monius to assume that such instances are indeed rare, rather than just neglected. One generalization that can be made is that chemical communication in general among fishes may be on a low level of organization in terms of the hierarchy of levels[14]. Because of the critical position of reproductive behavior in species survival, it is normal to find that interactions during reproduction include the highest levels of organization and behavior of which the species is capable. In the case of chemical stimuli, reproductive behavior in fishes does not attain the level of signal or communication (as defined by TAVOLGA[14]), with a very few exceptions.

[14] W. N. TAVOLGA, in *Nonverbal Communication* (Eds. L. KRAMES, P. PLINER and T. ALLOWAY; Plenum Press, New York 1974), p. 51.

Electroencephalography of the Olfactory Bulb in Relation to Prespawn Homing

by W. E. HAHN

Department of Anatomy, University of Colorado School of Medicine, 4200 East Ninth Avenue, Denver (Colorado 80220, USA).

The purpose of this brief survey is to place in perspective electroencephalographic (EEG) responses of the olfactory bulb as they relate to prespawn homing behavior of salmon. No attempt will be made to review the numerous experiments in this area since they have been recently reviewed by HARA[1,2].

EEG and behavior

Spontaneous electrical activity in the brain was first observed by CATON in 1875 (BRAZIER[3], 1961) and first recorded from humans by BERGER[4] in 1929. Continuous oscillations in electric potential can be measured between electrodes placed on the brain. Oscillations differ in frequency and amplitude from region to region and the parameters of frequency and amplitude can be altered by sensory input, hormones, metabolites, blood gas level, etc. In theory the EEG might serve as a direct measure of the qualitative aspects of brain activity, but in fact the relationship between behavior and EEG is not understood. However, in humans some states of altered brain function may be diagnosed by EEG. Relative to an actual behavioral response the EEG response must be considered to be very crude in terms of yielding qualitative information. For example odiferous substances which evoke behavioral responses in fish do so at concentrations several orders of magnitude below that required to evoke a change in the EEG of the olfactory bulb. This is not surprizing when one considers that changes in EEG require the simultaneous firing of complex networks of neurons.

Bulbar EEG evoked by natural waters

Having recognized the great disparity between evoked changes in EEG and actual behavioral responses the question arises as to whether it is meaningful to draw any behavioral conclusions from EEG studies. To address this question, the relationship between prespawn homing behavior and evoked bulbar EEG responses to natural waters will be discussed. The focus is on studies of homing salmon (various species of *Oncorhynchus*) since more detail is available from these studies. As discussed earlier in this article, the homing salmon is dependent upon olfaction. Hara et al.[5] first showed that when the olfactory epithelium of salmon *Oncorhynchus tshawytscha* and *O. kisutch* was irrigated with water taken from the home stream a high amplitude, synchronized response was recorded from the surface of the olfactory bulb. Originally it was found by UEDA et al.[6] that *only* water from the home stream evoked the high amplitude synchronized bulbar response as shown in Figure a. UEDA et al. showed that waters transversed during migration were stimulatory, but the evoked bulbar response was much less than when home stream water was used as the stimulant.

Subsequently OSHIMA et al.[7] showed that the bulbar response to natural waters in homing salmon was not the 'all of none' situation which was suggested from earlier studies of UEDA et al.[6]. OSHIMA et al.[7] found that, although a high amplitude bulbar response always occurred when home stream water was profused into the nasal cavity, all natural waters evoked some response and in some instances non-home water evoked a response similar to the response to home water, Figure b. OSHIMA et al.[8] also showed that bulbar re-

[1] T. J. HARA, J. Fish. Res. Bd. Canada *27*, 565 (1970).
[2] T. J. HARA, Progr. Neurobiol. *5*, in press (1975).
[3] M. BRAZIER, *A History of the Electrical Activity of the Brain. The First Half-Century* (MacMillan, New York 1961).
[4] H. BERGER, Acta nova Leopold. *6*, 173 (1938).
[5] T. J. HARA, K. UEDA and A. GORBMAN, Science *149*, 884 (1965).
[6] K. UEDA, T. J. HARA and A. GORBMAN, Comp. Biochem. Physiol. *21*, 133 (1967).
[7] K. OSHIMA, W. E. HAHN and A. GORBMAN, J. Fish. Res. Bd. Canada *26*, 2111 (1969).
[8] K. OSHIMA, W. E. HAHN and A. GORBMAN, J. Fish. Res. Bd. Canada *26*, 2123 (1969).

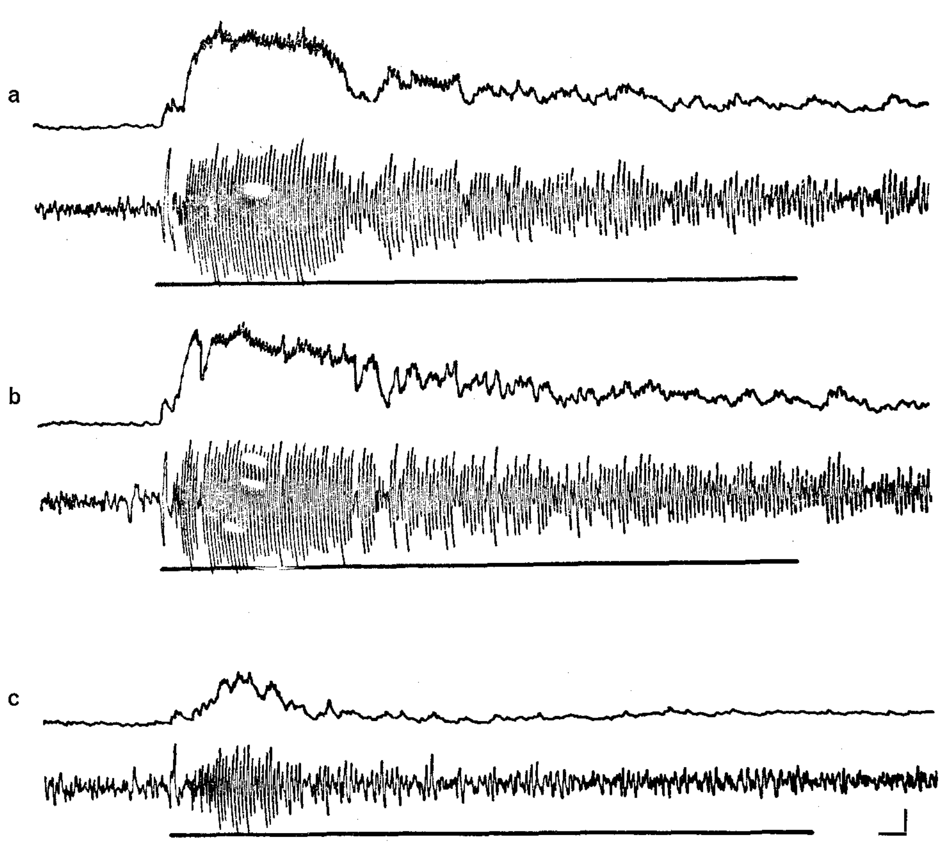
sponses similar to that evoked by water from the home stream occurred when waters taken at various intervals along the fresh water migratory route were profused over the olfactory epithelium. From this latter study it was suggested that homing salmon were not following an odor gradient emanating from the homestream, but rather fish are stimulated by a succession of olfactory clues along the migratory route. Hence, the bulbar EEG, as analyzed by pattern and magnitude, was found not to be specific for only the home stream water. However, in general, discrimination between home route waters and waters taken from *different* drainage areas was usually observed.

The high amplitude synchronized bulbar EEG was also found to be evoked by substances from fish. Water which failed to evoke a high amplitude synchronized response in chinook salmon did so when chinook or coho were placed in the water for a few hours prior to testing. Water containing chinook evoked the greatest response. Since olfaction is probably important in schooling and species identification (HARA[2]) these results are not surprizing. This finding is presented to illustrate the point that the bulbar EEG, viewed simply in terms of overall pattern and magnitude, is a quantitative reflection of intense, excitatory, olfactory stimulation. The *qualitative* aspect of this EEG 'language' still remains obscure.

Qualitative analyses of electrophysiological responses

To observe a qualitative aspect of the bulbar EEG during exposure to natural waters RAJI et al.[9] used a computer to analyze the frequency spectrum of the bulbar EEG. They observed temporal changes in frequency which were different for individual waters or solutions L-serine and concluded that spectral patterns seemed to reflect qualitative differences even when overall magnitudes of some of the responses were similar. The spectral patterns were analyzed at a resolution of 0.25 cycles/sec. However, the validity of the spectral pattern approach is still open to question since the variation observed between individuals as well as repeated responses given by an indivudal animal to the same stimulus often differ nearly as much as responses to certain different natural waters or test solutions (HARA, personal communication).

Another approach to obtain qualitative electrophysiological information on olfactory responses to homestream water is to measure activities of single bulbar neurons. DÖVING et al.[10] have shown that differential responses to waters, in which different fish had been held, occur in individual bulbar neurons of the migratory Arctic Char. As with EEG, relating single unit activity to the problem of understanding behavior remains a difficult task. Single unit studies, however,



Shown are olfactory bulb EEG's recorded from chinook salmon during stimulation of the olfactory epithelium with various natural waters. a) Response to home water; b) response to non-home water from the same drainage area as the home area; c) response to non-home water from a drainage area different from that of the home area. Solid line under the EEG indicates perfusion of water over the epithelium. Upper trace is the integration of the total baseline deviation of the EEG. Scale is given at lower right: horizontal, 1 sec; vertical 50 μV (from OSHIMA et al.[7]).

have alerted us to the possibility that the bulbar EEG may be influenced by a variety of non-olfactory stimuli which are registered on the olfactory epithelium. For example SATO and SUZUKI[11] found 4 types of functionally differentiated fibres in the olfactory tract of the carp, *Carassius auratus*. They described chemosensitive, thermosensitive, mechanosensitive and chemothermosensitive fibres. Also they differentiated two types of thermosensitive and two types of chemosensitive fibres. Considering that a similar array of fibres exist in other fish such as salmon, it is important that electrophysiological studies be controlled in terms of parameters such as the temperature of test waters, force with which the olfactory epithelium is perfused, etc.

Variables which alter the bulbar EEG

As suggested from the single unit work there are a variety of parameters which influence both quantitative and qualitative aspects of the bulbar EEG recorded during olfactory stimulation. COOPER and HASLER[12] have shown in bass that the EEG response can vary with the temperature of the test water. The pH also has some effect on the response (COOPER and HASLER[13]). The period during the migratory season when fish are tested may also be a variable at least in some instances. COOPER and HASLER[13] found that homing coho salmon obtained during the *peak* of the season, which had been in part 'imprinted' on morpholine as fingerlings, gave a stronger bulbar response to morpholine than fish which were early or late arrivals. This may be due to the endocrine state differences of fish arriving at the home stream at different times. Estradiol, for example, may increase the bulbar EEG response (HARA[14]). The time intervals in which various test waters are presented during recording of the EEG may produce variation in the bulbar response. Also the amplitude of the evoked potential may change with the number of times a given test water is presented. A 'priming' effect is sometimes observed in which the first exposure evokes a small response which increases to maximum after several exposures to the test water (OSHIMA, personal communication). The manner and the location of the placement of recording electrodes on or just beneath the surface of the olfactory bulb may also alter the pattern and intensity of the recorded EEG (HARA et al.[15], OSHIMA and HAHN (unpublished data).

Discrimination at the bulbar level

Experiments have been done to determine if a 'discriminatory' EEG can be recorded from the olfactory bulb after bilateral tract section. In preparations of this type the olfactory bulb is isolated from the rest of the brain but afferent neurons from the nasal mucosa remain operative. Immediately after tract section home and non-home waters were presented. While the magnitude and pattern of the EEG was decreased, the ratio of the home water response to non-home water response was similar to that observed in the intact brain (OSHIMA et al.[7]). This experiment suggests that discrimination between natural waters may occur at the bulbar level. Experiments of this type also show that the bulbar EEG is markedly modified by centrifugal feedback from higher brain regions.

Summary remarks

It is evident that the bulbar EEG is a complex response which can be influenced by several methodological and stimulant variables. What EEG patterns tell us about actual behavior remains obscure. The bulbar EEG which is evoked by homestream water is not necessarily a reflection of olfactory memory. The evoked bulbar EEG also does not necessarily demonstrate the salmon has distinguished the home-water from another water in terms of migrational orientation. Despite lack of absolute specificity, a correlation between bulbar EEG and actual behavioral performance has been observed even though some non-home waters evoke responses similar to that of the home water. In general it has been found that the home water response can be distinguished from the response to other natural waters. Failure to obtain complete specificity may be due to a variety of variables which have been alluded to earlier in this section. Thus considering that the evoked EEG is a reflection of the integration of a diverse afferent input, further electrical and computer analyses may eventually permit the decoding of the EEG in terms of behavior. However, if the EEG proves to be more a quantitative rather than qualitative reflection of brain activity, relating EEG to behavior will prove to be of limited value. Since afferent responses in the olfactory bulb are influenced by impulses from higher brain centers, studies on centrifugal aspects during olfactory stimulation may be useful in gaining some qualitative understanding of the home water evoked EEG of the olfactory bulb.

[9] S. RAJI, M. SATOU, Y. KUDO, K. UEDA and A. GORBMAN, Comp. Biochem. Physiol. *51 A*, 711 (1975).
[10] K. B. DÖVING, H. NORDENG and B. OAKLEY, Comp. Biochem. Physiol. *47 A*, 1051 (1974).
[11] Y. SATO and N. SUZUKI, J. Fac. Sci. Hokkaido Univ. *17*, 208 (1969).
[12] J. C. COOPER and A. D. HASLER, Fish. Res. Bd. Canada Tech. Rep. *415*, 44 (1973).
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[15] T. J. HARA, M. FREESE and K. R. SCOTT, Jap. J. Physiol. *23*, 325 (1973).