Ekológia (Bratislava) Vol. 19, Supplement 3, 171-180, 2000

ELECTRORETINOGRAPHIC MODULATION BY DOPAMINE AND NORADRENALINE IN THE SPIDER *LYCOSA TARENTULA* (ARANEAE: LYCOSIDAE)

ARTURO MUÑOZ-CUEVAS[1], PIERRE CARRICABURU[2]

[1] Laboratoire de Zoologie-Arthropodes, MNHN-CNRS, 61 rue de Buffon, 75231 Paris Cedex 05, France. E-mail: jkamc@cimrs1.mnhn.fr
[2] 21 rue du Commandant Mouchotte, 94160 Saint-Mandé, France.

Abstract

Muñoz-Cuevas A., Carricaburu P.: Electroretinographic modulation by dopamine and noradrenaline in the spider *Lycosa tarentula* (Araneae: Lycosidae). In Gajdoš P., Pekár S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 171-180.

Injections of dopamine, or noradrenaline, produced modifications of the amplitude, latency and profile of the electroretinograms (ERGs) in a lycosid spider. Each type of eye showed its own ERG modifications. Dopamine-treated anterior-median and lateral eyes showed opposite modifications of the amplitudes of ERGs which increased (AME) or decreased (ALE) compared with controls; the latencies were increased in both cases. Dopamine induced a significant decrease of the amplitudes and an increase of the latencies of ERGs of posterior-median (PM) and lateral (PL) eyes. The effect of noradrenaline was less marked. The antagonist haloperidol produced an opposite effect on ERGs of ALE for all dark adaptation times. The study of visual neuromodulation opens a way towards the control of visually-guided behaviours such as predation, sexual display and orientation in *Lycosa tarentula.*

Introduction

Catecholamines are well known as neuromodulators and neurotransmitters in vertebrates. Dopamine, mainly, has been widely studied in relation to the modulation of vertebrate visual systems (review by Nguyen-Legros, 1996).

The action of cataecholamines on arthropod visual system has very rarely been studied. Konopka (1972) observed very low concentrations of dopamine in mutants *tan* of *Drosophila melanogaster* which showed striking abnormalities of their electroretinograms (Hotta, Benzer, 1969). Noradrenaline plays a role in screening pigment regulation of a sphingid moth, *Deilephila elpenor* (Juse et al., 1987). Most studies of this kind on neuromodulation

in Arthropoda do not involve the visual system. However, the effects of biogenic amines, octopamine and serotonine on the modulation of ERG have been studied in scorpions and opilions (Arachnida) (Carricaburu, Muñoz-Cuevas, 1987; Muñoz-Cuevas, Carricaburu, 1990). In the central nervous system of spiders, evidence was provided by Meyer et al. (1984) concerning the comparative distribution and contents of important neurotransmitters and neuromodulators. Injections of modafinil (R), a drug able to induce in vertebrates an awakening effect via an effective central α 1- adrenergic tone, induce modifications of the amplitude and latency of electroretinograms (ERGs) in the spider *Lycosa tarentula* (Linnaeus) during dark adaptation (Carricaburu, Muñoz-Cuevas, 1998). Dopamine, adrenaline and noradrenaline have been found in Lycosidae (Meyer, 1991; Meyer, Jehnen, 1980; Meyer et al., 1984). The amounts of noradrenaline in the central nervous system of hunting spiders (Salticidae, Lycosidae) exceed that of dopamine, while amounts of both substances are about the same in web-building families (Agelenidae, Araneidae). Based on these findings, an analysis of the effects of dopamine and its antagonist haloperidol, which blocks dopamine receptors in vertebrates, on the ERGs of *Lycosa tarentula* is reported below.

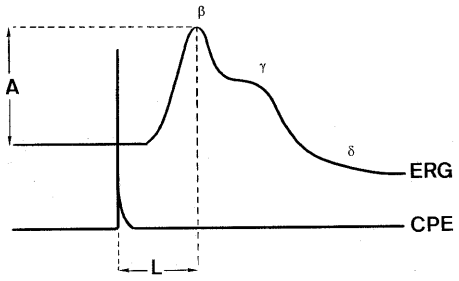


Fig. 1. ERG- electroretinogram; β and γ negative waves; δ positive wave. CPE- photo electric cell. A- amplitude; L- latency.

Material and methods

Lycosa tarentula (Lycosidae) females from Canto Blanco (Madrid, Spain) were maintained in the laboratory, in Paris, at 20°C and under natural light-dark cycles (LD: 10/14). Animal mass was about 2 g.

Nocturnal and diurnal electroretinograms were obtained by using a technical device described earlier (Carricaburu et al., 1990). The light stimulus was an electronic flash of white light, which produced 45 000 lx/s; the duration of the flash was a few milliseconds. Spiders were positioned in a Faraday cage in total darkness. Electric signals were amplified and directly photographed from the cathode ray oscilloscope screen (Fig. 1). ERG recordings were obtained in each eye type for 1s, 2s, 5s, 10s, 20s, 60s and 300s of dark adaptation.

The following *drugs* were tested: dopamine (hydroxytryptamine hydrochloride, Sigma), noradrenaline (norepinephrine hydrochloride, Aldrich), both substances were used in 0.0001M water solutions, haloperidol (4-[chlorophenyl)-4-hydroxy-1-piperidinyl]-1-(4-fluorophenyl)-1-butanone, Sigma) (0.0001M in 20% DMSO). Microquantities of these drugs were injected through a Hamilton microsyringe into the dorsal vessel of the spiders.

Results

Effects of dopamine during daytime (morning)

Anterior-median (AME) and lateral eyes (ALE)

Injection of dopamine (3µl) at 10.00 h, after recording of a control ERG, induced a slight increase (about +0.3 mV) of the amplitude one hour later in AME for 10s to 300s of dark adaptation (Fig. 2). On the other hand, the amplitude of ERGs of ALE decreased (up to -1.5 mV) for 1s to 10s of dark adaptation and did not vary for longer adaptations; the decrease compared with the control amplitude was only 0.5 mV for 300s of dark adaptation (Fig. 3).

Latencies were increased after dopamine treatment in AME as well as in ALE. In the case of AME, control latencies showed two distinct levels, one up to 10 or 20s of dark adaptation, and another much higher one for longer adaptations. These two levels of latency were greatly increased in dopamine-treated animals (Fig. 2). Latency of ALE control specimens was 50ms for all dark adaptation times; the injection of dopamine induced a slight lengthening of the latency for short dark adaptation times but from 10s to 20s of adaptation, latency was much increased, reaching 76ms, a value which did not change for longer times of adaptation.

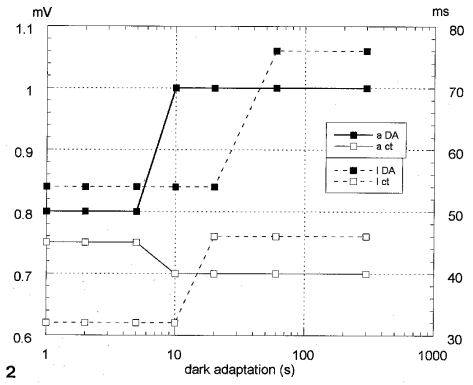
Posterior-median (PM) and lateral (PL) eyes

A striking decrease of the amplitudes appeared in ERGs of PM and PL eyes of dopamine-treated spiders recorded at 11.00 h. For PME, control amplitudes, at 10.00 h, were 5 mV (or nearly so) for all times of dark adaptation. After dopamine injection, ERG amplitudes of PME were much smaller (from 1.2 to 2.4 mV) (Fig. 4). The latencies, shorter than normal for 1s of dark adaptation, reached 72 ms from 60s of dark adaptation on, a value much higher than the normal one (46 ms) (Fig. 4).

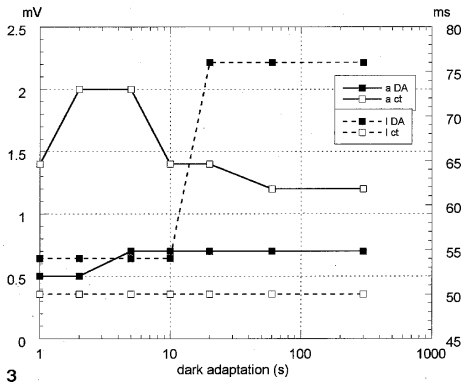
The amplitudes of PLE responses after dopamine injection decreased from 4 mV (control value) to 0.8 mV for 1s of dark adaptation. For longer adaptation times, control amplitudes showed smaller and smaller values up to 60 s of dark adaptation for which 2 mV were recorded, while the experimental amplitude was 1 mV. On the other hand, experimental latencies reached 76 ms for 60 s of dark adaptation, while control latencies were constantly 46 ms (Fig. 5).

Effects of noradrenaline during daytime (afternoon)

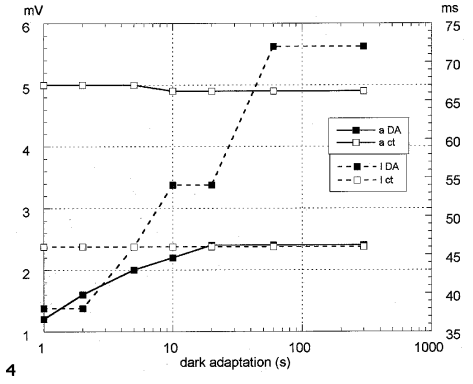
The injection of a noradrenaline solution (5 µl) at 15.00 h resulted, one hour later, in ERG amplitudes of PME a little higher (+ 0.5 mV) than for the controls, which did not exceed 4.1 mV at 17.00 h for short times of dark adaptation (Fig. 6). From 10s to 60s of dark adaptation, the experimental amplitudes were severely dropping up to 2.6 mV, 0.8 mV less than the control one. The latencies were much higher than normal for all dark adaptation times in ERGs of PME or PLE, reaching 64 ms for 300s dark-adapted spiders (Fig. 6, 7).



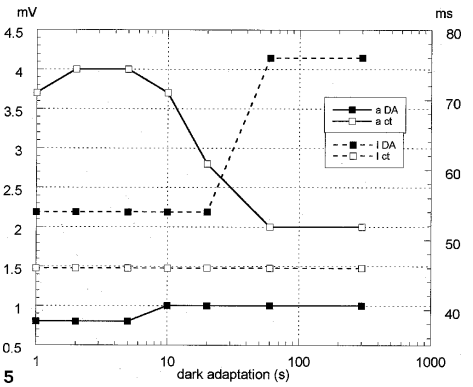
2



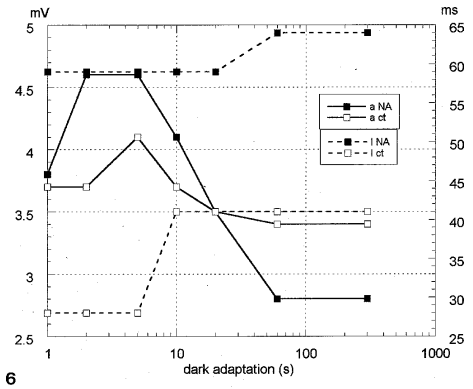
3



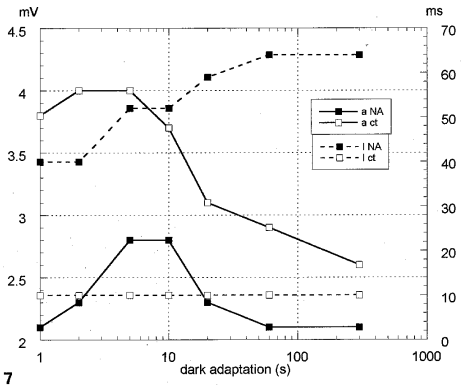
4



5



6



7

Figs 2-3. Effects of dopamine (DA), in the morning, on the amplitudes (mV) and latencies (ms) of ERGs for different times of dark adaptation. a: amplitude, ct: control, l: latency, s: seconds; ticks on X axis are on a log scale. 2. Anterior-median eye (AME); 3. Anterior-lateral eye (ALE).

Figs 4-5. Effects of dopamine, in the morning, on the amplitudes (mV) and latencies (ms) of ERGs of posterior-median (PME, Fig. 4) and lateral eyes (PLE, Fig. 5) for different times of dark adaptation. Same labels as in Figs 2-3.

Figs 6-7. Effects of noradrenaline (NA), in the afternoon, on the amplitudes (mV) and latencies (ms) of posterior-median (PME, Fig. 6) and lateral eyes (PLE, Fig. 7).

The effect of noradrenaline on ERGs of PLE were also expressed as a decrease of the amplitudes, more important (-1.2 mV) for short than for long dark adaptation (-0.5 mV) (Fig. 7).

Effects of dopamine and noradrenaline on the ERG-wave form

Dopamine injected in the morning induced a downturn of the curves, much accentuated for more than 20s dark adaptation times. In posterior eyes, an attenuation of the γ wave and the disappearance of the δ wave took place, after noradrenaline treatment; both waves were obvious in ERGs of posterior eyes of control spiders at the corresponding time. During the night, dopamine as well as noradrenaline did not induce any modification of the ERG-wave form.

Effects of haloperidol on ERGs of ALE

Effects of haloperidol, an antagonist of dopamine, were studied on the ERGs of ALE in daytime and at night.

Test 1

Control ERGs were first recorded at 12.00; then 3 µl of dopamine solution were injected and other ERGs were recorded 300s later. At 12.30 h, 10 µl of haloperidol solution were injected. ERGs of ALE recorded at 13.30 h showed an amplitude about 4 times as high as that recorded from control or dopamine treated animals, for all dark adaptation times (Fig. 8).

Test 2

The effect of haloperidol was also studied for longer periods. A 10 µl injection of haloperidol was made at 12.30 h. ERG recordings were performed 1, 2, 20, 29, 30, 31 and 33 hours after the injection for 300s of dark adaptation. ERG amplitudes appeared progressively increased up to 31 h after the injection, then a slight decrease was recorded (Fig. 9). It should be noted that a comparison with control amplitude of ALE ERGs at times of the day nearly corresponding to some of the experimental recordings showed that the maximum increase of amplitude had been recorded one or two hours after haloperidol injection.

Test 3

In the third experiment, control ERGs were recorded at 11.30; 10 µl of haloperidol solution were injected at 11.40 h; a second injection (20 µl) was made 4 hours later (at 15.45 h). ERGs recorded 6 hours after the first injection showed largely increased amplitudes (+ 4.1 mV) compared with those of control ERGs (at 17.15 h) for short times of dark adaptation. From 10s and more of dark adaptation, the experimental amplitudes decreased faster than the control ones; for 300s of dark adaptation, experimental and control amplitudes of ERGs differed only by 1.3 mV (Fig. 10). Eleven hours after the first injection, at 22.40 h, the increase of amplitudes, compared with the control recorded at 00.35 h, varied from + 3.6 mV for 1s to + 1.6 mV for 5 min of dark adaptation (Fig. 10).

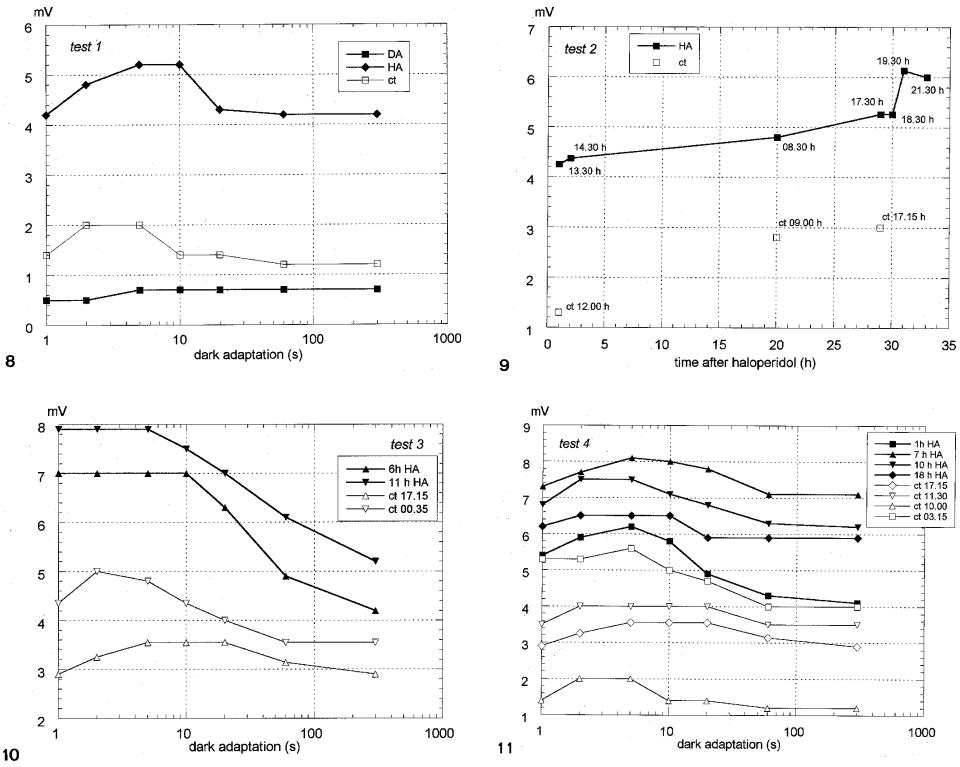


Fig. 8. Effect of dopamine (DA) and haloperidol (HA) on the amplitudes (mV) of ERGs of ALE for different times of dark adaptation. Test 1: in daytime. ct: control.
Fig. 9. Long-term effect of haloperidol (HA) on the amplitudes (mV) of ERGs of ALE. Test 2: for each value of amplitude, time of recording is indicated; control (ct) amplitudes at three corresponding times are included; ERGs were recorded for 5 min dark adaptation.
Fig. 10. Effect of a double injection of haloperidol (HA) on the amplitudes of ERGs of ALE for different dark adaptation times (Test 3).
Fig. 11. Effect of haloperidol (HA), at night, on the amplitudes of ALE recorded from 1 to 18 hours after injection, for different times of dark adaptation (Test 4).

Test 4

Recordings of ALE ERGs were performed as controls at night, at 03.15 h; 30 µl of haloperidol solution was injected at 03.25 h and ERGs were recorded 1, 7, 11 and 18 hours after the injection, that is at 04.30 h, 10.30 h, 13.30 h and 21.30 h respectively. The amplitudes of control ERGs were higher at 03.15 h than in daytime: a maximum of 5.2 mV was reached for 5s of dark adaptation. In all recordings following haloperidol injection, ERG amplitudes were higher than control amplitudes; the highest amplitude was recorded 7 hours

after the injection (Fig. 11). One hour after the injection, the amplitudes of ERGs were only a little higher than for the controls. The largest increase of amplitude was recorded after 7 hours, when it reached 8 mV, that is 4 times the control amplitude for 5s of dark adaptation. The effect of haloperidol 10 or 18 hours after the injection was less significant, the amplitudes reaching only twice the control values.

Effect of haloperidol on ERG-wave form

In the ERGs recorded in daytime, the γ wave was accentuated and the δ wave slowly decreased to much lower than the basal line after 5 min of dark adaptation. At night, γ and δ waves were similar to those of control ERGs.

Discussion

The physiological role of dopamine in the vision process has been investigated on a few species of vertebrates. Two aspects of dopamine activity have been treated: the modifications of ERG and the structural changes in neurons induced by dopamine. Citron et al. (1985), studying the amphibian *Rana pipiens*, have shown that 6-hydroxydopamine injected in the vitreous body, reducing the amount of dopamine in the retina, induces an increase of the b-wave and the amplitude of oscillation potential (OP). Apomorphine, an antagonist of dopamine, reverses the process. The action of dopamine and its antagonist, haloperidol, was tested on chicken ERG by Sato et al. (1987), Wioland et al. (1990) and Rudolf et al. (1991). The common results obtained by these authors are an increase of the amplitude of c-wave of ERG after dopamine and a strong decrease of b and c-waves after haloperidol; the c-wave may even disappear (Sato et al., 1987).

Biochemistry and cell electrophysiology methods have been used to localise the site and elucidate the mode of action of dopamine in the retina of other vertebrates such as teleost fishes (Dowling, 1991; Nguyen-Legros, 1996). It is now well established that the b-wave and, most of all, the oscillation potential of ERG are related to the activity of interplexiform cells of the retina, some of which are dopaminergic cells. Dowling, Ehinger (1978) have shown that dopamine released at specific synaptic sites in the fish retina modulates the activity of horizontal cells. Dopamine application to the fish retina results in a decrease of the amplitude of responses to light of horizontal cells and in a reduction of the electrical coupling between these cells. Dopamine exerts its multiple effects via cyclic AMP and protein kinase A (Dowling, 1991).

The modulation of ERG by catecholamines has never been experimentally studied in arthropods. However, modifications of ERG, in mutants ital. (or ital.) of *Drosophila melanogaster* (Hotta, Benzer, 1972), have been related to very small amounts of dopamine in the mutant ital., in juveniles as well as in adults (Konopka, 1972).

Dopamine and noradrenaline have an indirect effect on adaptation to light (NA) and darkness (DA). Both substances stimulate the release of red- or black-pigment-concentrat-

ing hormones (RPCH or BPCH) from chromatophore cells in the crab *Uca pugilator* (KULKARNI, FINGERMAN, 1986). In the sphingid moth *Deilephila elpenor*, JUSE et al. (1987) have found that noradrenaline alters pigment migration in the compound eyes: pigment migration is reversed by noradrenaline application after light stimulation. A similar, but less marked effect is obtained with dopamine.

Dopamine and its antagonist haloperidol influence the behaviour of insects also. Aggression between individuals of the ant *Formica rufa* is stimulated by dopamine and moderated by haloperidol (KOSTOWSKI et al., 1975). According to GERM (1997), variations of the concentration of biogenic amines, such as dopamine, in the visual tissue, during the postembryonic development of the mantids *Tenodera sinensis* and *Polyspilota* sp., is most probably correlated with the development of the visually-guided predatory behaviour of these species.

Dopamine and noradrenaline modulate the electroretinographic responses of *Lycosa tarentula*. In this species, the effects of catecholamine treatments on ERGs are not the same (1) for all eye types, (2) for each eye type when ERGs are recorded at different times of the day. The rhythmic process of rhabdom structural changes during 24 hours also follows a particular timing for each eye type (KOVOOR et al., 1995). In the morning the slight increase of ERG amplitude of AME contrasts with the strong decrease of ERG amplitude of the indirect eyes, ALE, PME and PLE. Rhabdom renewal of AME retinae occurs partly during the daytime (ORTEGA et al., 1997). It can therefore be assumed that ERGs of AME will not be affected by dopamine in the morning. It has been shown that the rhythmic renewal of rods of rat (REMÉ et al., 1986) or ox retinae (MASRI et al., 1996) is slowed down under the action of dopamine. The decrease of the amplitudes of ERG is not as marked in ALE as in PME or PLE which function in daytime. In these cases, dopamine seems to induce an amplification of the diurnal functioning, which is less effective in ALE than in posterior eyes. Parallel to this physiological difference between anterior median and other eyes of *L. tarentula*, an important neuroanatomical difference is obvious. Anterior-median retinae are connected to the side of the brain via two small optic neuropiles, isolated from the three neuropiles of the other eyes, which are partly interconnected (KOVOOR et al., 1992).

Applied in the afternoon, noradrenaline induces only a moderate decrease of the amplitude of PLE ERGs; for PME, the amplitude is increased for 2 and 5s dark adaptation but it is decreased for the longest times of adaptation while a large increase of latencies is observed for both eyes, as under the action of dopamine in the morning.

From the four experiments performed with haloperidol, some characteristics of the effect of this antagonist of dopamine on ERGs of ALE clearly appear. This drug reverses the effect of dopamine in daytime; it has no effect at night (04.00 h); it has a long-term action on the amplitude of ERG which is still largely increased 33 hours after the injection.

Modulation of ERGs under the action of biogenic amines has been studied in scorpions and opilions (CARRICABURU, MUÑOZ-CUEVAS, 1987; MUÑOZ-CUEVAS, CARRICABURU, 1990). The visual system of scorpions differs from that of opilions and in both orders it is never as complex as in spiders. Octopamine appears to be the main neurotransmitter for scorpions, as for xiphosures; it is responsible for the modulation of the ERG of the median eyes. The

nocturnal effect of octopamine is inhibited by phentolamine which blocks the adenylate-cyclase sensible to octopamine. In opilions Gonyleptidae (*Discocyrtus dilatatus* SÖRENSEN), serotonine modulates the ERG amplitude which is higher during daytime than at night. By blocking S1 receptors of serotonine in the CNS with cyproheptadine, a striking decrease of ERG amplitude occurs. The modifications of ERGs induced by catecholamines in *Lycosa tarentula* are more subtle and diverse. They differ from one eye type to another and express (or follow) the circadian rhythm of activity of each eye type.

In the natural habitat of *L. tarentula*, light intensity reaches 30 000 or even 50 000 lx during the photophase, when the spider is hunting prey, visually discriminating objects (ORTEGA et al., 1994) and using polarised light of the sky for orientation. It would be of interest to study the modulatory action of catécholamines and other neuromodulators on the expression of visually-guided behaviours of *L. tarentula*.

Acknowledgements

We are greatly indebted to Dr J. Nguyen-Legros (INSERM, Paris) who gave us opinions and advice that were greatly appreciated. Many thanks are due to Prof. J. Ortega-Escobar (UAM, Madrid) who provided us with specimens of *Lycosa tarentula*; we benefited from his accurate knowledge of the behaviour of this species and from useful discussions with Dr. J. Kovoor (CNRS-MNHN) who shared unpublished data on circadian modifications of retinae in *L. t.*

References

CARRICABURU, P., MUÑOZ-CUEVAS, A., 1987: La modulation du rythme visuel circadien par l'octopamine chez les scorpions et l'adaptation à la vie souterraine. Comptes-Rendus des Séances de l'Académie des Sciences Paris, *305*, p. 285-288.

CARRICABURU, P., MUÑOZ-CUEVAS, A., 1998: Action du Modafinil sur l'électrorétinogramme de *Lycosa tarentula* en relation avec le rythme de l'activité visuelle (Araneae,Lycosidae). C. R. Soc. Biol. *192*, p. 1163-1173.

CARRICABURU, P., MUÑOZ-CUEVAS, A., ORTEGA-ESCOBAR, J., 1990: Electroretinography and circadian rhythm in *Lycosa tarentula.* Acta Zoologica Fennica, *190*, p. 63-67.

CITRON, M.C., ERINOFF, L., RICKMAN, D., BRECHA, N.C., 1985: Modification of electroretinograms in dopamine-depleted retinas. Brain Research, *345*, p. 186-191.

DOWLING, J.E., 1991: Retinal neuromodulation: the role of dopamine. Visual Neuroscience, *7*, p. 87-97.

DOWLING, J.E., EHINGER, B., 1978: The interplexiform cell system. I. Synapses of dopaminerdic neurons of the goldfish retina. Proceedings of the Royal Society (London), *201*, p. 7-26.

GERM, M., 1997: Dopamine, N-acetyldopamine and serotonin concentrations in the visual system of praying mantis during postembryonic development. Comparative Biochemistry and Physiology, *116A*, p. 379-386.

HOTTA, Y., BENZER, S., 1969: Abnormal electroretinograms in visual mutants of *Drosophila*. Nature, *222*, p. 354-356.

JUSE, A., HÔGLUND, G., HAMDORF, K., 1987: Reversed light reaction of the screening pigment in a compound eye induced by noradrenaline. Zeitschrift für Naturforschung, *42c*, p. 973-976.

KONOPKA, R.J., 1972: Abnormal concentrations of dopamine in a *Drosophila* mutant. Nature, *239*, p. 281-282.

KOSTOWSKI, W., TARCHALSKA, B., WANCHOWICZ, B., 1975: Brain catecholamines, spontaneous electrical activity and aggressive behavior in ants (*Formica rufa*). Pharmacological Biochemistry of Behavior, *3*, p. 337-342.

KOVOOR, J., MUÑOZ-CUEVAS, A., ORTEGA-ESCOBAR, J., 1992: Le système visuel de *Lycosa tarentula fasciiventris* (Araneae, Lycosidae). I. Organisation des nerfs et des premiers ganglions optiques. Annales des Sciences naturelles, Zoologie, Paris, 13čme Serie, *13*, p. 25-36.

Kovoor, J., Muñoz-Cuevas, A., Ortega-Escobar J., 1993: Microanatomy of the anterior median eyes and its possible relation to polarized-light reception in *Lycosa tarentula* (Araneae, Lycosidae). Bollettino di Zoologia, *60*, p. 367-375.

Kovoor, J., Muñoz-Cuevas, A., Ortega-Escobar, J., 1995: Diel morphological changes in the photoreceptors of *Lycosa tarentula* (Araneae, Lycosidae). Biological Rhythm Research, *26*, p. 272-291.

Kulkarni, G.K., Fingerman, M., 1986: Distal retinal pigment of the fiddler crab, *Uca pugilator*: evidence for stimulation of release of light adapting and dark adapting hormones by neurotransmitters. Comparative Biochemistry and Physiology, *84C*, p. 219-224.

Masri, H., Goureau, O., Hecquet, C., Simon, A., Guyen-Legros, N., 1996: La dopamine ralentit la phagocytose des bâtonnets par l'épithélium pigmentaire de boeuf *in vitro* grâce à un récepteur D1. Comptes-Rendus des Séances de l'Académie des Sciences Paris, *319*, p. 687-691.

Meyer, W., 1991: The biology of excitatory neurotransmitters in the central nervous system of spiders (Arachnida : Araneida). Neurological Chemistry (Life Science Advances), *10*, p. 85-103.

Meyer, W., Jehnen, R., 1980: The distribution of monoamine oxidase and biogenic monoamines in the central nervous system of spiders (Arachnida: Araneida). Journal of Morphology, *164*, p. 69-81.

Meyer, W., Schlesinger, C., Poehling, H.M., Ruge, W., 1984: Comparative quantitative aspects of putative neurotransmitters in the central nervous system of spiders (Arachnida: Araneida). Comparative Biochemistry and Physiology, *78C*, p. 357-362.

Muñoz-Cuevas A., Carricaburu, P., 1990: Modulation in electroretinograms during 24 hours by serotonin of *Discocyrtus dilatatus* (Chelicerata, Opiliones, Gonyleptidae). Acta Zoologica Fennica, *190*, p. 287-291.

Nguyen-Legros, J., 1996: Retinal dopamine: basic mechanisms and clinical implications. In Stone, T.W. (ed.): CNS Neurotransmitters and Neuromodulators: Dopamine, CRC Press, USA, p. 233-250.

Ortega-Escobar, J., Fernandez-Montraveta, C., Fernandez, E., 1994: Señalizacion activa de la disposicion a la copula y discriminacion visual del macho en la hembra de *Lycosa tarentula fasciiventris*. Etologia, *4*, p. 11-18.

Ortega-Escobar, J., Kovoor, J., Muñoz-Cuevas, A., 1997: Circadian structural changes in the retinae of *Lycosa tarentula* (Araneae, Lycosidae). Chronobiology International, *14*, Suppl. 1, p. 129.

Remé, C.E., Wirz-Justice, A., Rhyner, A., Hofmann, S., 1986: Circadian rhythm in the light response of rat retinal disk shedding and autophagy. Brain Research, *369*, p. 356-360.

Rudolf, G., Wioland, N., Allart, I., 1991: Is dopamine involved in the generation of the light peak in the intact chicken eye? Vision Research, *31*, p. 1841-1849.

Sato, T., Yoneyama, T., Kim, H.K., Suzuki, T.A., 1987: Effect of dopamine and haloperidol on the c-wave and light peak of light-induced retinal responses in chick eye. Documenta Ophthalmologica, *65*, p. 87-95.

Wioland, N., Rudolf, G., Bonaventure, N., 1990: Electrooculographic and electroretinographic study in the chicken after dopamine and haloperidol. Documenta Ophthalmologica, *75*, p. 175-180.