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Report to the William and Flora Hewlett Foundation

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REPORT TO THE WILLIAM AND FLORA HEWLETT FOUNDATION

by

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Experiments on Unconstrained Environmental Systems

From April to December, 1978, I have been on Sabbatical Leave from the Headship of the Department of Applied Physics, University of Strathclyde, Glasgow, U.K.. From April through August, I was supported by Grants from the North Atlantic Treaty Organization and from my hosts. Since then, my support has been a much appreciated Grant from the Hewlett Foundation. This has enabled me to work without undue financial worry. This period has been by far the most productive of my Leave.

The work done before September has been described in the report attached hereto. Building on that work, I have been attempting to model the environmental-physiological system (the thermal regulatory system of a mouse) on which my colleagues and I had earlier made dynamic measurements, and to test the models by comparing their behavior with the experimental results.

The Experimental Results

In those experiments, the temperature of the mouse's environment was varied sinusoidally (with amplitude of a few degrees Celsius), at different periodicities (ranging from 22 to 250 minutes) in different experiments. The oxygen consumption was measured continuously, and was found to vary greatly, in a very complicated fashion, presumably because the mouse's basal metabolic rate fluctuates, and because it was free to eat, drink, excrete, run about or sleep, all activities which affect oxygen consumption. Nevertheless, it was possible to extract (by Fourier analysis) in each experiment the component of variation that had the same frequency as the temperature excitation (more details and references are given in the earlier report). The experimental results, shown in Fig. 1, are the amplitudes and phases of those components, as functions of frequency of excitation. This "frequency response" of the system is believed to be a property that is determined by the internal processes in the mouse. The results are rich in distinguishing features that any model would have to explain. In particular, only certain kinds of models can show a peak in the amplitude response.

Modelling

Keeping Occam's Razor firmly in mind, we start with the simplest model, and elaborate it only as far as the experiments demand. The simplest possible model of thermal regulation is that of a body whose temperature is uniform throughout, in which heat is generated at a constant rate, and which is surrounded by an insulating layer, corresponding to fur. Such a body, if placed in an environment whose temperature fluctuates, will experience smaller fluctuations in its internal temperature, because of the thermal resistance of the fur, and its own thermal capacity. However, if the external temperature fluctuates very slowly, the internal temperature will fluctuate just as much -- only higher frequencies of fluctuation are attenuated. This would be physiologically unsatisfactory. Furthermore, such a model implies no link between oxygen consumption and environmental temperature, yet the experiments emphatically show that there is such an effect.

In order to make this link, the heat supply to the body was supposed to vary linearly with body temperature, the rate of heat production falling as the temperature rises. The ratio of the change in heat production to the change in body temperature causing it is a parameter (h) of the model, to be determined by fitting to the experiment results. So also are the thermal capacity of the body (C) the heat-transfer coefficient of the fur (K), and the volumes of oxygen required to produce a unit of heat by metabolism (α). C and α are already known with enough accuracy from general studies on mammals. Thus, the model would leave two parameters, h and K, to be determined from the experiments. (The result for K must lie within fairly narrow limits to be plausible.)

Unfortunately, this simple model has a frequency response where amplitude has a maximum only at zero frequency. This is clearly at variance with the observations, and we must therefore elaborate. The physiologically most plausible elaborations were to make the heat production depend, not on the temperature at that moment, but on that at time T earlier, and also to make the oxygen consumed from the air correspond to heat production T_1 earlier. Indeed, these elaborations are required by the knowledge that all physiological processes that are not mediated solely by nerve signals, have rather long response times. These may be in the responses of "transducers", or in the transport of hormones. The delays, T and T_1, would be further parameters to be determined from the data (they might, of course, come out to be small).

Within this model, it was indeed possible to produce a very reasonable fit with the data. However, the values of the parameters then found, though apparently physiologically reasonable, correspond to an unstable model. This was clearly unacceptable. No remotely reasonable fit to both the amplitude and phase could be found for any stable configuration, though the amplitude data alone could be fitted. Thus, even further elaboration was required by the data.

Even though the features so far built into the model were insufficient, they would all have to be part of any satisfactory model eventually found. However, the further features added to the model are choices from among physiologically plausible mechanisms.

The best fit that was eventually obtained was with a model that supposed heat was lost not only through the skin, but also through the breath -- what is called "panting" when it becomes extreme -- and that the rate of heat loss by this mechanism responds to the air temperature direct, and not to the internal body temperature. As the mouse has bare skin, and presumably temperature sensors, in nose, ears, feet and tail, this is not implausible. It was also supposed that heat was supplied under the skin by two mechanisms, one responding quickly, the other slowly; these might correspond to vasodilation, and to shivering and exercise, respectively.

With this model, a good fit was obtained to the amplitude data, and tolerable fit to the phase data, as shown in Fig. 2. However, the divergence fo phase is still systematic, not random, so that further features are called for. However, I doubt if these further features can usefully be added without considerable physiological insight, which I lack. From my point of view, this study has gone far enough. I intend to publish this work.

Computation

The modelling was done by solving the differential equations analytically, and computing the resulting response functions. Ideally, this should have been done on a flexible, interactive computing system with visual display.

To my astonishment and disappointment, the Computing Center at LBL does not provide ready access to such a system for the inexperienced user. Further, I was warned by my colleagues that it was not worth going through the complicated procedures needed, as the interactive computing system itself was very unsatisfactory.

I therefore did the early computing on a programmable desk calculator, which had to be shared with another user. When the data forced me to more complex models, this became impossibly tedious, and visual display became imperative in the evaluation of the results.

At that point I was fortunate in meeting Dr. David Auslander, of the Department of Mechanical Engineering, on the UCB campus. He gave me access to an interactive system based on a minicomputer in his Department, and it was there that the bulk of this work was done. I cannot overstress my appreciation of this help by Dr. Auslander, without which the work could not have succeeded.

I think it is remarkable that satisfactory facilities for work of this kind do not appear to be readily available at LBL.

Relevance to Ecosystems

This work has been done on the influence of an environmental variable (temperature), on a physiological variable (oxygen consumption of a mammal). This system was chosen because it was readily available, small, quick in response, and because the variables were readily measurable. However, I believe that the method is even more relevant to measurements on ecosystems, and I hope that such experiments will soon follow. The basic reason for doing sinusoidal experiments is to produce a dynamic as opposed to a static, description of the system under study. This is needed for two reasons. (1) It allows prediction of both transient and steady-state responses of a system to disturbance; often the most important responses are transient. (2) The dynamic description contains enormously more, and more significant, information about the system than does a static one. This is clearly seen in the way I was able to reject certain models unambiguously, not because they were implausible, but because they could not fit the data. This is "falsification of hypothesis" in the fundamental sense of scientific method.

However, both these aims can be achieved by measuring the response to an impulse, to a "step", or to "pseudo-random binary signals". Unfortunately, these methods cannot usually be used in environmental or especially in ecological systems because they require too much control over the "natural" variations of the systems being examined. The sinusoidal input provides the greatest ability to reject "noise" (that is, irrelevant variations) and establish an unambiguous relationship between cause and effect.

My experience with attempts at modelling this system has shown how even relatively crude data allow one to reject whole classes of models, to draw attention to indispensable features of models, and to suggest further experiments. It re-emphasizes the need for experiments in the environmental sciences, rather than reliance on untested models and simulation.

In this sense, I believe that what has already been done is valuable. Dr. John Harte and I are hoping to do experiments of this kind, if funds can be found, with the aquatic microcosms he has in his laboratory.

Acknowledgments

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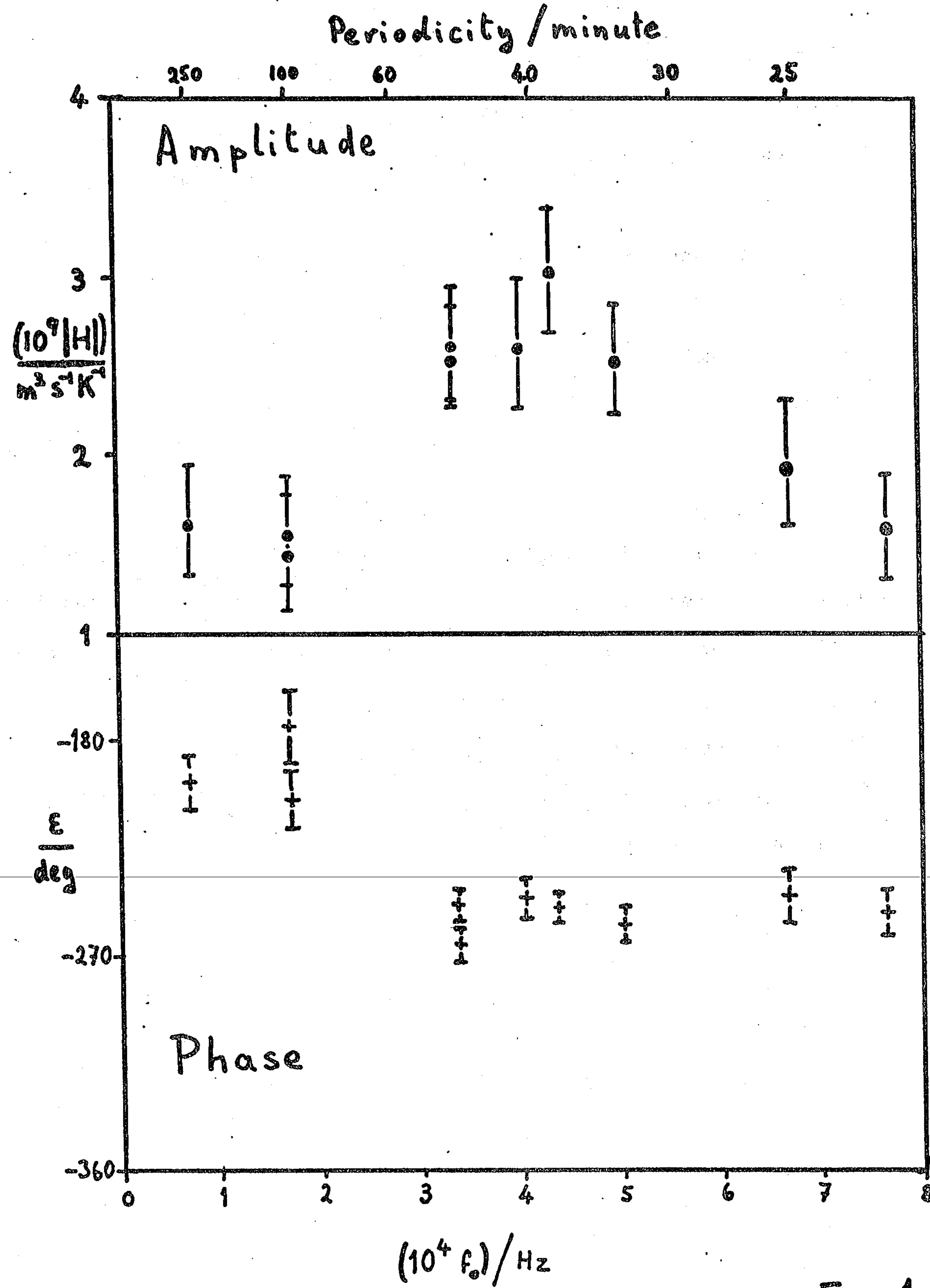

Fig. 1

Measurements of the amplitude and phase of the response of rate of oxygen consumption to variation in ambient temperature, at different frequencies, f_o.

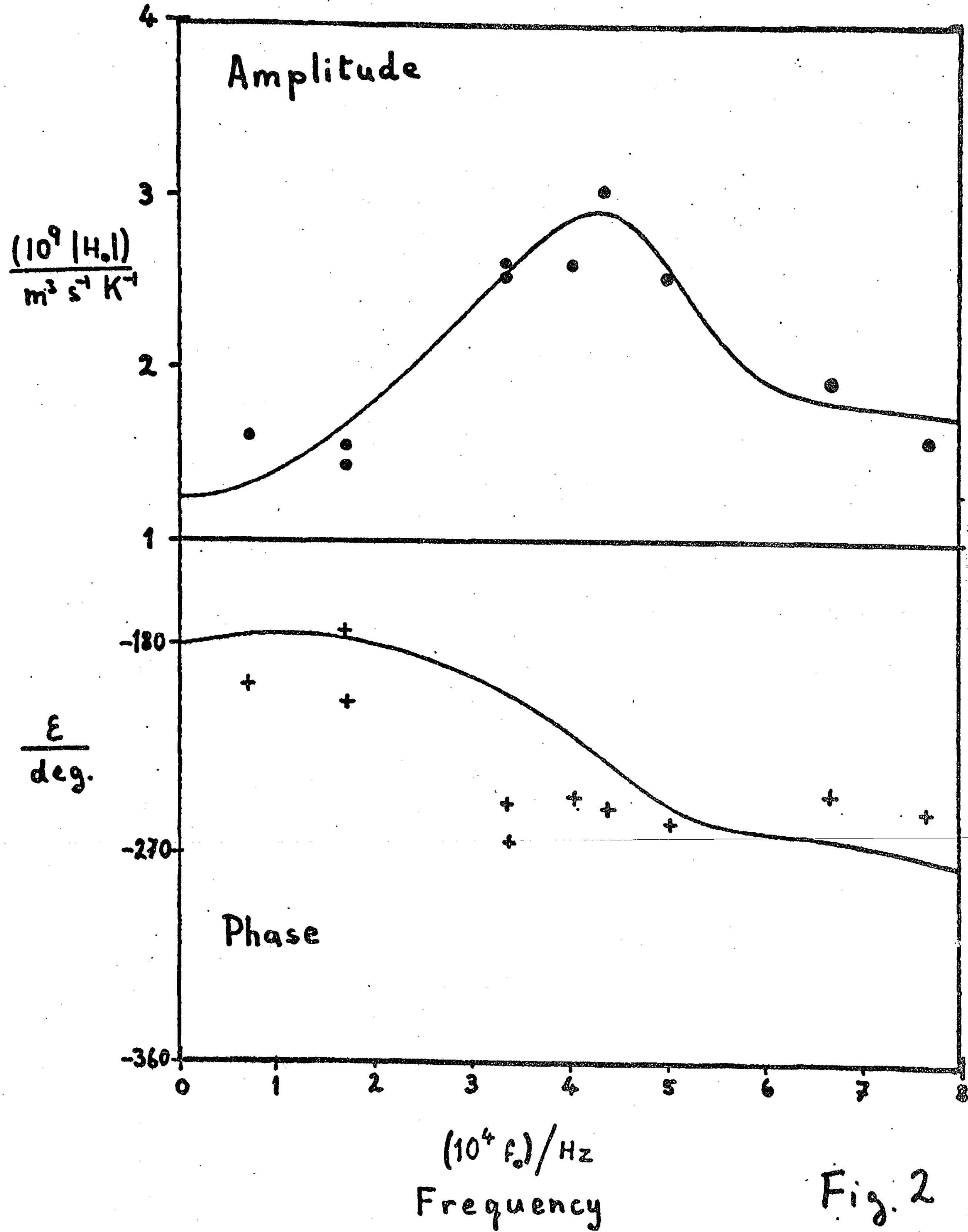

Fig. 2

Best fit obtained with physical model.