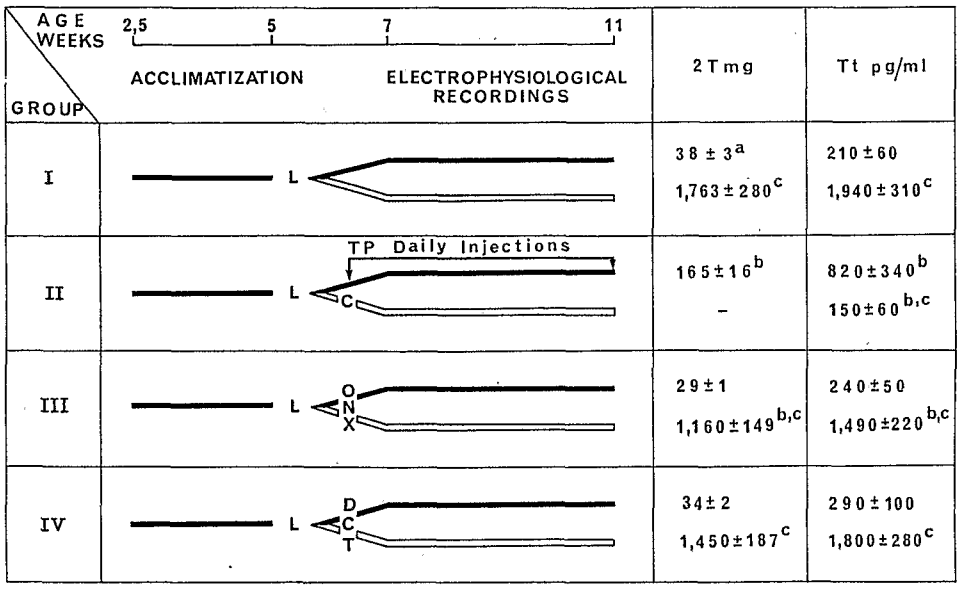

Fig. 1. Experimental groups and testicular function. 2T = Combined testes weight (mg); Tt = plasma testosterone level (pg/ml); TP = testosterone propionate; L = control laparotomy; C = castration; DCT = retroparaolfactory disconnection; ONX = optic nerve section. ■ = 6L:18D; □ = 18L:6D. [a] Mean ± SEM (n = 9); [b] $p < 0.01$ vs. controls (I); [c] $p < 0.01$ (18L:6D) vs (6L:18D). Body weights ranged between 100 ± 8 and 138 ± 7 g.

Materials and Methods

Young (2.5 week-old) immature quail were reared in individual cages, under controlled temperature (26 ± 1 °C) and at short daily photoperiods ($6L_{9-15,\ 150\ lux}$:18D). Surgical interventions were performed on 5 week-old birds, under sodium pentobarbital anesthesia (Nembutal, Abbott Lab., 5 mg/100 g body weight). At the beginning of all experiments, the quail were subjected to intercostal laparotomy in order to control that the testes were quiescent. Four experimental groups of 18 quail were constituted (fig. 1). In each group, half of the birds was retained under short days (6L:18D) and the other half was subjected to long daily photoperiods ($18L_{6-24,\ 150\ lux}$:6D). Group I included intact nonphotostimulated and photostimulated controls. Group II was made up of birds whose plasma testosterone levels were inverted, i.e., photostimulated quail had been castrated before being transferred to long days and nonphotostimulated quail received 250 µg/100 g body weight of testosterone propionate (Testoviron) intramuscularly, daily. Group III comprised blinded birds (bilateral optic nerve section). The skin was incised dorsally to the eyeball. A small curved hook was slipped behind the eyeball and passed under the optic nerve which was cut with small scissors. In group IV, transection of the brain (retroparaolfactory disconnection) isolated the *lobus paraolfactorius* from its caudal afferents. A thin blade was vertically lowered, immediately caudal to the paraolfactory lobe, and a see-saw motion of the blade in the frontal plane allowed to completely section the brain.

The birds were left to rest for 2 weeks after control laparotomy, photoperiodic change and surgical interventions. Electrophysiological records were obtained between 7 and 11 weeks of age and then the birds were sacrificed. Autopsy data (fig. 1) included body weight and combined testes weight. Plasma testosterone levels were determined using radioimmunoassay kits (Bio-Mérieux, Paris). Student's t test was used for statistical calculations.

Control and experimental birds were prepared for electrophysiological exploration according to a procedure previously described

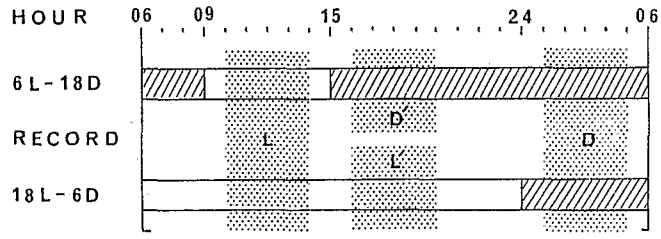

Fig. 2. Position of recording sessions with respect to the daily photoperiods. L = Morning session (light); D = night session (dark); L'/D' = afternoon session (light or dark).

[20]. The head was fixed in a stereotaxic frame (David Kopf 900) in order to trepan the calvarium and fix the electrode holder to the skull, at the anterior and lateral coordinates of the paraolfactory lobe [3]: A+7.5, L+1. Recording sessions began 48 h later. A platinum-irridium (70/30) elctrode [35] pointed to a diameter of 10 µm was mounted in its carrier and the complete outfit (electrode and carrier) was inserted in the holder fixed on the skull. A microdrive device allowed the electrode to be lowered through the brain to the vertical coordinate (H+2.2) of the paraolfactory lobe.

The electrode was connected to a Grass preamplifier (P511) via a Grass cathode follower. The preamplified MUA was fed into a Didac 800 transient computer (Intertechnique) and monitored on a Tektronix 515 A oscilloscope. Neuronal spikes were separated from baseline interference by means of a voltage gate and overbrillancy. The MUA was monitored for 15 min allowing stabilization. Records were obtained in scotopic or photopic environments according to the phase of the photoperiod (fig. 2). All morning sessions (from 09.00 to 13.00 h) were carried out in light and all night sessions (from 01.00 to 05.00 h) in dark surroundings in both long and short daily photoperiods. The afternoon sessions were carried out in light and dark surroundings for photostimulated (18L:6D) and nonphotostimulated (6L:18D) birds, respectively. In the fol-

lowing, morning records will be designated L, night records D and afternoon records either L′ or D′.

Either spontaneous or flash-altered MUA was obtained during sweeps of 1 s (200 addresses of 5 ms) and integrated for 200 s. Every sweep was triggered at a rate of 1 cps either by a current pulse generator (spontaneous MUA) or by the photostimulator (flash-altered MUA: white flashes, 50 µs in duration, 400 lux in intensity).

Nonanesthetized resting birds were used during recording sessions that lasted no more than 2.5 h. Artefacts of muscular origin were avoided by placing the body of the quail in a small box and restraining its head movements.

Results

Photosexual Response

Combined testes weights and plasma testosterone levels are indicated for the various groups in figure 1. Small testes (2T = less than 40 mg) and low testosterone concentrations (Tt = less than 300 pg/ml) were found in quail exposed to short days, except for group II, i.e., in birds receiving daily androgen injections which exhibited significantly higher testosterone levels (820 pg/ml) and slightly heavier testes (165 mg) than in untreated ones. On the contrary, exposure to long days for more than 2 weeks led to markedly increased testicular weights (1-2 g) and testosterone levels (1,500-2,000 pg/ml). Obviously, photostimulated castrated quail constituted a group on its own. Moreover, the photosexual response in optic-nerve-sectioned birds appeared to be moderately restrained.

On the whole, body weights were rather low in all groups probably due to some troubles in feeding resulting from the fixation of the electrode holder to the skull.

Light Regime and Paraolfactory MUA in Intact Controls (fig. 3: group I)

Spontaneous MUA recorded from the *lobus paraolfactorius* of intact quail was always higher during light than dark phases of the photoperiod (between 35 and 50%). Comparison of nonphotostimulated (6L:18D) to photostimulated (18L:6D) birds indicated that morning values (L) were significantly (20%) lower in the later group whereas dark (D) MUA was fairly similar in both photoperiods.

Repetitive flashes led to reduced firing rates in all records (L, L′, D′, D) but this effect was more significant in sexually quiescent quail (approximately 30%) than in sexually developped ones (approximately 14%).

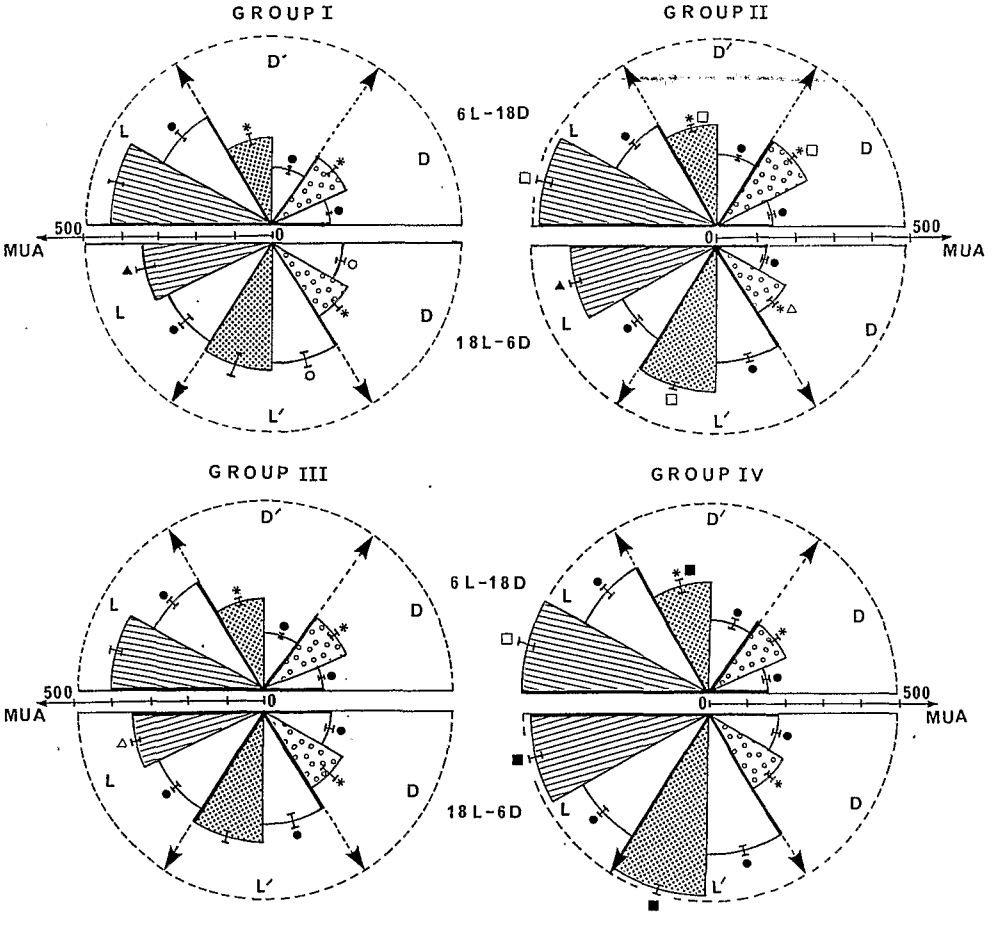

Fig. 3. Paraolfactory multiunit activity (MUA/200 s, mean ± SEM) correlates of long (18L:6D) and short (6L:18D) day lengths in control and experimental groups. Group I = Intact quail; group II = short-day androgenized and long-day castrated quail; group III = blinded quail (optic nerve sectioned); group IV = retroparaolfactory disconnected quail. ▤ = Spontaneous MUA from the morning (L); ▦ = spontaneous MUA from the night (D); ▨ = spontaneous MUA from the afternoon (L′, D′); □ = flash-altered MUA. * = $p < 0.01$ spontaneous MUA D,D′ or L′ vs. L; ▲ $p < 0.01$ and △ = $p < 0.05$ spontaneous MUA 18L:6D vs. 6L:18D; ■ = $p < 0.01$ and □ = $p < 0.05$ spontaneous MUA, groups II, III or IV vs. group I; ● = $p < 0.01$ and ○ = $p < 0.05$ flash vs. spontaneous MUA.

Effects of Altered Testosterone Levels on Paraolfactory MUA (fig. 3: group II, Tt and C)

Daily administration of propionate testosterone moderately increased spontaneous firing rates in the paraolfactory lobe of nonphotostimulated quail by 10–25%, whereas castration did not significantly alter the values of birds reared during long daily photoperiods (except for afternoon records). As in controls, morning values (L) were markedly higher (45%) than night values (D) in short as well as in long day periods. As to flash-altered MUA, it was significantly lowered – from 20 to 40% – with respect to spontaneous MUA in all, testosterone-treated or castrated, quail.

Paraolfactory MUA in Blinded Birds (fig. 3: group III)

Spontaneous firing rates were never drastically modified after bilateral optic nerve section, as compared to controls (group I) and D values remained also markedly lower than L ones (30–40%). However, the difference between 6L:18D and 18L:6D birds (L values) became almost negligible. As to acute photic stimulations they exhibited a 15–30% inhibitory effect on paraolfactory MUA in both photoperiods and in all L, D, L′ or D′ records.

Results of Retroparaolfactory Disconnection (fig. 3: group IV)

In all records except those obtained in the night, high spontaneous firing rates were observed in the caudally disconnected *lobus paraolfactorius* (15–40% more than in controls). The levels of MUA corresponding to the light phases of the photoperiod were strongly raised – about 50% – with respect to the dark phase values.

In this group, as in the preceding one (optic nerve section group) comparison of photostimulated and nonphotostimulated quail revealed no further influence of the photoperiodic regime on spontaneous MUA levels. On the contrary, marked effects of repetitive white flashes were visible in all lots (20–30% decrease).

Discussion

Surgical intervention (optic nerve section or retroparaolfactory disconnection) per se never appeared to modify drastically the testicular conditioning. Both parameters, testicular weight and plasma testosterone level, were low and high according to the daily photoperiods (6L:18D and 18L:6D) in controls as well as after optic nerve section and after retroparaolfactive disconnection. However, testicular weight and testosterone concentration in the long-day blinded quail were lower than in the long-day intact ones. Bilateral section of optic nerves did not inhibit light-induced testicular growth in various avian species: the drake [4, 5], the chicken [14, 28], the quail [17, 18, 29], the sparrow [9, 34], the canary [16] and the white-crowned sparrow [10, 33]. Here, the testes of the long-day blinded birds were indeed heavier and the testosterone levels higher than those of the short-day blinded or intact quail but also smaller than those of the long-day intact birds. Considering the short time interval between the operation and autopsy, it is possible that a temporary feeding impairment, due to blinding, could partly account for such a difference between controls and optic-nerve-sectioned animals. It is not surprising that retroparaolfactory disconnection did not alter the photoinduced gonadal stimulation since complete hemispherectomy was found not to inhibit such a response [1].

Daily injections of testosterone propionate led a medium-sized increase in plasma testosterone level of the nonphotostimulated quail (820 pg/ml). It might be that exogenous androgen weakly stimulated the testicular development since the testes were slightly heavier than in controls. Spermatogenesis could also be induced by testosterone propionate in the regressed testes of *Quelea quelea* [15] and silastic implants of androgen were capable of initiating some testicular development in immature quail [7]. However, this treatment was far less effective in hypophysectomized than in intact birds [7] and testosterone propionate injections appeared to merely retard the hypophysectomy-induced increase in testicular weight and the degeneration of the germinal epithelium in Coturnix quail [2].

We previously observed [20, 21] that the MUA that was recorded from the infundibular complex of the quail was increased after flashes were delivered. To the contrary, present results indicate that the paraolfactory MUA was markedly reduced following flash-light stimulations. Some examples of poststimulus-time-histograms and of integated MUA patterns are given in figure 4 and demonstrate that such a decrease in firing rates regularly developed during the whole recording sweep, i.e., 1 s. A similar pattern of flash-altered MUA was previously observed in the pineal organ [11] and in the habenular nuclei [*Herbuté*, unpublished data] of quail. There is, however, a difference between the epithalamic and the paraolfactory responses to acute photic stimulations. The flash-induced epithalamic decrease in MUA depends upon retinal information since it disappeared after bilateral optic nerve section [12], whereas this effect was still visible in the paraolfactory lobe of blinded Japanese quail (optic nerve section group). This paraolfactory response to flashes was still extant also after retroparaolfactory disconnection. Consequently, it appears that light flashes may modulate directly the rhinencephalic MUA, without any participation of neither retinal receptors nor cerebral structures located caudally to the level of the septomesencephalic tract. This can be taken as an argument favoring the existence of some deep photoreception, in the paraolfactory lobes, although we do not know its nature.

Some evidence that the environmental lighting exerts a direct influence upon the activity of paraolfactory neuronal

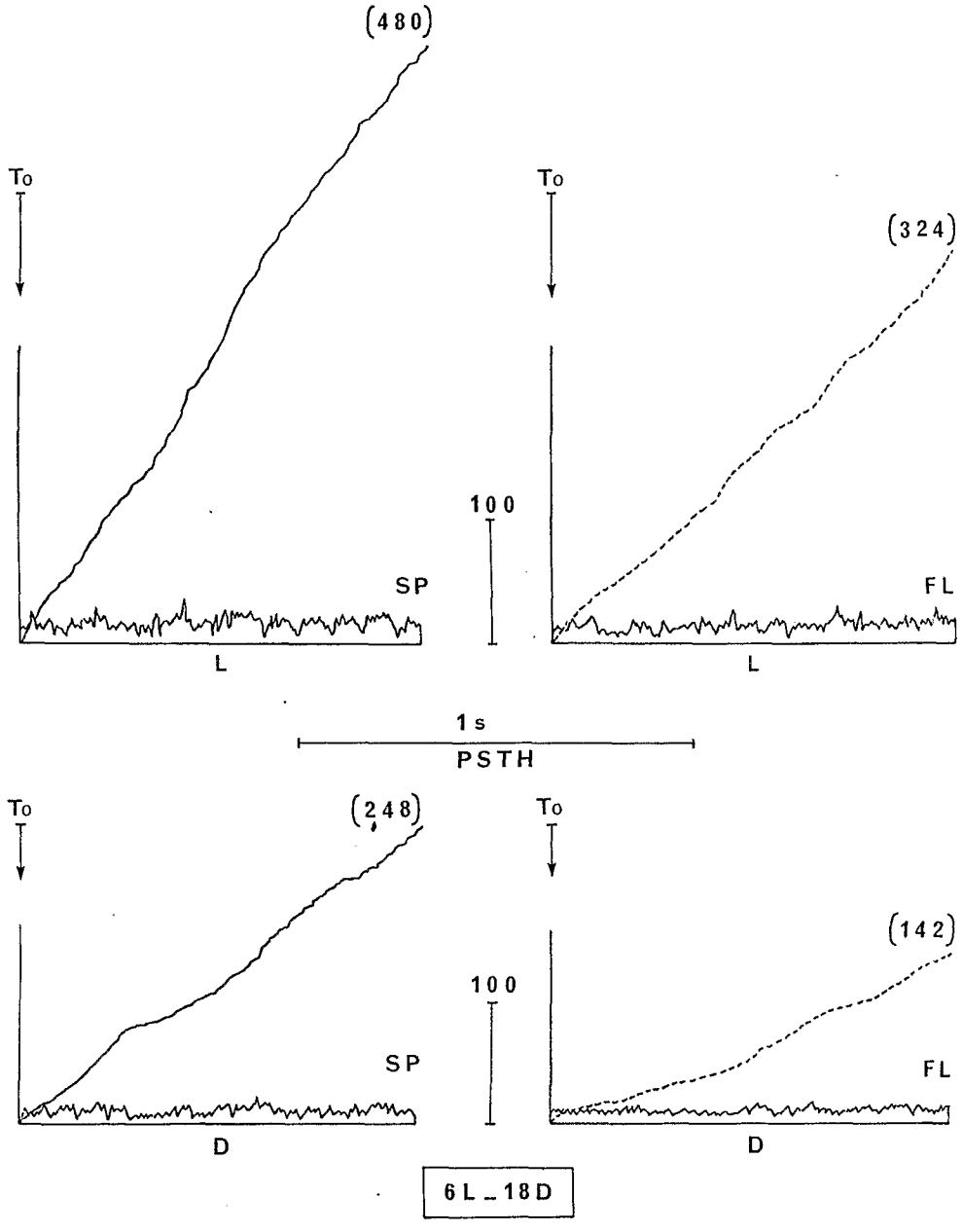

Fig. 4. Poststimulus-time-histograms (PSTH) and integrated MUA patterns in non-photostimulated (6L:18D) intact quail. L = Morning (light phase) records; D = night (dark phase) records; SP = spontaneous MUA (——); FL = flash-altered MUA (· · · · ·); (values) indicate the integrated firing rates/200 s; TO = trigger of sweeps.

populations can also be raised from the variations of the spontaneous MUA in our experimental groups. In all, photostimulated (18L:6D) or nonphotostimulated (6L:18D), birds, and especially in blinded and retroparaolfactory disconnected quail, as well as in controls, the MUA values recorded during the light phases (L or L′) were plainly higher than the levels observed during the dark phases (D or D′) of the photoperiods. In both the blinded and the retroparaolfactory disconnected groups, obviously no retinal signals could be involved in the light/dark fluctuation of paraolfactory firing rates.

It is interesting to note that the difference between L-L′ and D-D′ values was more important in retroparaolfactory disconnected quail than in controls. Therefore, it can be suggested that some modulating influences on the paraolfactory photoreactivity, originating from cerebral structures located caudally to the level of the septomesencephalic tract, were exerted in intact birds. Moreover, if one considers the paraolfactory firing rates measured during the morning records in intact quail, these L values were found to be signifantly different according to the daily - long or short - photoperiods. 18L:6D birds exhibited MUA levels de-

creased by 20% with respect to 6L:18D animals. A similar phenomenon was still observed in the blinded quail of group III, i.e., a 13% reduction of L values in photostimulated quail as compared to nonphotostimulated ones. This again underlines the modulating influence of the environmental lighting on paraolfactory neuronal populations without any noticeable participation of retinal signals. In retroparaolfactory disconnected animals, however, morning (L) values of paraolfactory MUA were found to be at the same high levels whatever the daily photoperiods were 18L:6D or 6L:18D. The modulating influence exerted by the light regime no longer appeared when posterior regulating mechanisms were excluded. On the other hand, unpublished data [*Sicard, Oliver and Baylé,* in preparation] show that the infundibular gonadotropic neurons are reciprocally influenced by the paraolfactory cells.

It is well known that the controlling system that governs the gonadotropic axis of male quail includes at least two hypothalamic regions. The tubernal (infundibular) complex [18, 30] and the preoptic-suprachiasmatic area [8, 22, 23] are essential for photoinduced testicular development, but we do not know how basal and anterior parts of the hypothalamus are functionally correlated. It was postulated [26] that some extrahypothalamic formations are involved in the interrelationships between infundibular and anterior hypothalamic gonadotropic structures. The paraolfactory lobe which was explored in the present experiments could participate in these regulating extrahypothalamic mechanisms. In our opinion the paraolfactory lobe has another interest. If one accepts, as we suggest, that some paraolfactory cells are endowed with an intrinsic photosensitivity, they can provide an experimental model allowing for further investigations on deep, extraretinal photoreceptors.

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