CHAPTER 5

Adaptation as Stability

5/1. THE concept of 'adaptation' has so far been used without definition; this vagueness must be corrected. Not only must the definition be precise, but it must be given in terms that conform to the demand of S. 2/8.

5/2. The suggestion that an animal's behaviour is 'adaptive' if the animal 'responds correctly to a stimulus' may be rejected at once. First, it presupposes an action by an experimenter and therefore cannot be applied when the free-living organism and its environment affect each other reciprocally. Secondly, the definition provides no meaning for 'correctly' unless it means 'conforming to what the experimenter thinks the animal ought to do'. Such a definition is useless.

Homeostasis

5/3. I propose the definition that *a form of behaviour is* **adaptive** *if it maintains the essential variables* (S. 3/14) *within physiological limits*. The full justification of such a definition would involve its comparison with all the known facts—an impossibly large task. Nevertheless it is fundamental in this subject and I must discuss it sufficiently to show how fundamental it is and how wide is its applicability.

First I shall outline the facts underlying Cannon's concept of 'homeostasis'. They are not directly relevant to the problem of learning, for the mechanisms are inborn; but the mechanisms are so clear and well known that they provide an ideal basic illustration. They show that:

(1) Each mechanism is 'adapted' to its end.

(2) Its end is the maintenance of the values of some essential variables within physiological limits.

(3) Almost all the behaviour of an animal's vegetative system is due to such mechanisms.

5/4. As first example may be quoted the mechanisms which tend to maintain within limits the concentration of glucose in the blood. The concentration should not fall below about 0·06 per cent or the tissues will be starved of their chief source of energy; and the concentration should not rise above about 0·18 per cent or other undesirable effects will occur. If the blood-glucose falls below about 0·07 per cent the adrenal glands secrete adrenaline, which makes the liver turn its stores of glycogen into glucose; this passes into the blood and the fall is opposed. In addition, a falling blood-glucose stimulates the appetite so that food is taken, and this, after digestion, provides glucose. On the other hand, if it rises excessively, the secretion of insulin by the pancreas is increased, causing the liver to remove glucose from the blood. The muscles and skin also remove it; and the kidneys help by excreting glucose into the urine if the concentration in the blood exceeds 0·18 per cent. Here then are five activities all of which have the same final effect. Each one acts so as to *restrict* the fluctuations which might otherwise occur. Each may justly be described as ' adaptive ', for it acts to preserve the animal's life.

The temperature of the interior of the warm-blooded animal's body may be disturbed by exertion, or illness, or by exposure to the weather. If the body temperature becomes raised, the skin flushes and more heat passes from the body to the surrounding air; sweating commences, and the evaporation of the water removes heat from the body: and the metabolism of the body is slowed, so that less heat is generated within it. If the body is chilled, these changes are reversed. Shivering may start, and the extra muscular activity provides heat which warms the body. Adrenaline is secreted, raising the muscular tone and the metabolic rate, which again supplies increased heat to the body. The hairs or feathers are moved by small muscles in the skin so that they stand more erect, enclosing more air in the interstices and thus conserving the body's heat. In extreme cold the human being, when almost unconscious, reflexly takes a posture of extreme flexion with the arms pressed firmly against the chest and the legs fully drawn up against the abdomen. The posture is clearly one which exposes to the air a minimum of surface. In all these ways, the body acts so as to maintain its temperature within limits.

The water content of the blood is disturbed by the intake of water at drinking and eating, by the output during excretion and secretion, and by sweating. When the water content is lowered, sweating, salivation, and the excretion of urine are all diminished; thirst is increased, leading to an increased intake, and the tissues of the body pass some of their water into the blood-stream. When the water content is excessive, all these activities are reversed. By these means the body tends to maintain the water-content of the blood within limits.

The pressure of the blood in the aorta may be disturbed by haemorrhage or by exertion. When the pressure falls, centres in the brain and spinal cord make the heart beat faster, increasing the quantity of blood forced into the aorta; they make the small arteries contract, impeding the flow of blood out of it. If the pressure is too high, these actions are reversed. By these and other mechanisms the blood pressure in the aorta is maintained within limits.

The amount of carbon dioxide in the blood is important in its effect on the blood's alkalinity. If the amount rises, the rate and depth of respiration are increased, and carbon dioxide is exhaled at an increased rate. If the amount falls, the reaction is reversed. By this means the alkalinity of the blood is kept within limits.

The retina works best at a certain intensity of illumination. In bright light the nervous system contracts the pupil, and in dim relaxes it. Thus the amount of light entering the eye is maintained within limits.

If the eye is persistently exposed to bright light, as happens when one goes to the tropics, the pigment-cells in the retina grow forward day by day until they absorb a large portion of the incident light before it reaches the sensitive cells. In this way the illumination on the sensitive cells is kept within limits.

If exposed to sunshine, the pigment-bearing cells in the skin increase in number, extent, and pigment-content. By this change the degree of illumination of the deeper layers of the skin is kept within limits.

When dry food is chewed, a copious supply of saliva is poured into the mouth. Saliva lubricates the food and converts it from a harsh and abrasive texture to one which can be chewed without injury. The secretion therefore keeps the frictional stresses below the destructive level.

The volume of the circulating blood may be disturbed by haemorrhage. Immediately after a severe haemorrhage a number of changes occur: the capillaries in limbs and muscles undergo constriction, driving the blood from these vessels to the more essential internal organs; thirst becomes extreme, impelling the subject to obtain extra supplies of fluid; fluid from the tissues passes into the blood-stream and augments its volume; and clotting at the wound helps to stem the haemorrhage. A haemorrhage has a second effect in that, by reducing the number of red corpuscles, it reduces the amount of oxygen which can be carried to the tissues; the reduction, however, itself stimulates the bone-marrow to an increased production of red corpuscles. All these actions tend to keep the variables ' volume of circulating blood ' and ' oxygen supplied to the tissues ' within normal limits.

Every fast-moving animal is liable to injury by collision with hard objects. Animals, however, are provided with reflexes that tend to minimise the chance of collision and of mechanical injury. A mechanical stress causes injury—laceration, dislocation, or fracture—only if the stress exceeds some definite value, depending on the stressed tissue—skin, ligament, or bone. So these reflexes act to keep the mechanical stresses within physiological limits.

Many more examples could be given, but all can be included within the same formula. Some external disturbance tends to drive an essential variable outside its normal limits; but the commencing change itself activates a mechanism that *opposes* the external disturbance. By this mechanism the essential variable is maintained within limits much narrower than would occur if the external disturbance were unopposed. The narrowing is the objective form of the mechanism's adaptation.

5/5. The mechanisms of the previous section act mostly within the body, but it should be noted that some of them have acted partly through the environment. Thus, if the body-temperature is raised, the nervous system lessens the generation of heat within the body and the body-temperature falls, but only because the body is continuously losing heat to its surroundings. Flushing of the skin cools the body only if the surrounding air is cool; and sweating lowers the body-temperature only if the surrounding air is unsaturated. Increasing respiration lowers the carbon dioxide content of the blood, but only if the atmosphere contains less than 5 per cent. In each case the chain of cause and effect passes partly through the environment. The mechanisms that work wholly within the body and those that make extensive use of the environment are thus only the extremes of a continuous series. Thus, a thirsty animal seeks water: if it is a fish it does no more than swallow, while if it is an antelope in the veldt it has to go through an elaborate process of search, of travel, and of finding a suitable way down to the river or pond. The homeostatic mechanisms thus extend from those that work wholly within the animal to those that involve its widest-ranging activities; the principles are uniform throughout.

5/6. Just the same criteria for 'adaptation' may be used in judging the behaviour of the free-living animal in its learned reactions. Take the type-problem of the kitten and the fire. When the kitten first approaches an open fire, it may paw at the fire as if at a mouse, or it may crouch down and start to 'stalk' the fire, or it may attempt to sniff at the fire, or it may walk unconcernedly on to it. Every one of these actions is liable to lead to the animal's being burned. Equally the kitten, if it is cold, may sit far from the fire and thus stay cold. The kitten's behaviour cannot be called adapted, for the temperature of its skin is not kept within normal limits. The animal, in other words, is not acting homeostatically for skin temperature. Contrast this behaviour with that of the experienced cat: on a cold day it approaches the fire to a distance adjusted so that the skin temperature is neither too hot nor too cold. If the fire burns fiercer, the cat will move away until the skin is again warmed to a moderate degree. If the fire burns low the cat will move nearer. If a red-hot coal drops from the fire the cat takes such action as will keep the skin temperature within normal limits. Without making any enquiry at this stage into what has happened to the kitten's brain, we can at least say that whereas at first the kitten's behaviour was not homeostatic for skin temperature, it has now become so. Such behaviour is 'adapted': it preserves the life of the animal by keeping the essential variables within limits.

The same thesis can be applied to a great deal, if not all, of the normal human adult's behaviour. In order to demonstrate the wide application of this thesis, and in order to show that even Man's civilised life is not exceptional, some of the surroundings which he has provided for himself will be examined for their known physical and physiological effects. It will be shown that each item acts so as to narrow the range of variation of his essential variables.

The first requirement of a civilised man is a house; and its first effect is to keep the air in which he lives at a more equable temperature. The roof keeps his skin at a more constant dryness. The windows, if open in summer and closed in winter, assist in the maintenance of an even temperature, and so do fires and stoves. The glass in the windows keeps the illumination of the rooms nearer the optimum, and artificial lighting has the same effect. The chimneys keep the amount of irritating smoke in the rooms near the optimum, which is zero.

Many of the other conveniences of civilisation could, with little difficulty, be shown to be similarly variation-limiting. An attempt to demonstrate them all would be interminable. But to confirm the argument we will examine a motor-car, part by part, in order to show its homeostatic relation to man.

Travel in a vehicle, as contrasted with travel on foot, keeps several essential variables within narrower limits. The fatigue induced by walking for a long distance implies that some variables, as yet not clearly known, have exceeded limits not transgressed when the subject is carried in a vehicle. The reserves of food in the body will be less depleted, the skin on the soles of the feet will be less chafed, the muscles will have endured less strain, in winter the body will have been less chilled, and in summer it will have been less heated, than would have happened had the subject travelled on foot.

When examined in more detail, many ways are found in which it serves us by maintaining our essential variables within narrower limits. The roof maintains our skin at a constant dryness. The windows protect us from a cold wind, and if open in summer, help to cool us. The carpet on the floor acts similarly in winter, helping to prevent the temperature of the feet from falling below its optimal value. The jolts of the road cause, on the skin and bone of the human frame, stresses which are much lessened by the presence of springs. Similar in action are the shock-absorbers and tyres. A collision would cause an extreme deceleration which leads to very high values for the stress on the skin and bone of the passengers. By the brakes these very high values may be avoided, and in this way the brakes keep the variables ' stress on bone ' within narrower limits. Good headlights keep the luminosity of the road within limits narrower than would occur in their absence.

The thesis that ' adaptation ' means the maintenance of essential variables within physiological limits is thus seen to hold not only over the simpler activities of primitive animals but over the more complex activities of the ' higher ' organisms.

5/7. Before proceeding further, it must be noted that the word ' adaptation ' is commonly used in two senses which refer to different processes.

The distinction may best be illustrated by the inborn homeostatic mechanisms : the reaction to cold by shivering, for instance. Such a mechanism may undergo two types of ' adaptation '. The first occurred long ago and was the change from a species too primitive to show such a reaction to a species which, by natural selection, had developed the reaction as a characteristic inborn feature. The second type of ' adaptation ' occurs when a member of the species, born with the mechanism, is subjected to cold and changes from not-shivering to shivering. The first change involved the development of the mechanism itself ; the second change occurs when the mechanism is stimulated into showing its properties.

In the learning process, the first stage occurs when the animal ' learns ' : when it changes from an animal not having an adapted mechanism to one which has such a mechanism. The second stage occurs when the developed mechanism changes from inactivity to activity. In this chapter we are concerned with the characteristics of the developed mechanism. The processes which led to its development are discussed in Chapter 8.

5/8. We can now recognise that '*adaptive*' *behaviour is equivalent to the behaviour of a stable system, the region of the stability being the region of the phase-space in which all the essential variables lie within their normal limits.*

The view is not new (though it can now be stated with more precision):

> 'Every phase of activity in a living being must be not only a necessary sequence of some antecedent change in its environment, but must be so adapted to this change as to tend to its neutralisation, and so to the survival of the organism. . . . It must also apply to *all* the relations of living beings. It must therefore be the guiding principle, not only in physiology . . . but also in the other branches of biology which treat of the relations of the living animal to its environment and of the factors determining its survival in the struggle for existence.'
>
> (Starling.)

> 'In an open system, such as our bodies represent, compounded of unstable material and subjected continuously to disturbing conditions, constancy is in itself evidence that agencies are acting or ready to act, to maintain this constancy.'
>
> (Cannon.)

> 'Every material system can exist as an entity only so long as its internal forces, attraction, cohesion, etc., balance the external forces acting upon it. This is true for an ordinary stone just as much as for the most complex substances; and its truth should be recognised also for the animal organism. Being a definite circumscribed material system, it can only continue to exist so long as it is in continuous equilibrium with the forces external to it: so soon as this equilibrium is seriously disturbed the organism will cease to exist as the entity it was.'
>
> (Pavlov.)

McDougall never used the concept of 'stability' explicitly, but when describing the type of behaviour which he considered to be most characteristic of the living organism, he wrote:

> 'Take a billiard ball from the pocket and place it upon the table. It remains at rest, and would continue to remain so for an indefinitely long time, if no forces were applied to it. Push it in any direction, and its movement in that direction persists until its momentum is exhausted, or until it is deflected by the resistance of the cushion and follows a new

> path mechanically determined. . . . Now contrast with this an instance of behaviour. Take a timid animal such as a guinea-pig from its hole or nest, and put it upon the grass plot. Instead of remaining at rest, it runs back to its hole; push it in any other direction, and, as soon as you withdraw your hand, it turns back towards its hole; place any obstacle in its way, and it seeks to circumvent or surmount it, restlessly persisting until it achieves its end or until its energy is exhausted.'

He could hardly have chosen an example showing more clearly the features of stability.

Survival

5/9. The forces of the environment, and even the drift of time, tend to displace the essential variables by amounts to which we can assign no limit. For survival, the essential variables *must* be kept within their physiological limits. In other words, the values of the essential variables must stay within some definite region in the system's phase-space. It follows therefore that unless the environment is wholly inactive, stability is *necessary* for survival.

5/10. If an animal's behaviour always maintains its essential variables within their physiological limits, then the animal can die only of old age. Disease might disturb the essential variables, but the processes of repair and immunity would tend to restore them. But it is equally clear that the environment sometimes causes disturbances for which the body's stabilising powers are inadequate; infections may prove too virulent, cold too extreme, a famine too severe, or the attack of an enemy too swift.

The possession of a mechanism which stabilises the essential variables is therefore of advantage: against moderate disturbances it may be life-saving even if it eventually fails at some severe disturbance. It promotes, but does not guarantee, survival.

5/11. Are there aspects of 'adaptation' not included within the definition of 'stability'? Is 'survival' to be the sole criterion of adaptation? Is it to be maintained that the Roman soldier who killed Archimedes in Syracuse was better 'adapted' in his behaviour than Archimedes?

The question is not easily answered. It is similar to that of S. 3/4 where it was asked whether all the qualities of the living organism could be represented by number ; and the answer must be similar. It is assumed that we are dealing primarily with the simpler rather than with the more complex creatures, though the examples of S. 5/6 have shown that some at least of man's activities may be judged properly by this criterion.

In order to survey rapidly the types of behaviour of the more primitive animals, we may examine the classification of Holmes, who intended his list to be exhaustive but constructed it with no reference to the concept of stability. The reader will be able to judge how far our formulation (S. 5/8) is consistent with his scheme, which is given in Table 5/11/1.

Behaviour	Non-adaptive			Useless tropistic reaction. Misdirected instinct. Abnormal sex behaviour. Pathological behaviour. Useless social activity. Superfluous random movements.
	Adaptive	Self-maintaining	Sustentative	Capture, devouring of food. Activities preparatory, as making snares, stalking. Collection of food, digging. Migration. Caring for food, storing, burying, hiding. Preparation of food.
			Protective	Against enemies—fight, flight. Against inanimate forces. Reactions to heat, gravity, chemicals. Against inanimate objects.
			Ameliorative	Rest, sleep, play, basking.
		Race-maintaining	(with these we are not concerned, S. 1/3).	

TABLE 5/11/1 : All forms of animal behaviour, classified by Holmes.

For the primitive organism, and excluding behaviour related to racial survival, there seems to be little doubt that the 'adaptiveness' of behaviour is properly measured by its tendency to promote the organism's survival.

The stable organism

5/12. A most impressive characteristic of living organisms is their mobility, their tendency to change. McDougall expressed this characteristic well in the example of S. 5/8. Yet our formulation transfers the centre of interest to the resting state, to the fact that the essential variables of the adapted organism change *less* than they would if they were unadapted. Which is important: constancy or change?

The two aspects are not incompatible, for *the constancy of some variables may involve the vigorous activity of others.* A good thermostat reacts vigorously to a small change of temperature, and the vigorous activity of some of its variables keeps the others within narrow limits. The point of view taken here is that the constancy of the essential variables is fundamentally important, and that the activity of the other variables is important only in so far as it contributes to this end.

5/13. So far the discussion has traced the relation between the concepts of 'adaptation' and of 'stability'. It will now be proposed that 'motor co-ordination' also has an essential connection with stability.

'Motor co-ordination' is a concept well understood in physiology, where it refers to the ability of the organism to combine the activities of several muscles so that the resulting movement follows accurately its appropriate path. Contrasted to it are the concepts of clumsiness, tremor, ataxia, athetosis. It is suggested that the presence or absence of co-ordination may be decided, in accordance with our methods, by observing whether the movement does, or does not, deviate outside given limits.

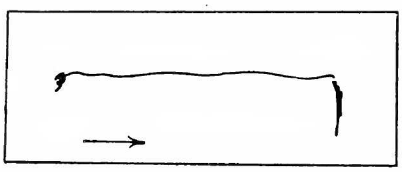

FIGURE 5/13/1.

The formulation seems to be adequate provided that we measure the limb's deviations from some line which is given arbitrarily, usually by a knowledge of the line followed by the normal limb. A first example is given by Figure 5/13/1, which shows the line traced by the point of an expert fencer's foil during a lunge.

Any inco-ordination would be shown by a divergence from the intended line.

A second example is given by the record of Figure 5/13/2. The subject, a patient with a tumour in the left cerebellum, was asked to follow the dotted lines with a pen. The left- and right-hand curves were drawn with the respective hands. The tracing shows clearly that the co-ordination is poorer in the left hand. What criterion reveals the fact? The essential distinction is that the deviations of the lines from the dots are larger on the left than on the right.

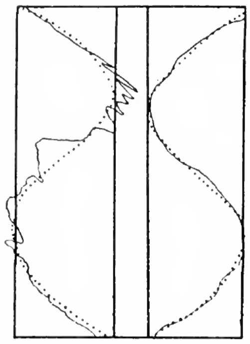

FIGURE 5/13/2: Record of the attempts of a patient to follow the dotted lines with the left and right hands. (By the courtesy of Dr. W. T. Grant of Los Angeles.)

The degree of motor co-ordination achieved may therefore be measured by the smallness of the deviations from some standard line. Later it will be suggested that there are mechanisms which act to maintain variables within narrow limits. If the identification of this section is accepted, such mechanisms could be regarded as appropriate for the co-ordination of motor activity.

5/14. So far we have noticed in stable systems only their property of keeping variables within limits. But such systems have other properties of which we shall notice two. They are also shown by animals, and are then sometimes considered to provide evidence that the organism has some power of 'intelligence' not shared by non-living systems. In these two instances the assumption is unnecessary.

The first property is shown by a stable system when the lines of behaviour do not return directly, by a straight line, to the resting state (e.g. Figure 4/5/3). When this occurs, variables may be observed to move away from their values in the resting state, only to return to them later. Thus, suppose in Figure 5/14/1 that the field is stable and that at the resting state R x and y have the values X and Y. For clarity, only one line of behaviour is drawn. Let the system be displaced to A and its subsequent behaviour observed. At first, while the representative point moves towards B, y hardly alters ; but x, which started at X', moves to X and goes past it to X''. Then x remains almost constant and y changes until the representative point reaches C. Then y stops changing, and x changes towards, and reaches, its resting value X. The system has now reached its resting state and no further changes occur. This account is just a transcription into words of what the field defines graphically.

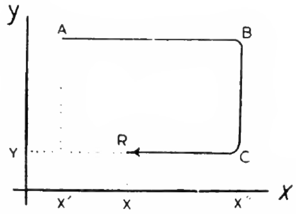

FIGURE 5/14/1.

Now the shape and features of any field depend ultimately on the real physical and chemical construction of the 'machine' from which the variables are abstracted. The fact that the line of behaviour does not run straight from A to R must be due to some feature in the 'machine' such that if the machine is to get from state A to state R, states B and C must be passed through of necessity. Thus, if the machine contained moving parts, their shapes might prohibit the direct route from A to R; or if the system were chemical the prohibition might be thermodynamic. But in either case, if the observer watched the machine work, and thought it alive, he might say: 'How clever! x couldn't get from A to R directly because this bar was in the way; so x went to B, which made y carry x from B to C; and once at C, x could get straight back to R. I believe x shows foresight.'

Both points of view are reasonable. A stable system may be regarded both as blindly obeying the laws of its nature, and also as showing a rudimentary skill in getting back to its resting state in spite of obstacles.

5/15. The second property is shown when an organism reacts to a variable with which it is not directly in contact. Suppose, for instance, that the diagram of immediate effects (S. 4/12) is that of Figure 5/15/1; the variables have been divided by the dotted line into 'animal' on the right and 'environment' on the left, and the animal is not in direct contact with the variable marked X. The system is assumed to be stable, i.e. to have arrived at the 'adapted' condition (S. 5/7). If disturbed, its changes will show co-ordination of part with part (S. 5/14), and this co-ordination will hold over the whole system (S. 4/15). It follows that the behaviour of the 'animal'-part will be co-ordinated with the behaviour of X although the 'animal' has no immediate contact with it.

In the higher organisms, and especially in man, the power to react correctly to something not immediately visible or tangible

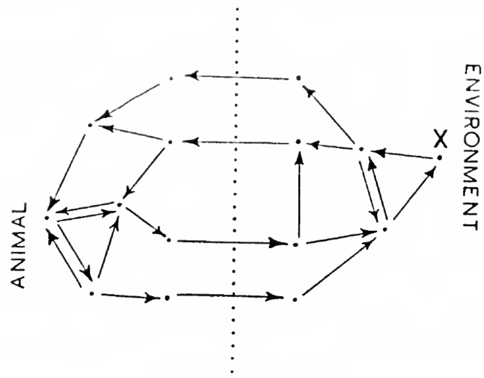

FIGURE 5/15/1.

has been called 'imagination', or 'abstract thinking', or several other names whose precise meaning need not be discussed at the moment. Here we should notice that the co-ordination of the behaviour of one part with that of another part not in direct contact with it is simply an elementary property of the stable system.

5/16. At this stage it is convenient to re-state our problem in the new vocabulary. If, for brevity, we omit minor qualifications, we can state it thus : A determinate 'machine' changes from a form that produces chaotic, unadapted behaviour to a form in which the parts are so co-ordinated that the whole is stable, acting to maintain certain variables within certain limits—how can this happen ? For example, what sort of a thermostat could, if assembled at random, rearrange its own parts to get itself stable for temperature ?

It will be noticed that the new statement involves the concept of a machine changing its internal organisation. So far, nothing has been said of this important concept ; so it will be treated in the next two chapters.

References

ASHBY, W. ROSS. Adaptiveness and equilibrium. *Journal of Mental Science*, **86**, 478 ; 1940.
Idem. The behavioral properties of systems in equilibrium. *American Journal of Psychology*, **59**, 682 ; 1946.
CANNON, W. B. *The wisdom of the body.* London, 1932.
CONFERENCE ON TELEOLOGICAL MECHANISMS. *Annals of the New York Academy of Science*, **50**, 187 ; 1948.
GRANT, W. T. Graphic methods in the neurological examination : wavy tracings to record motor control. *Bulletin of the Los Angeles Neurological Society*, **12**, 104 ; 1947.
HOLMES, S. J. A tentative classification of the forms of animal behavior. *Journal of Comparative Psychology*, **2**, 173 ; 1922.
McDOUGALL, W. *Psychology.* New York, 1912.
PAVLOV, I. P. *Conditioned reflexes.* Oxford, 1927.
ROSENBLUETH, A., WIENER, N., and BIGELOW, J. Behavior, purpose and teleology. *Philosophy of Science*, **10**, 18 ; 1943.
SOMMERHOFF, G. *Analytical biology.* Oxford, 1950.