Chemical Aspects of Stimuli

by H. KLEEREKOPER

Texas A & M University, Department of Biology, College of Science, College Station (Texas 77843, USA).

The initiative to dedicate an issue of Experientia to the role of the chemical senses in the reproductive behaviour of fishes is in itself evidence for the scientific interest in the many facets of this biologically important and fascinating problem.

Although even from a strictly descriptive point of view the part played by the chemical senses in that behaviour has become known only superficially, there remains no doubt as to the importance of their involvement in a number of behaviour patterns related to reproduction in these animals, from orientation in migration to social behaviour and parental care. It may be expected that continuing research in this area will reveal the dependence of many more behavioural functions in reproduction on chemical communication which is potentially one of the most versatile biological mechanisms for the transfer of precise and unequivocal information so essential in many phases of reproduction. The many fascinating results of modern physiological investigations of behaviour related to reproduction in insects and, to a lesser extent, in mammals are strongly suggestive as to what similar efforts may yield with respect to that behaviour in fishes.

The information available on the role of the chemical senses in the behaviour of fish generally is largely descriptive in that inquiries into the chemical identity of the substances involved are almost entirely non-existent. The few attempts described in the literature, including my own, which have yielded some information on chemical characteristics, have dealt with olfactory stimuli related to orientation (food localization) and alarm substances.

Having been invited by you to prepare for this issue of Experientia a short review of the present status of our knowledge on the chemical aspects of stimuli involved in reproductive behaviour in fish, I exhaustively searched the literature on information that may be even remotely related to the problem at hand. I cannot remember any other of the many literature searches carried out by me over the years that was as totally negative as the one in question. I have occasionally emphasized the urgent need for an intensive and highly sophisticated chemo-analytical approach to the problem of odour identity of the waters of spawning grounds and migratory pathways and was well aware of the great void in meaningful knowledge on this aspect which is extraordinarily complex and whose solution is technically difficult and expensive. However, it is far less obvious why, apparently, so few efforts have been made to ascertain the chemical nature, not to speak of the identity, of substances involved in less complex chemical communication such as is likely to be involved in sexual discrimination. It seems reasonable to speculate that, in many cases, we may be dealing with fairly simple steroids whose identification should not present too great problems.

Allow me to, once more, express the opinion that advances in knowledge on the fundamental processes in chemical communication in general and, in the context of the present issue of your journal, on that related to reproductive behaviour in fishes will be dependent on precise information on the chemistry of the substances involved. The analogy with the great advances in physiology of reproductive behaviour in insects, following biochemical identification of many pheromones, is obvious. However, the analytical problems are bound to be considerable and complex in most cases and would call for the application of the advanced techniques not generally accessible to the general and behavioural biologist. Collaborative efforts with organic and biochemists would be required in serious investigations of this type.

Conclusion

by M. DOMINIQUE CRAPON DE CAPRONA

Abteilung Mittelstaedt, Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, (Germany).

The previous articles, demonstrating the importance of chemoreception in many aspects of fish reproduction, can be summarized in the following way.

When breeding is limited to certain periods of the year, chemoreception promotes spawning synchrony by bringing together many individuals of a given species. This is accomplished either through migration to spawning grounds, or by an increase of the reproductive activity and receptiveness of the individuals. This assures a greater variety of prospective partners, consequently an efficient spreading and mixing of the gene 'capital' of a population (and possibly even sexual selection).

Hybridization is sometimes prevented by the use of highly specific signals, which enable the fish to find not only a partner ready to spawn, but to recognize the partner of the right species (TODD 1971). The role of chemoreception in species preservation is evident.

As studies on the social behaviour of the Bullhead have shown (ATEMA 1969; ATEMA, TODD, BARDACH 1969), chemoreception is also a means of individual recognition, and is probably active in species capable of strong individual pair-bonding.

During breeding, chemoreception is present in many aspects of communication between sexes: females obviously stimulate males (TAVOLGA 1956, BELDING 1934), but the other combinations are also true (males excite males (LOSEY 1969), males females (EGGERT 1931, ROULE 1931), probably females females).

In species showing strong broodcare, chemoreception enables the parents to recognize their own brood, or, at least, to distinguish their own species' broods from those of other species (MYRBERG 1966, 1975; KÜHME 1963; GREENBERG 1963).

In a few cases, the environment itself produces chemical stimulants: spawning in the Pacific herring, *Clupea pallasii*, seems to be stimulated by lowered salinity (OUTRAM 1951); parental fanning of the eggs in the stickleback is elicited by a change in the chemical composition of the 'nest water' (VAN IERSEL 1953); the odor of its own nest and slime enhances the sexual activity of the three-spined stickleback (LEINER 1930). Migrating fish use chemical substances as orientation cues (see HASLER above).

Individual, species, sex and brood recognition, all rely, often heavily, on chemical stimuli produced by the fish themselves or the environment.

If the responses observed are analyzed quantitatively, they can be characterized not only by immediate increases in rates of behavioural events, but also by long-term effects spreading the arousal over several days (CRAPON DE CAPRONA 1975).

The sense involved in the detection of these substances, although evidence is scarce, is usually smell. Taste, however, is certainly involved in courtship using tactile information, i.e., bringing taste buds in contact with parts of the partner's body (Barbel-play in the catfish, and maybe the mouthing of the male's genital papilla by the female of *Tilapia macrochir*). The outer surfaces (body, barbels, lips, gillrakers) are known to be receptive to chemical substances (HASLER 1957, BARDACH and CASE 1965, HERRICK 1903). As to the nature of the pheromones themselves, very little can yet be said (see KLEEREKOPER above).

Their source is mostly a matter for speculation. The fluids from gravid female ovaries (in *Bathygobius soporator* (TAVOLGA 1956), and *Alosa alosa* (ROULE 1931), as well as secretions from special glands presented to the partner during courtship (in Glandulocaudines, NELSON 1964) may account for the production of some of these pheromones. Secretions from the cutaneous anal glands in the male *Blennius pavo* attract females (EGGERT 1931).

Chemosensory acuity is, of course, more or less specialized, its role in reproduction more or less essential, according to the relative importance of other systems of communication in the species chosen: visual, acoustical, electrical, tactile. One interesting aspect of chemoreception has been pointed out by TODD, ATEMA and BARDACH (1969). Their study is based on anatomical descriptions of fish brains, comparisons between species which are either primarily visual or olfactory, and their relationships to behaviour. According to these authors, a brain possessing an exaggerated development of the optic lobes will lead to very stereotyped, i.e. predictable behaviour; on the other hand, a brain where the olfactory bulbs are dominant, allows sophisticated and plastic, i.e. versatile, behaviour.

All these ideas about the nature of the functions of chemoreception in fish reproductive behaviour, as well as its relations to other types of communication, obviously need to be strengthened. An efficient collaboration between thorough anatomical and histological studies of the fish brain (especially olfactory and gustatory areas), chemical analyses of the substances produced, neurophysiological, endocrinological studies and behavioural investigations is necessary.

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SPECIALIA

Etude photophysique de la ptérobiline

Photophysical Study on Pterobilin

R. GAUTRON[1], P. JARDON[1], C. PÉTRIER[1], M. CHOUSSY[2], M. BARBIER[2] et M. VUILLAUME[3,4]

Laboratoire de Photochimie de l'Université Scientifique et Médicale, Boîte postale 53, Centre de Tri, F–38041 Grenoble Cédex (France); Institut de Chimie des Substances Naturelles CNRS, F–91190 Gif-sur-Yvette (France); et Laboratoire de Zoologie, Ecole Normale Supérieure, F–75005 Paris (France), 29 mars 1976.

Summary. The first results of a photophysical study on pterobilin (biliverdin IX γ, a Lepidopter blue bile pigment) are presented. From the absorption and fluorescence spectra, it is deduced that the low yield of fluorescence indicates a desactivation of the excited singlet state occurring mainly by a non-radiative process. Analyses of the chemical compounds formed after irradiation of pterobilin in methanol show that it is rearranged into a series of new blue pigments among which phorcabilin and sarpedobilin (the two neobiliverdins IX γ isolated from Lepidopters) have been identified.

De la cuticule et de l'hémolymphe des larves ainsi que de la membrane alaire des imagos d'un certain nombre de Lépidoptères, ont été isolés des pigments biliaires bleu-vert de la série IX γ: la ptérobiline (ou biliverdine IX γ), la phorcabiline et la sarpédobiline. Cette dernière dont la structure complète n'est pas encore connue, n'a pu être étudiée que dans les ailes d'imagos[5–10]. Ces pigments sont biosynthétisés par les Lépidoptères et proviennent de l'ouverture de la protoporphyrine IX au niveau du pont γ[11].

La biliverdine IX α a été trouvée dans la cuticule et l'hémolymphe de divers Insectes Orthoptères[12,13]. McDONAGH[14] met en évidence un rôle d'inhibiteur de l'oxygène singulet pour cette substance et pense qu'elle peut agir efficacement pour protéger les Insectes contre les photoxydations néfastes. Une telle possibilité avait été suggérée par VUILLAUME[15,16].

L'analyse de l'action de la lumière sur la ptérobiline se fera sur plusieurs plans. L'étude photophysique dont nous présentons ici les premiers résultats, doit permettre de déterminer les caractéristiques des états photoexcités de ce pigment et de mettre en évidence certains modes de désactivation de la molécule. L'étude photochimique est orientée vers la détermination des produits formés après irradiation et du comportement éventuel de la ptérobiline vis-à-vis d'autres réactions photochimiques. Enfin, la