Brainstem Temperature Affects Gill Ventilation in the California Scorpionfish

Abstract. *California scorpionfish,* Scorpaena guttata, *were implanted with a pair of thermodes which straddled the anterior brainstem. When the fish were in water of about 20°C, warming the thermodes to temperatures above 20°C caused a proportional increase in the ventilatory minute volume. Cooling the thermodes below 20°C caused a proportional decrease in the ventilatory minute volume. It is concluded that the anterior brainstem temperature provides an important input to the respiratory control center in teleost fish.*

Activity and temperature can rapidly change the oxygen requirements of fish. Although marked increases in gill ventilation occur during exercise, arterial and venous oxygen tensions change only slightly. It appears likely that activity produces proprioceptive or other input to the respiratory control center and thus alters ventilation in an appropriate manner (*1*). Increasing water temperatures are also a major source of stress in fish. For example, an increase from 10° to 20°C increases the standard oxygen uptake in goldfish by 254 percent (*2*). Temperature increases do produce increases in gill ventilation (*3*), but there is no evidence that gill ventilation is directly affected by temperature except through an effect on the metabolic rate of the entire animal (*4*).

During experiments dealing with behavioral thermoregulation in fish, it was noticed that shifts in the anterior brainstem temperature affected the rate and magnitude of opercular movements. The study reported here is an investigation of this effect.

The volume of water passing over the gills per minute (ventilatory minute volume) was measured by the method of Van Dam (*3*). A thin rubber membrane fitted over the head served to separate the inspired from the expired water. A set of siphons was arranged so that water which passed through the gills could be collected and measured. The California scorpionfish (*Scorpaena guttata*) was chosen for use because it is a sedentary species and tolerates long periods of confinement. The fish were collected locally and maintained in a tank supplied by the seawater system at the Scripps Institution of Oceanography. Water from this source was also used during the experiments and was usually between 19.0° and 21.0°C, with a much narrower temperature range during a particular experiment.

Each fish was implanted with a pair of thermodes which straddled the anterior brainstem. Circulating water of the appropriate temperature through the thermodes kept the adjacent brain tissue at the desired temperature. The temperature of the water leaving the thermodes was continuously monitored, and will be referred to here as the anterior brainstem temperature. Heart rate and ventilation frequency were obtained by recording from a pair of electrodes positioned just ventral to the heart.

At the beginning of each experiment the fish was lightly anesthetized with tricaine (MS 222). The electrodes were then positioned, and the fish was placed in the apparatus. The experiments were typically started about 1 hour later. The apparatus was shrouded during the experiments since detection of motion by the fish usually led to an immediate, although transitory, decrease in ventilation volume.

Figure 1 shows the effect of periodic heating and cooling of the anterior brainstem on heart rate, ventilation frequency, and ventilatory minute volume. Ventilation volumes were collected for 30 seconds, and heart rate and ventilation frequency were calculated for the same 30-second period. The left side of Fig. 1 shows that ventilatory minute volume and ventilation frequency decrease as the anterior brainstem is cooled to 9°C. There appears to be little change in the heart rate during the period of brainstem cooling. The right side of Fig. 1 shows the effect of heating the anterior brainstem to 29°C. During each period of brainstem heating there is an increase in the ventilatory minute volume. Ventilation frequency bears no obvious relation to brainstem temperature in this case, although it appears that there may be a slight effect on heart rate. The gradual downward trend in ventilation volume seen in Fig. 1 likely represents a gradual decrease in the oxygen requirements of the fish. Occasionally the fish would struggle to free themselves. These bouts of activity usually occurred after 3 or 4 hours in the chamber and always resulted in large increases in the ventilation volume.

To obtain the data in Figs. 2 and 3 the anterior brainstem temperature was shifted to various levels and the ventilation rate (milliliters per minute) was measured over a 1-minute period. The mean of the ventilation rates obtained immediately before and after

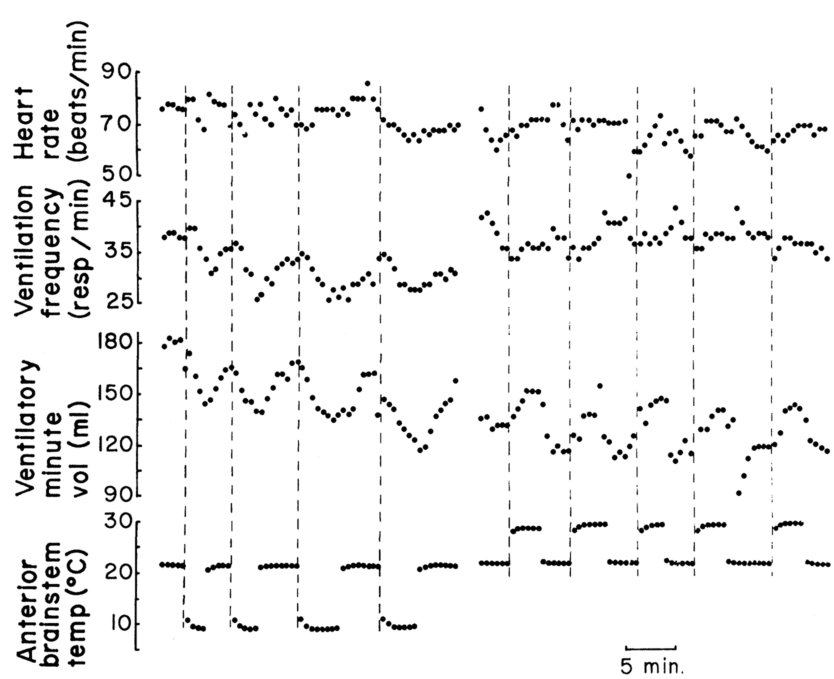
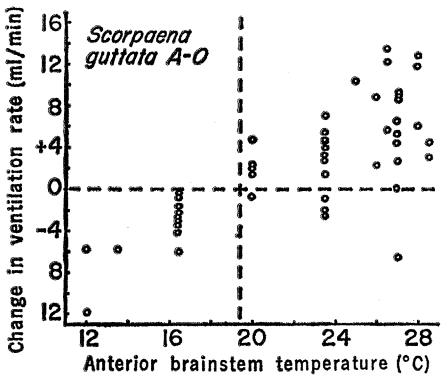


Fig. 1. Effect of displacements of the anterior brainstem temperature on ventilatory minute volume, ventilation frequency, and heart rate in California scorpionfish A-1. The break in the records represents a 1-hour interval.



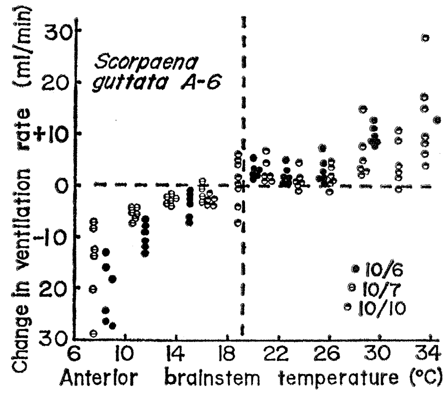


Fig. 2 (left). Effect of graded displacements of the anterior brainstem temperature on ventilation rate in fish A-0. The vertical dashed line shows the body temperature of the fish (exclusive of the anterior brainstem) during the experiment. Fig. 3 (right). Effect of graded displacements of the anterior brainstem temperature on ventilation rate in fish A-6.

the change in brainstem temperature was subtracted from this rate, and the difference was expressed as the change in ventilation rate. The vertical dashed line represents the temperature of the water (and the fish) during the experiment. Heart rate and ventilation frequency were not measured in these experiments.

Figures 2 and 3 demonstrate that as the anterior brainstem temperature was raised above the temperature of the fish the ventilation rate increased, and as the brainstem temperature was dropped below the temperature of the fish the ventilation rate decreased. Moreover, the change in ventilation appears to be proportional to the change in brainstem temperature.

Figure 4 illustrates the location of the thermodes in fish A-1, A-0, and A-6 in a ventral view of the brain. Four implanted fish did not alter their ventilation rates when the thermode temperature was changed. In two of these the thermodes were 3 mm anterior to the location shown in Fig. 4, and in the other two the thermodes were in the proper anteroposterior location but were displaced so that one thermode pierced the medial brainstem and caused considerable damage. The overall lengths of fish A-1, A-0, and A-6 were 29, 19, and 23.5 cm, respectively.

In one experiment a thermocouple was placed in the dorsal muscle just superior to the rib cage, and the anterior brainstem of the fish was heated to 31°C for 10 minutes. No increase in dorsal muscle temperature was detected.

Activity (*1*) and now temperature have been shown to directly affect the teleost respiratory control center, although the major inputs to this center probably come from structures within the body sensitive to respiratory gas concentrations (*4*). The neural signals produced by changes in activity and anterior brainstem temperature likely aid in minimizing the deviation in blood oxygen levels which might otherwise occur under conditions where activity or ambient temperature changes rapidly. The ventilatory response to temperature change is probably present in all teleosts, since increases in the magnitude and rate of opercular movements have been observed in Arctic sculpin (genus *Myoxocephalus*) and brown bullheads (*Ictalurus nebulosus*) during periods of anterior brainstem heating (*5*).

If the anterior brainstem temperature is transduced into a neural signal which aids in the regulation of blood oxygen levels, then changes in the ventilation rate should be mirrored by similar changes in the rate of blood flow through the gills. Although no major changes in heart rate were observed in this study, the cardiac

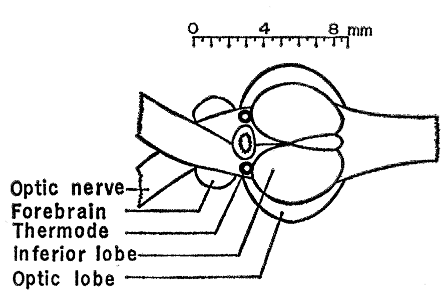


Fig. 4. Schematic drawing of the ventral side of the brain of *Scorpaena guttata*, illustrating the position of the thermodes in fish A-1, A-0, and A-6.

output may have been augmented by an increased stroke volume. Indeed, changes in the cardiac output of fish are typically associated with large changes in stroke volume and small changes in heart rate (*6*). The increased heart rates associated with higher body temperatures in fish are thought to be due to a direct effect on the pacemaker cells of the heart (*7*). The temperature of the heart was not altered in the present experiments. In rainbow trout, increased rates of artificial perfusion of the gills are accompanied by an increased cardiac output (*8*). Thus, increased ventilation alone may increase cardiac output.

Rodbard *et al.* (*9*) and Heath *et al.* (*10*) found that increasing and decreasing the local hypothalamic temperature of turtles led to increased and decreased blood pressures, respectively. Both groups suggested that such pressure changes might reflect a neurogenically controlled cardiovascular response tuned to the increased metabolic needs that ectotherms encounter with increases in temperature. If this response is similar to that of the scorpionfish, then changes in the respiratory minute volume of reptiles would also be expected during heating or cooling of the anterior brainstem.

Anterior brainstem heating and cooling in fish may provide an alternate means for determining the energy requirements of gill ventilation. Such studies have been plagued by the lack of means for persuading fish to increase gill ventilation without otherwise affecting oxygen consumption (*4, 11*).

This study suggests that long before the evolution of endothermy in birds and mammals, fish had evolved a neural output from the anterior brainstem which provided a signal proportional to deviations in local temperature. This neural output probably developed to control thermoregulatory behavior (*12*) and to coordinate autonomic responses in preparation for conditions caused by changes in body temperature. Further evolution may have involved the same neurons in a system to regulate autonomic responses so as to minimize changes in body temperature.

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References and Notes

1. E. D. Stevens and D. J. Randall, *J. Exp. Biol.* **46**, 307 (1967); A. M. Sutterlin, *Physiol. Zool.* **42**, 36 (1969).
2. F. E. J. Fry and J. S. Hart, *Biol. Bull.* **94**, 66 (1948).
3. L. van Dam, thesis, University of Groningen (1938).
4. G. Shelton, in *Fish Physiology*, W. S. Hoar and D. J. Randall, Eds. (Academic Press, New York, 1970), vol. 4, p. 293.
5. H. T. Hammel and L. I. Crawshaw, personal observations.
6. D. J. Randall, *Amer. Zool.* **8**, 179 (1968).
7. P. Laurent, *Arch. Anat. Microsc. Morphol. Exp.* **51**, 337 (1962).
8. J. C. Davis and J. M. Cameron, *J. Exp. Biol.* **54**, 1 (1971).
9. S. Rodbard, F. Samson, D. Ferguson, *Amer. J. Physiol.* **160**, 402 (1950).
10. J. E. Heath, E. Gasdorf, R. G. Northcutt, *Comp. Biochem. Physiol.* **26**, 509 (1968).
11. G. M. Hughes and G. Shelton, *Advan. Comp. Physiol. Biochem.* **1**, 275 (1962).
12. H. T. Hammel, S. B. Strømme, K. Myhre, *Science* **165**, 83 (1969); L. I. Crawshaw and H. T. Hammel, *Life Sci.* **10** (part 1), 1009 (1971).
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Mathematical Modeling and Human Nutrition

Jean Mayer's article "Toward a national nutrition policy" (*1*) is an impressive report on the recent history and accomplishments of social contributions to the improvement of nutritional health in this country. Mayer is right in pointing out the causal relations between *improper diet* and malnourishment, and he is also right in listing the potentialities of institutional feeding programs, food labeling, education, and research as possible means of achieving improvement on a national scale. However, he is not specific as to how these factors can significantly affect the following of "proper diets" and thus eliminate the causes of malnutrition.

Most nutritionists seem to share the mistaken assumption that the knowledge of the nutrient composition of foods and the recommended dietary allowances is somehow sufficient to plan a diet, when in fact this information contains only part of the coefficients of the system of mathematical equations that must be solved to determine nonnegative quantities of food. Contrary to popular belief, the problem of diet *planning* is not a nutritional, but a mathematical one (*2*). Moreover, the term "proper diet" defies definition, both conceptually and operationally, unless the problem is cast into some mathematical model built upon the concepts of constrained optimization techniques. The scientific methodology to plan diets which are "proper" in the sense of satisfying consumers while meeting nutritional and budgetary allowances is already well developed (*3, 4*). Years of research and repeated comparisons in many institutions (*4, 5*) have consistently shown that diets planned with mathematical techniques on computers will cost less (by 10 to 30 percent), be preferred, and be better balanced nutritionally than diets planned by conventional means. It is laudable that increased federal funding is now available to extend participation in the school lunch and other volume feeding programs. But by changing from the conventional to the mathematical (computerized) method of diet planning, these programs could be extended to about 20 percent more people without extra funds.

Other disturbing signs point to the existing shortcomings in diet planning methods. One is the proposed rule of the Food and Drug Administration for nutrition labeling (*6*). Nutritionists without mathematical models have limited use for precise nutrient composition data; more data means only that more information will have to be ignored. The proposed labeling formally advocates shortcuts in determining the precision of nutrient values that do not benefit the consumer, yet place unnecessary constraints on the food packagers. In this process, the issue of the consumer's right to know and the method of using the information are confused.

It is consistent with this picture that the majority of the population is ignorant or indifferent about proper diets. Of the millions who "eat out," no one can purchase a balanced meal. A fixed combination of menu items that explicitly guarantees some specified fraction of recommended daily allowances (*7*) is yet to be included in the menus of our food service industry.

A move toward mathematical methods for meal planning will require an interdisciplinary approach, with the participation of fields not traditionally linked to that of human nutrition. Only with the aid of mathematics, mathematical statistics, psychometrics, operations research, and computer science can the vast amount of information generated by nutrition science be fully utilized in medical or economic decisions. Mathematical modeling is the key to the perspective Mayer envisions when he calls for the cooperation of the scientific community in reexamining "our policies and habits concerning food." Within this broad framework, however, three specific issues emerge that must have top priority in our national nutrition policy. These are the problems of data, education, and research.

Nutrition science is a quantitative field, routinely producing and using a large amount of tabulated data. It should be a fundamental part of our national nutrition policy to see that a reliable source of food nutrient composition data is available and easily accessible to the public through a central computerized data bank.

To help nutritionists begin to conceive diet problems in mathematical terms, a complete overhaul of the curriculum in dietary education is necessary. The recent report of a study commission on dietetics (*8*) omits any reference to this need. The recognition of the role and value of scientific methods in diet planning is the responsibility of the leading educators and researchers in nutrition science. Until this responsibility is met, cooperation between experts and other scientists who are now often considered "outsiders" will be hindered.

The art of mathematical modeling in the field of human nutrition is still in a developmental stage. With more and better data and with improved interdisciplinary cooperation, research teams could develop more sophisticated and acceptable models of diet planning that could be applied in hospitals, supermarkets, restaurants, and even to the cost-of-living index (*9*). Research in these areas demands both talent and funds, but the return in benefits to the public far outweighs the investment. The extension of funding for diet planning research should be an integral part of any program or policy which is aimed at the revitalization of nutrition science and the increase of its potential contributions to our life.

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