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The Physiology of Adaptation*

THE TITLE OF this lecture is misleading; a more accurate description of the subject matter would be "Some random remarks on physiological adaptation in man, illustrated by a description of personal experiences of studies on the effects of hot climates". Even this cumbersome subtitle is probably inadequate; adaptation is throughout limited to physiological adaptation.

The definition of adaptation can be attempted by considering its characteristics. There is a delay in the development of adaptation which distinguishes it from the immediate physiological response. If a man is put into a hot and humid environment, his skin blood flow will increase and he will sweat. If the environment is sufficiently severe his body temperature will rise and the sweat rate increase. If he leaves this environment and has a cold shower, he will rapidly return to his pre-exposure condition. The responses are those evoked by stimulation of the temperature regulating mechanisms. But, in addition, adaptative processes have been initiated and a subsequent exposure, provided it is not unduly delayed, will evoke qualitatively similar physiological responses, but they will be quantitatively altered. Reinforcement and time are needed to establish an adaptation, and the various modifications of physiological response do not necessarily follow the same time course. One modification may be easily aroused, another may need more stimulation before it becomes apparent. And so, in Adolph's phrase (Adolph, 1964), adaptation is a syndrome. Since for physiologists adaptation is environmentally determined, a definition could be that adaptation is any property of an organism which favours survival in a specific environment, particularly a stressful one (Prosser, 1964). The environments and conditions which have been studied particularly as far as man is concerned are: *high altitude*, *high pressure*, *heat*, *cold*, *high gravitational force*, *low calorie intake*, and *muscular work*. It appears to be true that all mankind has the capacity to adapt, as indeed Darwin (1859) himself stated:

> Hence I am inclined to look at adaptation to any special climate as a quality readily grafted on an innate wide flexibility of constitution, which is common to most animals.

But when we consider the diversity of man, it might be expected that marked differences of adaptation could be demonstrated. However, present evidence is inadequate to establish unequivocal differences. And where there is suggestive evidence we are unable to state with confidence the reason for such differences. The position to-day is not very different from that stated by Darwin (1859):

> How much of the acclimatization of species to any peculiar climate is due to mere habit, and how much to the natural selection of varieties having different innate constitutions, and how much to both means combined, is a very obscure question.

If evidence is to be obtained, then relatively large numbers of human beings have to be studied, and their responses to carefully standardized conditions compared with some precision. This is, of course, far easier to say than to do. The techniques involved in studying human physiology have become increasingly elaborate, as in all fields of research, and so have tended to be less applicable on a large scale in the field.

However, this very elaboration has now begun to make it possible to conceive of relatively large scale studies, due mainly to the development of miniature equipment which can be used by subjects without undue interference. My colleague, Mr. H. S. Wolff, has played a large part in this development, in which he has deliberately aimed to produce—in his phrase—"socially acceptable instruments".

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There has been so much work necessary within the fields of physiology that we have deliberately or perhaps, in some cases, acting in ignorance, confined ourselves to physiology without looking at the contributions from other disciplines.

Over the years, perhaps rather slowly, the many factors which can affect physiological responses have become clearer, not necessarily as subjects for study but rather for conditions to be controlled. Although this has meant an improvement in the results obtained, in the sense of isolating and controlling unwanted factors, it has also led to an awareness that physiology is not enough. We cannot ignore psychological effects, even if only for the reason that they are such a nuisance in spoiling one's results. Sometimes, of course, unexpected psychological or emotional responses are of great interest to physiologists. During the war, Henry Barcroft, McMichael, Sharpey Schafer and I planned some joint work on haemorrhage, combining plethysmography and the then new technique of cardiac catheterization. Our subjects were volunteers from the Friends Ambulance Unit, and were understandably apprehensive as apparently they gathered that a steel tube was to be pushed into the heart. All went well in the first experiment until we started to bleed the subject, when he fainted. Quite an unplanned event, but the results were dramatic. To our immense surprise, during the fall of blood pressure which accompanies fainting, the blood flow in the forearm went up, not down. So we happily set off to investigate this remarkable event, with to us most satisfactory results. Since then a number of emotional effects have been captured by the physiologists and studied by purely physiological techniques. As far as the circulation is concerned, emotions such as anger and fear have such obvious effects that they can be easily recognized and then studied. It has taken longer to realize what important effects they can have on other systems, such as those involved in temperature regulation.

What I am attempting to show, without over elaboration, are the profound effects of psychological events on physiological processes. Although these have certainly been recognized for a very long time by physiologists, undoubtedly in many cases—and particularly in human physiology—these have tended to be regarded as unwanted effects and our conduct and design of experiments have been carefully planned in attempts to exclude these effects. But if we are concerned as physiologists with studying man as he ordinarily exists and lives, as opposed to the highly artificial and abstract conditions we impose in the laboratory, then we must not only be aware of these disturbing influences, we must also include them in our studies. This is certainly the case if we wish, as we do, to bring in physiology to the study of human populations.

I may seem to be straying a long way from the physiology of adaptation in man, but if we want to examine the process of adaptation, even to such impressive changes in the environment as may be produced by ascending the highest mountains or travelling to the polar regions, or to the hottest climates, then also our study will be incomplete or inadequate to the degree that we fail to take into account all the factors in the situation. And a formidable list it is: age, sex, body form and composition, nutritional state, habitual activity, physical work capacity, climatic experience, genetic factors, cultural patterns and behaviour. No doubt this list is far from complete, but there is certainly enough to keep physiologists busy for a long time to come.

Effects of Hot Environments

As an illustration of the distance we have to travel, I propose to describe some of the work on the effects of hot environments on man. It would have been equally possible to look at studies of cold climates, or high altitudes, but not to discuss all three in the compass of a single lecture.

The problem of heat is chosen for several reasons, one of which is the obvious fact that a high proportion of the human race lives in regions which are hot, i.e. have a mean air temperature of 20° C or more during the daylight hours throughout the year. Very roughly, some two thousand millions, or two-thirds of the world's inhabitants, live in such climates. So the effects of heat on man and the way he adapts to these may be said to have wide application and be of some practical importance, as well as of considerable scientific interest.

The history of scientific investigations on the effects of hot climates has been sketched by several writers, and will not be repeated here. Although there were many important contributions during the earlier part of the century, one can date the period of intensive study to the Second World War, when the subject became a critical one to the armies and navies involved. Millions of men were moved to and from hot jungles and deserts back to temperate and frigid zones, and it was sufficiently evident that climatic factors could be of decisive military importance. Because of the difficulties involved in making detailed studies in the field, climatic chambers were constructed in which the various environments could be more or less reproduced and controlled. Very important field work was done, in spite of great difficulties, but the success of experiments in climatic chambers undoubtedly emphasized this mode of study, so they were continued after the war was over and, of course, continue still. The military emphasis made it inevitable that the subjects of these experiments were young, healthy, male adults and this also has continued. By far the largest number of experiments has been made on this particular group of the population.

Amongst the many important findings from chamber experiments are that men can develop heat adaptation or acclimatization (the terms are, to some extent, synonymous) even if they are only exposed for a short period each day, the rest of the time being spent in cool or temperate conditions. Originally the time required was thought to be four hours a day in a hot and humid environment in which the subject worked. More recently, Dr. R. H. Fox and his colleagues have shown that as short a time as one hour a day, provided the body temperature is significantly raised, can still produce adaptation (Fox, 1965). The second significant point is that all subjects tested, and there must be several thousands, have developed acclimatization to heat although they were all native to temperate climates and their ancestors were also. Implied is the third point, that the physiological changes which characterize heat adaptation are unequivocal and striking, with large alterations. The effective stimulus appears to be an increase in body temperature. But, surprisingly, man does not appear to adapt to a raised body temperature itself.

Studies in the Field

Since acclimatization to heat can be developed by short daily exposures, it might be predicted that performance in a hot climate would be similar in groups of men artificially or naturally acclimatized, and that both would have better performances than unacclimatized subjects. These predictions have been tested in a large scale field experiment but only partially verified.

The plan was initially to measure the responses of a group of sixty soldiers exposed to a hot and humid environment in which carefully standardized work was done. On the basis of their body temperature and pulse rate at the end of the four hours exposure, and their sweat rate, six men were rejected and the remaining fifty-four were divided into three matched groups whose average responses were similar. Subsequently, one group was sent to Aden for six weeks to become naturally acclimatized to a hot climate, a second group was exposed daily over four weeks in climatic chambers in London, to be artificially acclimatized, and the third group was sent to Scotland to act as controls. At the end of the treatment period all the subjects were re-assembled in London and were again tested in the climatic chambers. The physiological performance of the artificially acclimatized group was slightly better than that of the naturally acclimatized group; both groups were now significantly superior to the control group. All three groups were flown to Aden, where an arduous military exercise was carried out for twelve days. Measurements were made of body temperature and pulse rate on all subjects at approximately hourly intervals during the working day. In addition, body weight, fluid intake and urine output were measured, and some measurements of food intake were made. Cases of heat illness and other medical conditions were carefully recorded and military performance was assessed by a team of experienced officers.

Body temperatures were significantly higher in the control group than in the other two groups. The smallest rise was observed in the artificially acclimatized group, but there was relatively little difference between this group and the naturally acclimatized group. There were no significant differences between the three groups in water intake, food intake, urine output or loss of body weight. It would be expected that the group with the lowest mean body temperature had an important physiological advantage over the other two groups and particularly over the control group, and that this demonstrated the efficacy of artificial acclimatization. However, the casualty rates were much the lowest in the naturally acclimatized group, and although the control group during the first five days were significantly worse than the artificially acclimatized subjects, in the last part of the trial there was little difference between these two groups.

Furthermore, the military performance followed a similar pattern, with the naturally acclimatized group the best, the control group initially the worst, and the artificially acclimatized group rather better than the controls for the first five days but no different in the last part of the trial. In spite of a real physiological advantage, the artificially acclimatized group were, in terms of performance and liability to illness, only slightly more effective than the control group.

This unexpected result can, to a considerable extent, be explained by additional observations made during the trial and by further information. It was hoped, for example, that in matching the three groups on the basis of their physiological responses to heat, other factors would be randomly distributed. Such was not the case. Intelligence scores were significantly lower in the artificially acclimatized group than in the other two and their military experience was also the shortest, both factors which would have affected military performance. The morale of this group also appeared to be low as compared to the other two groups. The incidence of gastro-intestinal disorders was markedly higher in the artificially acclimatized and control groups, as compared with the naturally acclimatized group.

It was concluded that the natural situation is more complex than in the laboratory. In addition to acclimatization to heat, the group sent to Aden in the treatment phase had also acquired an adaptation to local micro-organisms as well as becoming familiar with the actual place. It would appear that the factors which can affect man's performance in the heat are not only those of acclimatization but also include (a) intelligence, (b) experience, (c) personality, (d) morale or discipline, and no doubt many others, including genetic constitution.

Accounts of this experiment have already been published (Edholm *et al.*, 1963; Edholm *et al.*, 1962), but it has been mentioned here in some detail as it illustrates the general theme that physiology is not enough. However, it also shows the feasibility of carrying out relatively large-scale studies in the field, and in subsequent experiments considerably more elaborate investigations have been completed successfully (Edholm *et al.*, 1964).

Although there have been extensive studies in climatic chambers and also in the field, these have been mainly on young, healthy, adult Caucasian males. But there have also been important studies of other ethnic groups, notably by Ladell amongst West Africans, Wyndham in South Africa, as well as some work on the American Negro and the Australian Aborigine. The main finding is the remarkable degree of similarity between apparently markedly different peoples. The chief difference is that peoples such as the West Africans, living in an essentially hot wet climate, regulate body temperature with a rather lower sweat rate than Europeans acclimatized to the heat (Ladell, 1964).

Among the difficulties of comparing groups from different peoples are body size and shape, and nutritional differences, as the most obvious. In many cases, a considerable number of subjects are needed before there can be any certainty of establishing differences.

Investigation on Indian Subjects

In one investigation carried out on Indian subjects, a comparison was made with British white subjects in which a deliberate attempt was made to select the Indians to match the British subjects in body size. These studies were made in

London, and the Indians were flown over at the end of September, having spent the hot season in Lucknow carrying out a moderately arduous training programme. They spent the winter in England, eating the same food as their British counterparts. It was thought that the Indians would on arrival be fully, or nearly fully, acclimatized to heat, and this could be demonstrated by high sweat rates, small or moderate increases in body temperature and pulse rate in the climatic room, and that there would be large differences with unacclimatized British subjects. It was also predicted that at the end of their four months stay in Britain their adaptation to heat, as judged by responses in the climatic chamber, would have decreased and might be more similar to unacclimatized British, but if they were re-acclimatized by daily exposure it was believed that they would re-adapt more quickly than the British. Only some of these predictions were realized. On the first test in the heat the Indians were, on the average, better than the British, but not much. Their sweat rates were a little higher, body temperature just significantly lower, and pulse rate was about the same. The difference was, to us, really surprisingly small. So the first prediction was not entirely confirmed.

The second prediction, about loss of acclimatization, was confirmed by the results of the second test after four months spent in England, when sweat rates were lower, body temperature and pulse rate higher than on their original test, and they were perhaps rather worse than the unacclimatized British. Incidentally, their health during the four months was remarkably good and there was little change in body weight. Then the two groups were acclimatized by daily exposure in the hot room for two weeks. We expected now, in spite of previous disappointment, that there would be a marked difference between the two groups in the rate of development of acclimatization, with the Indians winning. To our surprise, the Indians lost. The differences at the end of two weeks were highly significant, with the British having the better physiological performance (Edholm *et al.*, 1965).

These results certainly indicate the need for more detailed studies of different populations. They are difficult to explain and the very point of picking Indians with large body size may have been partly the reason. These subjects could not be said to be a representative or a random sample of the Indian population. They came from many different regions, but had all served for a number of years (five or more) in the Indian Army and led reasonably similar lives. But in the distribution of body size they came from the top end of the scale and conceivably they could be relatively poorly adapted compared with smaller Indian subjects.

The factors which might affect adaptation to heat have been listed above. Although some information is available about some of these factors, in most cases it is inadequate and as regards genetic constitution there is virtually no information at all.

There are other gaps, such as the effects of previous or existing disease states.

In the first part of this lecture I indicated my belief that physiology is not enough, but it is painfully clear that even now we do not have enough physiology. So it might seem that the proper way to proceed would be to extend carefully controlled physiological studies to begin to cover the glaring gaps. I want to argue an opposite, but not necessarily opposing, view. I feel that the opportunity to take part in population studies provides an essential stage in the evolution of investigations of human physiology. It was for this reason that, personally, I found the concept of the International Biological Programme so exciting. In this programme the objectives of the section devoted to Human Adaptability include joint work by geneticists, anthropometrists and physiologists in the study of populations, by the development of multidisciplinary teams. Selected populations would be examined to establish demographic features, genetic and anthropometric characteristics, as well as the pattern of disease. Cultural and sociological features would also be determined. The numbers involved in such studies would be relatively large, attempting a virtually complete cover of the selected population. Absolute numbers would clearly depend upon the particular population concerned, but could be 1,000 or considerably more.

It is perfectly feasible for such large-scale studies to be made in respect of genetics and anthropometry, but as far as the physiological side is concerned it is at present impracticable. Instead, we must work on samples of the defined population, and for some of the more elaborate tests we must use sub-samples.

Investigation in Israel

In these population studies, an essential objective is, wherever possible, to examine similar populations, i.e. genetically and preferably culturally similar people living in adjacent but contrasting environments, and for dissimilar peoples living in the same environment. Such situations do exist, and I have explored the possibility of one such situation, in Israel (Edholm, 1966). Here is a country which is geographically small; the greatest distance is rather more than Dan to Bathsheba, it is now Metullah to Eilat, but even this is not more than 250 miles, and in places it is not more than ten miles wide. Although it is so small, one can distinguish three climatic zones, apart from the coastal area. These are the desert area of the Negev, the mountain region of Judaea with an altitude of 1,000 metres, and the semi-tropical part of the upper Jordan area, including the region round the sea of Galilee.

Into this tiny area has poured a flood of peoples from all over the world. Although they are all Jews, this is a term which has proved remarkably difficult to define. This may not seem relevant either, but it is important to emphasize that these various groups coming from so many contrasting environments appear to be startlingly different from each other; certainly, as regards body size, the tiny Yemenites and the large hefty Kurds, for example; dark Cochin Jews from India and blonds from Russia.

What is more, there are many villages populated by one particular group; as, for example, a village group from Kurdistan remains as the same village group in Israel. So we have the position that in all the climatic zones mentioned there will be a Yemenite village next door to a Kurdish village, and in the next one all the habitants may be Cochin Jews.

Such a situation is enough to excite any climatic physiologist. Here we have the opportunity of studying contrasting, dissimilar people in the same environmental conditions, and in three contrasting environments. When it is added that in Israel demographic and medical data are available throughout the country and that there is a wealth of scientific talent and facilities, you may not be surprised at my eagerness to exploit the situation. Moreover, such opportunities do not necessarily persist, and intermarriage between the different communities will soon blur the distinctions which may exist.

Further Studies

I have described Israel because the problem of adaptation can so obviously be profitably looked at, but there are, of course, other populations and other localities where multidisciplinary studies can and will be carried out.

The final point I want to make is that extensive physiological field work is now practicable. The methods which are already available ensure this, and I have no doubt whatever that there will be rapid advances from now on which will extend our powers considerably. The great need is to develop a methodology which can be used in the field with many subjects, with the minimum of interference and a high order of accuracy. As one example, Wolff (1965) has developed a heart rate integrator which can provide us with information relevant to habitual physical activity. This can be used on a reasonably large scale, does not inconvenience the wearer or interfere with his activities. A basically similar device can be used to integrate other variables such as skin temperature. As physiologists, we have to learn the value of such devices in terms of the kind of information provided.

In conclusion, there is, I hope, another possible dividend from these population studies. We suffer from a shortage of physiologists interested in the whole animal or man. I believe, and I am of course biased, that the comparative neglect which this implies of work on the whole animal is unsatisfactory in terms of biology. The whole animal is more than an assemblage of parts; the study of the physiology of the whole man is certainly essential for an understanding of clinical problems, but it is also necessary to have a proportion of physiologists who are experienced investigators in these fields, otherwise we are in serious danger of becoming completely unbalanced. It would appear that the work that climatic physiologists are pursuing is not of sufficient interest to attract the recruits we need. Now, with the International Biological Programme developing, we can surely offer some exciting prospects, such as the possibility that we can hope to advance from the position that Darwin described over 100 years ago.

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