equivocal with respect to the dipsogenic effect of angiotensin. The lateral ventricles are also without active sites, as shown by the rats with interventricular blockage by lesion debris or cold cream plugs. Since the evidence points to a periventricular site, these data limit the area to the anterior-ventral part of the third ventricle at the preoptic and hypothalamic level. It is in this region that we suggest that further experimentation would be fruitful.

JAMES BUGGY*
ALAN E. FISHER
Psychobiology Program, Department of Psychology, University of Pittsburgh, Pittsburgh, Pennsylvania 15213
WILLIAM E. HOFFMAN
ALAN KIM JOHNSON
M. IAN PHILLIPS
Neurobehavior Laboratory, Department of Physiology and Biophysics, and *Department of Psychology, University of Iowa, Iowa City 52242*

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8. In the Iowa study, lesions were made by one penetration of Nichrome wire through an implanted guide shaft. Two-milliampere current was passed for 30 seconds. In the Pittsburgh study, three penetrations were made with steel insect pin electrodes, 1.5 ma for 15 seconds each. The Pittsburgh rats received angiotensin II (Ciba) doses of 100 or 200 ng/μl, while the Iowa studies used 100 or 500 ng/μl. For tests before and after lesions, each rat was tested with the same dose of angiotensin and drinking was recorded for a 30-minute test period. In both studies injections were of 1-μl total volume administered over 10 seconds. For Iowa rats, the first test after the lesion was on day 4 and the subsequent recovery test was on day 14. For Pittsburgh rats, the first test after the lesion was on day 4 for one rat, day 3 for eight rats, day 2 for one rat, and day 1 for two rats, while the recovery test was on day 8 for five rats, day 7 for three rats, day 4 for two rats, and day 10 for two rats.
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10. It should be noted Simpson and Routtenberg (*5*) also reported that in one of seven animals with SFO lesions there was no attenuation of drinking after intracranial injection of angiotensin.
11. Overall, cerebrospinal fluid flows from the lateral ventricles through the foramen of Monro to the third ventricle and then caudally through the aqueduct and fourth ventricle, exiting through the cisterna magna to subarachnoid space.
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* Present address: Department of Physiology and Biophysics, University of Iowa, Iowa City 52242.

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Light for All Reasons: Versatility in the Behavioral Repertoire of the Flashlight Fish

Abstract. *The flashlight fish,* Photoblepharon, *possesses headlight-like luminous organs situated in the orbit just below the eyes. On the basis of direct field and laboratory studies, it is postulated that the bioluminescence is used by the fish for many different functions: to assist in obtaining prey, to deter or escape predators, and for intraspecific communication. The fish also uses its light to see by.*

A biologically generated light may be used by an organism in different specific ways for several distinct functions (*1–3*). In most of the luminous organisms that have been analyzed, the proposed functions of light emission fall in three major categories. The first is assisting predation (offense). For example, certain of the mesopelagic ceratioid angler fish, such as *Melanocetus murrayi* (*4*) and *Oneirodes acanthias* (*5*), have a luminous organ (esca) which presumably functions as a lure (*1, 2*). Similarly, the firefly "femme fatale" (*Photuris versicolor*), in addition to using her light organ to signal the male of her own species, mimics the courtship signal of other species, attracting males whom she then eats (*6*). The second major function is

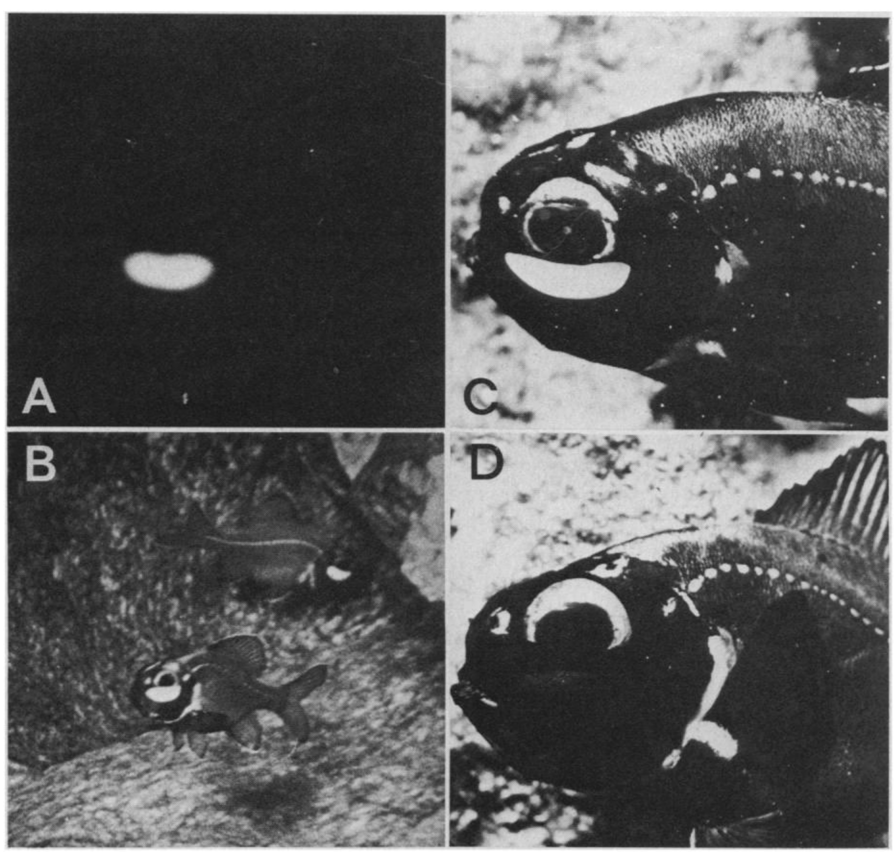

Fig. 1. The flashlight fish, *Photoblepharon palpebratus*, photographed at night along the reefs in the Gulf of Elat, Israel, by the light emitted from its own luminescent organ (A) and with an underwater strobe light (B, C, and D). The reflective areas of the lateral line, the edges of the fin rays, and the operculum are not luminescent. (B) A pair of *Photoblepharon* in their intertidal territory. (C) Closeup of *Photoblepharon* with the lid of the luminescent organ open. (D) Closeup with the lid closed. The fish are about 6.5 cm long.

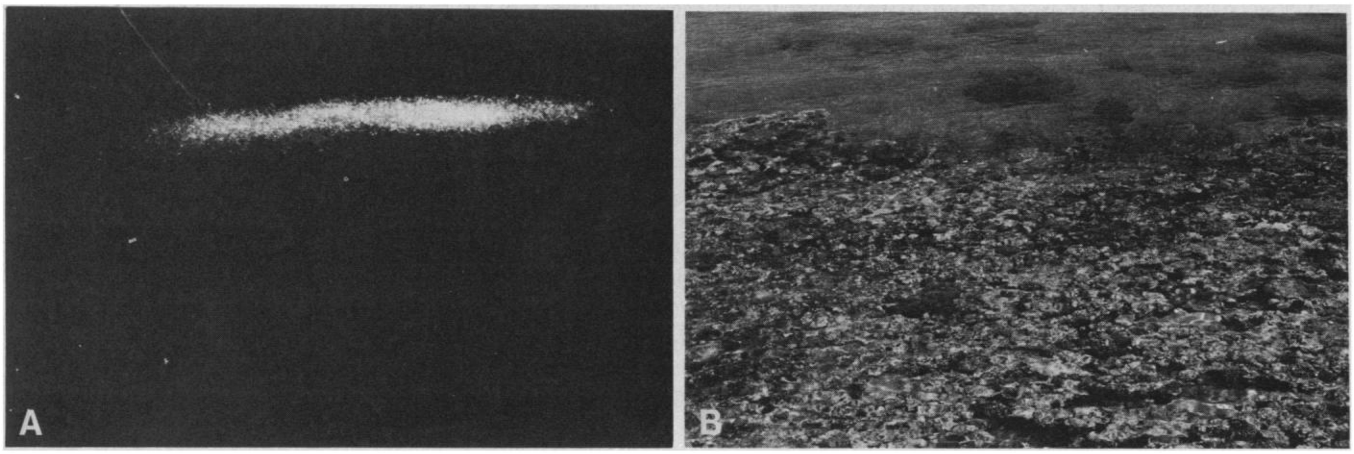

Fig. 2. Photographs of the same location at Marsa Mukebeila (A) by night and (B) by day. Each photograph encompasses the shallow water over the fringing coral reef edge (upper part of each photo) where *Photoblepharon* aggregate by night. (A) The night photograph was taken by the light being emitted from an aggregation of about 30 *Photoblepharon*. (Exposure about 15 minutes, Tri-X film, *f*/1.4.) (B) By day, the cleft at the edge of the reef (located about 12 m from the camera) is evident as the location where the fish congregate by night.

to aid in escaping or avoiding predators (defense). For example, a flash may frighten or divert a would-be predator, as in the case of the deep-sea squid *Heteroteuthis dispar* (*1*, pp. 281–283; *7*) and the crustacean *Cypridina hilgendorfii* (*1*, pp. 297–331), which squirt a luminescent substance into the water. Predators can also be avoided by luminescent camouflage, as in the case of pony fish (*8*), myctophids (*9*), and others (*3, 10*), which are postulated to match the light from above by ventral luminescence. Intraspecific communication, as in signaling between fireflies during courtship, constitutes the third general function of bioluminescence (*11*).

In 1973 we studied *Photoblepharon palpebratus* (Beryciformes; Anomalopidae) (*12, 13*) along the shallow fringing reefs of the Gulf of Elat in the Red Sea (*14–16*). This fish possesses headlight-like organs, packed with continuously emitting luminescent bacteria. The organs are situated just below the eyes, along the lower margin of the orbit, and have black lids that can cover them from below (*12, 13, 17, 18*) (Fig. 1). In different behavioral situations this fish appears to use its emitted light for all three of the general functions described above, being more versatile in this respect than any previously described bioluminescent organism, especially considering that all of the uses are mediated by a single type of light organ.

From the shore on moonless nights the light of the fish can be seen near the reef as a diffuse glow covering an area of several square meters (Fig. 2). Several such luminous patches may be visible, due to light from aggregations of about 10 to 100 or more fish; they characteristically remain in a relatively circumscribed area, but occasionally move slowly along the reef parallel to shore. Fish are also often observed at high tide in the intertidal area in pairs, small groups, or as individuals. Sometimes the groups or individuals join or depart from the aggregations.

The fish, observed from the shore, by snorkeling, or by using scuba, were easily seen underwater from distances up to 20 m. When carefully approached by a diver the aggregations appeared undisturbed at distances greater than 1 m, but the fish took evasive action if approached more closely. By using a bright underwater flashlight, we were able to temporarily "blind" the fish and capture them by hand for study in the laboratory, where they were maintained without difficulty. In the darkened laboratory, visual observations and photometric measurements were possible at all times of the day. In the field, however, observations could be made only during dark nights. The fish retreat into inaccessible caves in the reef during daylight and at night when the moon is bright.

Three patterns of bioluminescence were observed: (i) Infrequent blinking behavior (light on most of the time). In contrast to the flashing behavior [light off most of the time (*19*)] which is characteristic of many luminous organisms, *Photoblepharon* instead blinks. Although the rate may vary, the blink is rapid, so the light is effectively on most of the time (Fig. 3A). This pattern was seen in undisturbed fish at night, both in the field and in the laboratory. It could sometimes be induced at other times in the dark laboratory by feeding the fish. We measured the blinking frequency by using

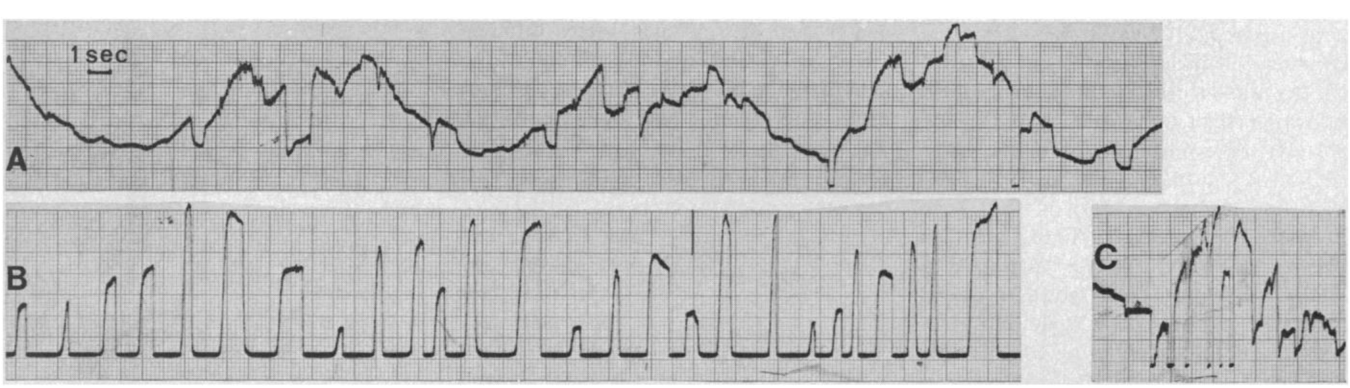

Fig. 3. Photometric records of the luminescent activity of an isolated *Photoblepharon* in the laboratory under constant dark conditions. The zero position of the pen was offset, so the baseline of the trace represents light off (lid covering the organ). The traces above the baseline show the variation in light being received by a fixed photomultiplier as the fish swims about the tank, sometimes turning abruptly. Each major time division represents 1 second. (A) Infrequent blinking pattern characteristic of night activity. There are two blinks toward the end of the record. (B) Equal on-off pattern characteristic of activity during daytime hours. (C) Rapid blinking pattern characteristic of blink-and-run activity.

four fish individually isolated in a dark room and recording for 3- to 5-minute periods at frequent intervals through the night. Twenty recordings showed an average of 2.9 blinks per minute, each blink having an average duration of 260 msec. (ii) Equal on-off behavior. An apparent circadian rhythm in the spontaneous blinking frequency was observed in undisturbed fish kept in continuous dark. The blinking rate was much higher during the daytime hours than during the night, and the duration of the blink was somewhat longer (Fig. 3B). The same four fish discussed above, isolated in the dark room and similarly measured during the daytime, exhibited an average frequency of 37 blinks per minute, each blink having an average duration of 800 msec. (iii) Blink-and-run behavior (light turned on and off rapidly along with a darting swimming pattern). The fish swims relatively slowly with the light on, it then blinks the light, and at the same time abruptly changes direction and increases swimming speed (Fig. 3C). When the light again comes on the fish is in a location not predictable from its previous course. This blink-and-run pattern was seen in the field when the fish swam over areas of the reef that offered little or no protection or when they were disturbed by predators or divers, and in the laboratory when the fish were disturbed. Ten recorded blink-and-run patterns from the four fish showed an average frequency of 75 blinks per minute and an average blink duration of 160 msec.

These distinct behavioral patterns, along with other field and laboratory observations, lead us to propose that the light of *Photoblepharon* can be used for all three of the different functions enumerated above.

1) To assist in predation, the light functions in at least two ways: to enable the fish to see, and to attract prey. In the otherwise dark laboratory we observed *Photoblepharon* capturing prey (adult *Artemia*) by the light of their own luminescent organs, which was also adequate for vision by the human eye. *Photoblepharon* swam in a scanning type of pattern, rolling and turning; this was recorded in the laboratory as changes in light intensity (Fig. 3A). Second, *Photoblepharon* feeds in the water column on crustaceans that have well-developed photoreceptors (*16*). Most of these plankters are positively phototactic (*20*) and we speculate that they are attracted to the light of the fish. The large aggregations of fish (Fig. 2) provide a bright and quite constant light covering a considerable area, which should be especially effective in this regard.

2) To avoid predation, three mechanisms involving luminescence appear possible. Although a luminous fish is presumably more vulnerable to predation than a dark one (*21*), the light organs may permit *Photoblepharon* to see and thus avoid predators. Second, the blink-and-run pattern, where evasive swimming is coordinated with blinking of the light, would seem effective in evading predators (*22*). Finally, aggregations, where they occur in diurnal fish, are assumed to confuse predators and thus to deter predation (*23*). A similar role may be assumed for the highly visible luminescent aggregations of *Photoblepharon*.

3) Use of the light in intraspecific communication is indicated by several behavioral patterns. When two aggregations approached to within about 3 m of each other, the fish in the leading part of each aggregation swam rapidly toward the others, and the two aggregations then streamed together to form a single large group. Second, pairs of fish (*24*) defended territories on the reef at night against other *Photoblepharon* (*16*). When intruding *Photoblepharon* approached, the female swam back and forth rapidly. She would then turn off her light, swim directly toward the intruder, and turn on the light when she was just next to the other fish. This was invariably effective in driving intruders away.

Other data indicating that the light serves for communication were obtained in laboratory experiments. Two fish were placed in adjacent tanks in the dark with a flat black panel between them. Basal blinking rates of about 10 per minute for one fish and 50 per minute for the other were recorded. When the panel was removed so that the fish could see one another, the blinking rates increased to about 40 and 60 per minute, respectively. A similar phenomenon was observed with one fish and a mirror, but no such change occurred when one of the fish was replaced by a nonluminescent species (*Siganus* sp.).

Thus, the bioluminescent behavioral repertoire of *Photoblepharon* is extensive and varied. It includes many different offensive, defensive, and communicative activities, and is especially unusual because only a single type of light organ is involved. The multiplicity of functions suggest that the organ is like a flashlight, whose owner can exercise options in its use.

James G. Morin*
Anne Harrington†
Kenneth Nealson‡
Neil Krieger§
Thomas O. Baldwin||
J. W. Hastings¶

Marine Biological Laboratory,
Hebrew University,
Elat, Israel

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14. Observations were made at numerous locations between Elat and Dahab, 150 km to the south. Most of the observations reported here were made at Marsa Mukebeila, 28 km south of Elat. In March 1975 a team of ichthyologists headed by J. McCosker collected *Photoblepharon* from the Comores Islands off the Malagasy Republic and brought them back alive to the United States, where they are now on display at the Steinhart Aquarium in San Francisco.
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25. This research was initiated and supported in large part by a grant from the Tobias Landau Foundation. Support was also provided by NIH grant 5-PO1-NSO-9546 to J.G.M. and NSF grant GB 31977X to J.W.H. We are especially grateful to D. Fridman and the staff of the Heinz Steinitz Marine Biological Laboratory, and to D. Por, M. Shilo, and A. Keynan for their interest in and support of this work. J. Kastendiek critically reviewed the manuscript and D. Diener determined the sex of the fish.
* Reprint requests should be addressed to J.G.M. at the Department of Biology, University of California, Los Angeles 90024.
† Present address: 30004 Stanford, Venice, Calif. 90291.
‡ Present address: Scripps Institution of Oceanography, University of California, La Jolla 92037.
§ Present address: Department of Pharmacology, Yale Medical School, New Haven, Conn. 06510.
|| Present address: Department of Biochemistry, University of Illinois, Urbana 61801.
¶ Present address: Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

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