Electroencephalographic Studies of Homing Salmon

Abstract. *When adult spawning salmon (*Oncorhynchus tshawytscha, O. kisutch*) arrive at the "home" pond, most regions of the brain are electrically inactive, but the olfactory bulbs and posterior cerebellum are relatively highly active. Infusion of various natural waters from nearby sources other than the home pond into the olfactory sac produces little or no change in spontaneous electroencephalographic patterns recorded from the olfactory bulbs. Water from the home pond, however, produces a vigorous response of high amplitude. These findings suggest that olfaction is an important factor in guidance during the final phases of homeward migration of salmon, and that olfactory discrimination occurs at the level of either the olfactory bulbs or the olfactory epithelium.*

Salmon usually return from the sea to spawn in precisely the stream or tributary in which they were reared. Many biologists have attempted to determine the clues and mechanisms by which such fish home on their objectives. Hasler and Wisby (*1, 2*) proposed that during the final stage of the migration—that is, when the fish are in fresh water—olfactory guidance is of prime importance, whereas a sun-compass mechanism plays a role in open-sea navigation. Observations of the behavior of the salmon and experiments in which the olfactory nerve has been sectioned (*3*) or the nasal-sac aperture plugged (*4*) have supported the idea that olfaction guides migrating salmon. Hasler and Wisby (*2*) showed that the sensitivity of olfactory receptors in salmon fingerlings is so great that they can discriminate between the odors of two different creeks after brief training; they suggested that young salmon are "imprinted" by a volatile organic substance of the home stream. A characteristic behavior response to home water by adult migrating sockeye salmon also has been reported (*5*). Thus, it seems clear that the chemical sense may play an important role in orienting adult salmon.

In our study we used electroencephalography to study features of central nervous activity that may correlate with the chemosensitive discriminatory activity in homeward migration. Spawning adult salmon were taken from their home pond on the Lake Washington Ship Canal, adjacent to the Department of Fisheries, University of Washington, Seattle, at the end of their migration. About 3 years previously they had been fertilized, hatched, and reared at this same place and then released. Fourteen male chinook salmon, *Oncorhynchus tshawytscha*, and 21 male coho (silver) salmon, *O. kisutch*, were used; they weighed between 0.5 and 3.3 kg. They were anesthetized lightly with MS-222 and immobilized with an intramuscular injection of either *d*-tubocurarine chloride (4 mg/kg of body weight) or flaxedil (gallamine triethiodide, 2 mg/kg of body weight). While the fish were tied firmly in a fitted holder placed in a plastic trough, the gills were perfused with tap water (2 liters/min at 10° to 13°C) throughout the experiment. The brain was exposed by removing skin and the roof of the cartilaginous skull with a dental saw.

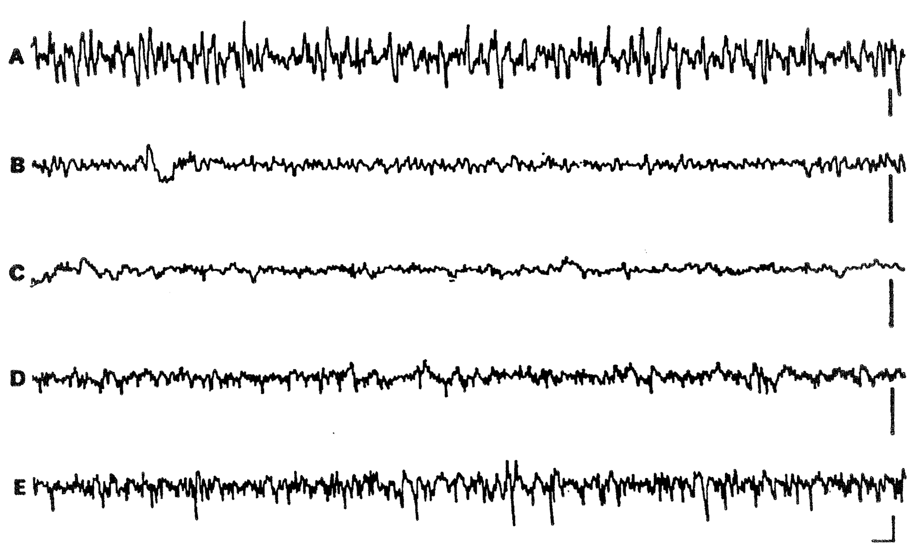

Fig. 1. Electroencephalographic records from the olfactory bulb (*A*), cerebrum (*B*), optic lobe (*C*), anterior cerebellum (*D*), and posterior cerebellum (*E*) of male silver salmon (length, 36 cm; weight, 0.5 kg). Vertical calibration, 50 μv; horizontal calibration, 1 second; temperature, 11°C.

Spontaneous electrical potentials were recorded from several different parts of the brain through silver–silver chloride bipolar electrodes (0.1 mm in diameter), the distance between electrodes being 1 mm. Electrodes were placed upon the dorsal brain surface in particular positions on each lobe of the brain, usually under visual observation with the aid of a dissecting microscope. Electroencephalographic (EEG) tracings were obtained by use of a Model D Grass polygraph and 5P5 preamplifier. Half-amplitude responses of this recording system were 1.5 cy/sec at low frequency and 60 cy/sec at high frequency. Experiments were carried out in a quiet room in subdued light.

Figure 1 illustrates typical EEG patterns of the spawning adult coho salmon. Activities in the olfactory bulb (dominant slow frequencies, 7 to 9 cy/sec; amplitudes, 35 to 65 μv) and in the posterior cerebellum near the median line (frequencies, 10 to 12 cy/sec; amplitudes, 25 to 40 μv) consistently had a much higher amplitude than those of the cerebrum or anterior cerebellum; amplitudes of the optic lobe were especially low. In some fish, in fact, the optic lobes were electrically "silent."

In contrast to adult salmon, young, hatchery-reared salmon about 15 cm long exhibited high activities in the olfactory bulb (frequencies, 8 to 10 cy/sec; amplitudes, 35 to 65 μv) and in the optic lobe (frequencies, 9 to 10 cy/sec; amplitudes, 25 to 50 μv). Cerebellar electrical activity in these younger specimens was not yet developed (Fig. 2). Electroencephalographic records were also made from brains of adult, nonmigratory rainbow trout (*Salmo gairdnerii*) and of goldfish (*Carassius auratus*), kept under the same conditions, for comparison with the adult salmon. In both of these nonmigratory species, spontaneous electrical activity in olfactory bulbs was relatively lower, while that of the optic lobes was much higher, than in adult spawning salmon.

The apparent specificity of the response of the adult migrating salmon to home water was confirmed as follows. A continuous flow of various samples of water (40 ml/min) was infused into the nasal cavities through glass tub-

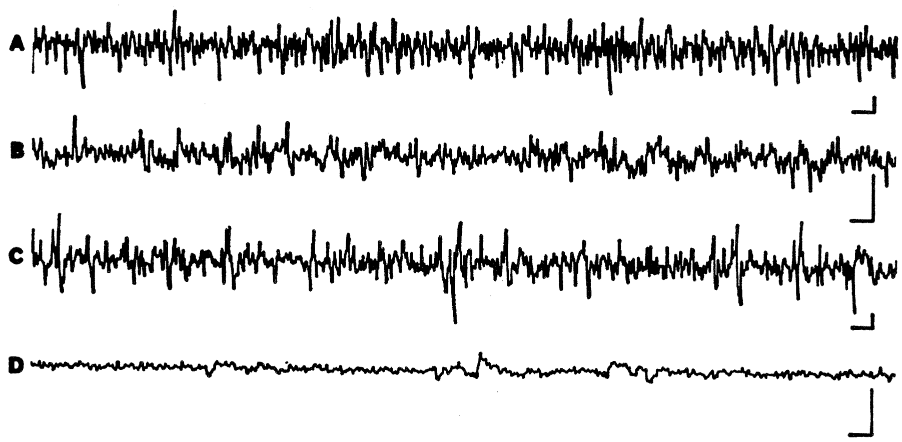

Fig. 2. Electroencephalographic records from the olfactory bulb (A), cerebrum (B), optic lobe (C), and cerebellum (D) of young chinook salmon (length, 16 cm; weight, 52 g). Vertical calibration, 50 μv; horizontal calibration, 1 second; temperature, 11°C.

ing under slight hydrostatic pressure from an elevated reservoir, while the gills were perfused with tap water. The samples of water were collected from (i) adjacent to the University of Washington College of Fisheries, in the canal leading from Union Bay to Portage Bay; (ii) the Washington State Hatchery at Seward Park on the shore of Lake Washington, about 8 km from the home pond; (iii) Green Lake, an isolated body of water in central Seattle; and (iv) Sammamish Lake, about 32 km east of Seattle but draining toward Lake Washington.

Figure 3 shows that infusion of home water into the olfactory receptor of the adult salmon produced a clear stimulation apparent in the EEG patterns from the olfactory bulb. This response may be considered stimulatory and dependent on a factor in the home water, since it disappeared only when the home water was diluted to at least 10 percent in distilled water. Samples of water from places other than the home pond produced little or no EEG change in the olfactory lobes. In order to test the specificity of the response to home water, it would be desirable to treat salmon from one or more other termini of migration with the series of waters used in this study, but the brevity of the spawning season and the difficulty of transporting and maintaining such large fish are serious problems.

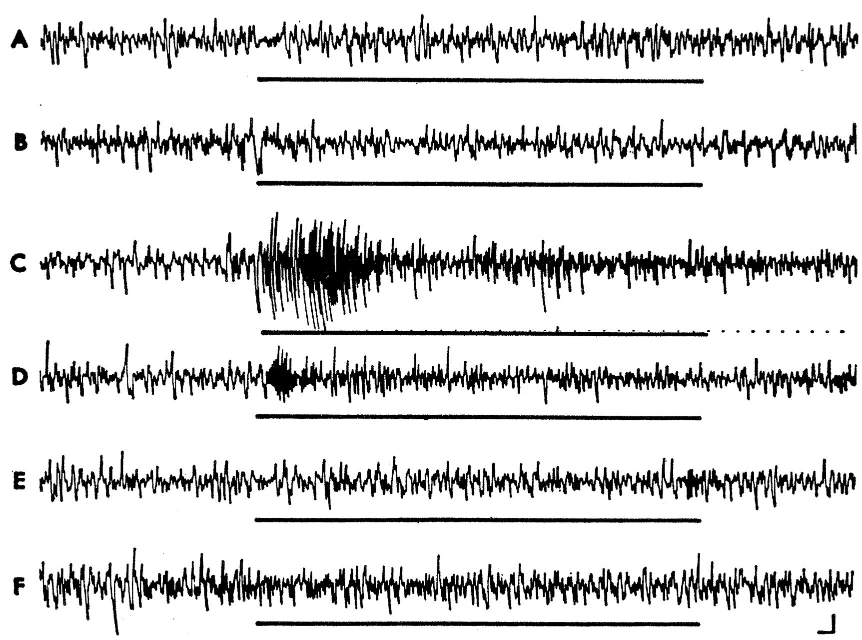

Fig. 3. Effects of infusion of different waters into the olfactory receptor upon EEG patterns in the olfactory bulb of an adult male silver salmon (length, 66.5 cm; weight, 3.3 kg). A, Distilled water; B, tap water; C, water from the home pond; D, Seward Park water; E, Green Lake water; F, Sammamish Lake water. Durations of stimuli are indicated by the heavy lines below. Vertical calibration, 50 μv; horizontal calibration, 1 second; temperature, 10.2°C.

All our results indicate that olfactory clues guide these anadromous fish in their migration to spawn. Furthermore, the very low electrical activity of the optic lobes of adult salmon suggests that visual clues may be of little use during the final stages of migration. Relatively high activity in the olfactory bulb of the young salmon also is consistent with the olfactory hypothesis; one may suppose (*4*) that they have to be imprinted by an odor of the home stream. An interesting aspect of our findings is that discrimination among the different waters tested is evident in the electrical response of olfactory bulbs. All the natural waters used in these tests presumably contained olfactory active chemicals, yet a selective and vigorous response occurred only when home water was infused.

Adult fish may be classified, according to Teichmann (*6*), into three types: (i) those in which optic and olfactory functions are well developed, such as *Phoxinus*; (ii) those in which optic function appears better developed than the olfactory, such as *Esox*; and (iii) those in which the olfactory sense is exceptionally well developed compared with the optic function, such as *Anguilla*. If this classification is meaningful, it is conceivable from the central neural activities described here that the salmon progresses through these types successively during the life cycle. It is possible that type (i) characterizes the young, freshwater salmon; type (i) or probably type (ii) applies to the stage of open-sea existence, during which salmon seem to navigate by a sun-compass mechanism; and type (iii) typifies the final stage of migration to spawn.

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References and Notes

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7. We thank L. R. Donaldson for the spawning salmon. This work was supported in part by NIH grant NB04887.

24 June 1965