The Behavioural Final Common Path

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Phil. Trans. R. Soc. Lond. B 1975 **270**, 265-293
doi: 10.1098/rstb.1975.0009

THE BEHAVIOURAL FINAL COMMON PATH

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(*Communicated by W. H. Thorpe, F.R.S. – Received* 22 *February* 1974)

CONTENTS

In this paper it is argued that any model of the motivational (i.e. reversible) processes governing the behaviour of an animal can be represented by means of isoclines in a multidimensional 'causal-factor space'. The argument is axiomatic, based upon the two prime assumptions: that (1) it is always possible to classify the behavioural repertoire of a species in such a way that the classes are mutually exclusive in the sense that the members of different classes cannot occur simultaneously, and (2) these incompatible actions are uniquely determined by a particular set of causal factors. The isoclines join all points in the space which present a given 'degree of competitiveness' of a particular 'candidate' for overt behavioural expression. The competition between candidates is an inevitable consequence of the fact that animals cannot 'do more than one thing at a time', and is envisaged as taking place in the behavioural final common path.

An empirical method of determining the motivational state (i.e. point in causal-factor space) is outlined. This is a 'relative' method, independent of the arbitrary calibration of the axes of the causal-factor space. It is shown that an arbitrary scale of measurement along any two axes of the causal-factor space is all that is necessary for empirical determination of the shape of a motivational isocline. Experiments in which this method has been applied to the measurement of hunger and thirst in doves are outlined, and the results are discussed in terms of their implications for motivation theory in general.

The behaviour of an animal may be regarded as the output of a multivariable adaptive control system, in which some of the inputs are observable, but others are hidden. Although a variety of quite sophisticated methods have been employed in the analysis of behavioural control systems (e.g. by Delius 1969; Heiligenberg 1973; McFarland 1971; Nelson 1964), their complexity is such than an almost infinite variety of interactions between variables seems possible. In attempting to narrow down the range of probable structures for such a complex system, a useful approach is to study the constraints acting upon the system.

The constraints may stem from the nature of the environment, and its roles in determining the 'climate' in which the animal finds itself (Sibly & McFarland 1974) and in determining the consequences of the animal's behaviour (McFarland & Sibly 1972). Another form of constraint is provided by the fact that the animal must use a limited set of muscles to carry out a wide range of activities. The term 'behavioural final common path' is appropriate here, because all influences upon behaviour converge at this point. This term is strictly relevant to consideration of motivational control in behavioural terms rather than the structure of the nervous system. Von Holst & von Saint Paul (1963) used the term 'initial common path' for competition at the perceptual level, and 'final common path' (after Sherrington 1906) for competition at the motor level. Both types of competition are envisaged as operating in the behavioural final common path, which thus involves the last type of interaction (see McFarland 1971) in the causal chain, the final 'decision' before a potential activity becomes overt. In other words, it is immaterial from the behavioural viewpoint, whether changes in behaviour are due to attentional or to motor competition.

Incompatible activities and motivational state

In observing behaviour the scientist notes a number of characteristics which he may regard as units of behaviour. Thus pecking at grains with an open bill is characteristic of feeding in pigeons, as are certain head movements, etc. Which characteristics he pays attention to are a matter of arbitrary choice and convenience. Within any given time period description of the behaviour will consist in specifying which characteristics are present. The observed characteristics at the given time will be a subset of all the characteristics in the animal's repertoire. Such a subset can be called an action. Actions which share characteristics may be said to be related. Actions may be arbitrarily grouped into mutually exclusive categories, which we shall call activities. It might be objected that some characteristics, such as pecking, might be common to a large number of actions, which could not then be split into different activities. At this point it may be useful to discuss a specific example, which will serve to outline the manner in which we envisage the process of behaviour classification taking place in practice.

When a pigeon feeds from a pile of grain, it takes the grains one at a time with a series of complex and highly stereotyped movement patterns that occur in rapid succession. Analysis of film records indicates that the feeding behaviour has three main characteristics (Zeigler 1974): *pecking*, which consists of a downward movement of the head with the bill initially closed, but gradually opening as it approaches the grain. Contact with the grain terminates this movement. *Mandibulation* involves an upward movement of the head synchronized with a series of tongue movements which propel the grain from the beak tip to the rear of the buccal cavity. *Swallowing* is initiated at this point, and this involves peristaltic movements of the oesophagus.

These three characteristics of the feeding response occur in a cyclic fashion, and may be said to constitute an action. Film analysis indicates that each action takes about 300 ms, and that the temporal relations between the three components are quite constant for an individual bird. Furthermore, the temporal characteristics of the action do not appear to vary with the motivational state of the bird. Although the feeding behaviour of a hungry pigeon involves an increase in the number of feeding responses per minute, this is attained by reducing the intervals between actions rather than by shortening the action itself. It would appear that we have here a paradigm case of an action, which we will label *eating*.

When a pigeon feeds from a source of food that is not homogeneous, it will often happen that mandibulation is not followed by swallowing, but by *ejection* of an inedible particle. In such cases the action of eating will not have been performed, and we recognize a different action which we may call *rejection*. This action has two characteristics in common with eating, and is thus said to be related to it. It may be that, while the characteristic pecking is identical in the cases of the two actions, mandibulation is not identical because the tongue movements prior to swallowing differ from those that precede ejection. The observer may not be able to distinguish the two types of mandibulation, or he may be able to distinguish them but not wish to classify them differently. The choice of characteristics is an arbitrary matter, and it is open to the observer to decide for himself whether to discriminate between the different types of mandibulation.

In practice, feeding behaviour will be found to involve a number of actions, such as *searching*, *probing*, etc., some of which may be related to eating and rejecting. We may wish to classify all these actions within a single activity, called *feeding*. However, it is important that activities should be classified in such a way that they are mutually exclusive. In some cases a set of related actions will form a natural group, there being no characteristics in common with actions outside the group. On the other hand, it will often be the case that an action is common to a number of such groups. For example, searching could be found as a component of feeding, drinking, and nest-building behaviour in pigeons.

The aim of the observer is to classify the behaviour of the animal into a number of mutually exclusive activities. It is perfectly legitimate for him to ignore certain actions. Thus *breathing* is an action common to all types of behaviour, and its inclusion in a classifying scheme would make the formation of mutually exclusive categories impossible. In the case of searching, it is legitimate for the observer to distinguish between searching for food, searching for water, etc. Close scrutiny may reveal that the various instances of searching differ in their exact form. Provided the observer has a consistent criterion, he may designate actions in an arbitrary manner, to suit his convenience.† We wish to assert that it is possible to classify behaviour into mutually exclusive categories, without specifying how it should be done, or what level of classification should be employed. It should be noted, however, that there will inevitably be classes of behaviour that are incompatible in the sense that the animal cannot perform them simul-

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† Note that actions are grouped into classes called activities, but the basis for this classification is not the conventional functional basis, by which behaviour patterns are classified according to their biological functions, such as feeding and reproduction. Functionally defined categories of behaviour (feeding, reproductive, etc.) may coincide with activities, but not necessarily so. We anticipate that certain ways of identifying actions will result in very few activities. For example, if walking were defined as an action, then all behaviour patterns of which walking is a constituent part would have to belong to the same activity. We wish to emphasize that the level at which an action is identified is a matter for the observer to decide, but that the exercise is likely to be more profitable if actions can be defined in such a way that there are as many activities as possible.

taneously. In his search for mutually exclusive activities, the observer would be well advised to direct his attention towards these incompatible aspects of behaviour.

Having outlined our attitude in this way, we can now turn to some more formal definitions and assumptions, which provide a generalized basis for our approach.

Assumption 1. It is always possible to classify the behavioural repertoire of a species in such a way that the classes, which we call activities, are mutually exclusive in the sense that the members, which we call actions, can only belong to one class.

Definition 1. An *action* is an identifiable pattern of behaviour, definable in such a way that it is possible to decide unequivocally whether the action has occurred or not. It is not possible for one action to occur at the same time as another.

Definition 2. An *activity* is a set of actions that are mutually exclusive from other activities. This means that no action can belong to more than one activity.

It is usual to assume that behaviour depends in a deterministic fashion upon a set of causal factors. These causal factors will include variables describing the animal's 'estimate' of stimuli present in the external environment (e.g. cues to the availability of food), and variables relevant to the animal's internal environment. The state of these causal factors can be represented in a space, the axes of which represent the causal factors. For example, the state of a (hypothetical) animal might be represented in a two-dimensional space (figure 4) with one axis corresponding to the degree of hunger, and the other to the strength of food cues (i.e. the animal's estimate of the availability of food).

We have said that behaviour depends upon the causal factors in a deterministic fashion. More precisely,

Assumption 2. The state of the causal factors uniquely determines which action will occur. This means that a particular state of the causal factors will always give rise to the same action, though a particular action might be determinable by more than one state of the causal factors.

At any time the causal factors relevant to a number of actions will be present, but by definition only one action can occur. The actions for which the relevant causal factors are present will be referred to as *candidates* for the control of ongoing behaviour. (By saying that a causal factor is 'relevant to an activity' we mean that changes of action within that activity can be induced by varying that causal factor. Note that a causal factor may be relevant to more than one activity.) Each candidate can be represented along an axis of a space, according to the activity to which it corresponds. We call this space the *candidate space*. The candidates can be ordered along each axis of the candidate space according to the following algorithm: 'In comparison with a particular candidate responsible for activity i, the candidates on any axis j are divided into those that displace i and those that do not.' (By displace is meant cause transference of behavioural control from one axis to another, so that a change in activity is observed.) This algorithm applied repeatedly for all candidates on axis i provides an ordering along axis j with respect to axis i (i.e. all possible candidates on axis j are sorted with respect to a moving binary criterion on axis i). For example, the algorithm shows that the candidates for two activities can be ordered along the axes of a two-dimensional candidate space (figure 1). It is possible to show that in general, given certain assumptions, not only can the candidates be ordered along the axes of the candidate space, but that the ordering is transitive (see appendix 1). Consider a three-dimensional candidate space in which candidates A, B and C correspond to actions α, β and γ respectively. Transitivity means that if candidates A, B and C are ranked so that $A > B$, so that action α is observed in a choice between A and B, and $B > C$ so that action β is observed in a choice between B and C, then $A > C$ and action α will be observed in a choice between A and C.

So far we have shown that the candidates can be ranked and that the ranking is transitive. This means that the candidate for a particular activity can be represented along an ordinal scale (Stevens 1951; Siegel 1956; McFarland 1971). Because an ordinal scale is involved, we are not justified in assuming that divisions between candidates are regularly spaced along each axis.

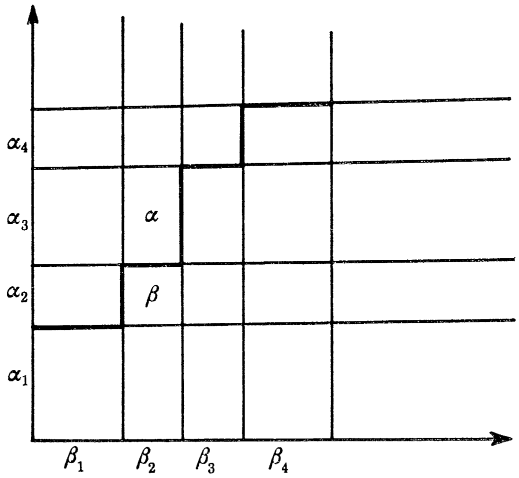

Figure 1. A two-dimensional candidate space with axes along which the candidates relevant to activities α and β can be ordered. Note that the ordering achieves an ordinal scale along each axis. For any given pair of candidates, either activity α or activity β will be observed, thus dividing the candidate space (thick line).

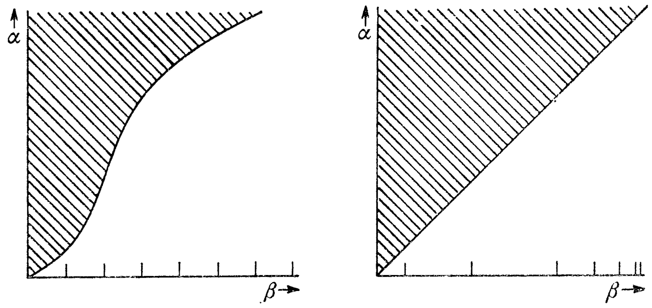

Figure 2. The switching line in candidate space can be made straight by a suitable nonlinear transformation of axis β (see text). (*Note*: the switching line is the thick line in figure 1, which is shown as a continuous curve here, because we are considering the limiting case, as explained in the text.)

The analysis will now be taken a step further: consider a two-dimensional candidate space with axes α and β (figure 2). In this example a particular candidate always displaces a candidate of lower rank, and equally ranked candidates are impossible (i.e. the shaded set in figure 2 is a closed set). All cases in which $A > B$ are shown as shaded areas in figure 2.

The two-dimensional space is divided by a 'switching-line' on one side of which activity α is observed, on the other side of which activity β is observed. In the limit this line becomes continuous and by means of a suitable nonlinear transformation of one axis (in this case axis β) the switching-line can be made straight. This example can be generalized to n dimensions (see appendix 2) to show that there is freedom of scaling along only one axis, if the switching-line is assumed straight. Then scales along all other axes can be read off by reference to the switching-line. A three-dimensional example is given in figure 3.

We now come to the problem of how the candidate space is related to the motivational state of the animal. We have seen that each action is controlled by a set of causal factors. The causal factors will include variables describing the animal's 'estimate' of the stimuli present in the external environment (e.g. cues to the availability of food), and variables relevant to the animal's internal state. We propose to represent the total motivational state in a *causal factor space*, in which there is an axis corresponding to each class of causal factor, with the classes defined in terms of some suitable arbitrary criterion. For example, a (hypothetical) animal might have a motivational state that can be represented in a two-dimensional space (figure 4), with one axis corresponding to the degree of hunger, and the other to the strength of food cues (i.e. the animal's estimate of the availability of food). Thus the causal factor space has axes corresponding to each class of causal factor, while the causal states relevant to each activity are represented along the axes of candidate space.

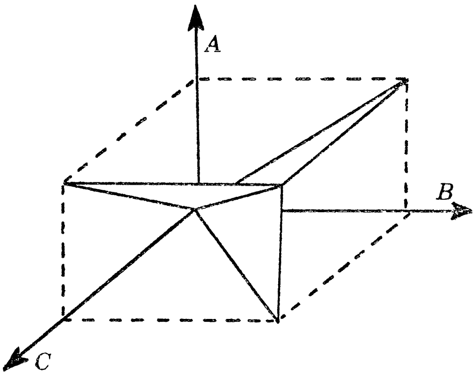

FIGURE 3. In a three-dimensional candidate space a switching-surface divides the space into three parts.

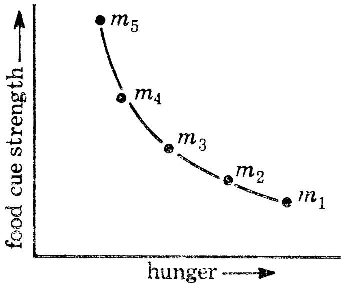

FIGURE 4. Two-dimensional causal factor space for feeding. The feeding strength is the same for points $m_1 \ldots m_5$, and the line joining these points is a motivational isocline.

THEOREM 1. Corresponding to every state in causal factor space there can be one and only one candidate state (see appendix 3 for proof).

However, the converse is not true, because there can be a set of points in causal factor space all mapping to the same candidate.

In terms of figure 4, it is clear that there are likely to be a number of motivational states that will map to the same feeding response strength in candidate space. For example, an animal may have a high hunger but low cue strength (m_1), giving the same feeding strength as if it had a low hunger and high cue strength (m_5). The line joining all those motivational states ($m_1 \ldots m_5$) which give the same feeding strength (F), is an example of a *motivational isocline*. Before going on to consider more precisely the possible combinations of causal factors that we may need to incorporate into any general theory, it may be useful to consider an hypothetical example in some detail.

Figure 5 is a Venn diagram showing two sets of causal factors, A, B, which may have overlapping elements. These map to two sets of candidates relevant to activities α, β, which must not have overlapping elements, because they are mutually exclusive. At any time, a candidate from α or β is observed as an action, and this will have been caused by a state of the causal factors in A or B.

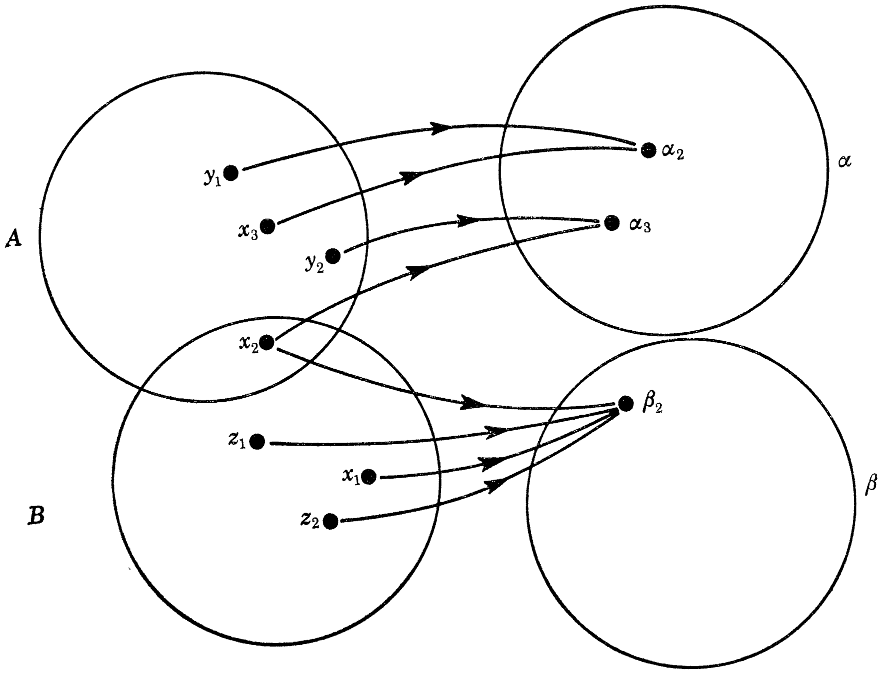

FIGURE 5. Venn diagram showing sets of causal factors, A, B, the elements of which (x_n, y_n, z_n) map to the candidates (α_n, β_n) responsible for particular actions. These causal states (candidates) are grouped into sets according to the mutually exclusive activities to which they belong.

Possible combinations of causal factors are illustrated in figure 5, namely (1) the causal factors (e.g. x_3, y_1) are only relevant to action α_2. (2) Some causal factors (e.g. y_2) may be exclusively relevant to one action (α_3), but others (e.g. x_2) may be relevant to more than one action (α_3, β_2). (3) An action (e.g. β_2) may be set up by alternative sets of causal factors (e.g. x_2, z_1, or x_1, z_2). In addition it will often be possible to group causal factors (e.g. x_1, x_2, x_3) having properties in common, but not necessarily relevant to the same activity. For example, x_1, x_2, x_3 might represent increasing levels of thirst, which induces one activity (β) at low, and another (α) at high levels. Thus β might result from the state of thirst below the 'thirst threshold' (Fitzsimons 1963; McFarland & McFarland 1968; Toates & Oatley 1970), and α from the state of thirst above the threshold. Morever, the state of thirst is itself the result of combinations of causal factors. For example, Oatley (1967) proposed that drinking is controlled by an additive combination of factors representing shrinkage of cellular and extracellular spaces, and there is now considerable evidence for such additivity (Fitzsimons & Oatley 1968; Fitzsimons 1969; Blass & Fitzsimons 1970). However, these factors are not individually represented in the causal factor space, because they are not independent. In terms of figure 5 activity α might represent drinking and β might represent feeding (α_2 and α_3 would be the drinking actions at different levels of thirst). This would imply that subthreshold thirst has a (presumably inhibitory) effect on feeding.

As in the case of candidate space, wherever causal factors can be grouped, and ranked within each group, it is possible to represent them along a single axis of the causal factor space. On this basis, figure 5 can be translated directly into figure 6, in which the causal factors are ordered along three axes x, y and z. Isoclines within this space join all those combinations of causal factors which lead to a single candidate.

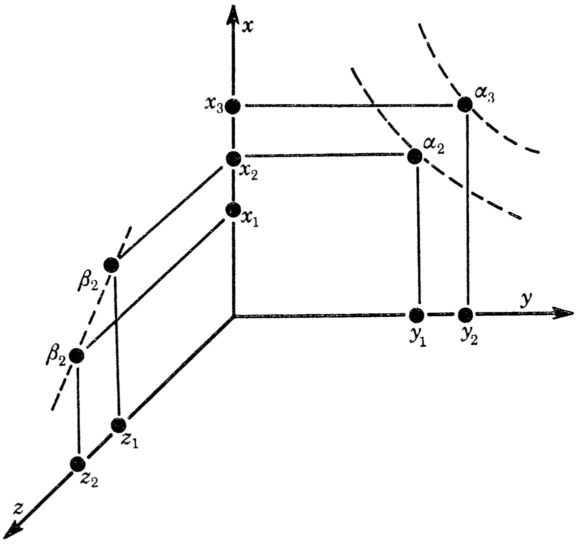

FIGURE 6. Causal factor space with axes x, y, z, along which the causal factors indicated in figure 5 are ranked. Isoclines are indicated by dotted lines.

INTERACTION OF INTERNAL AND EXTERNAL FACTORS CONTROLLING BEHAVIOUR

The necessity for distinguishing between internal and external causal factors controlling behaviour arises from the common observation that a given set of input conditions leads to different output phenomena from one occasion to another. Although the inferred change in internal state must, ultimately, derive from external factors, it is useful to distinguish between short-term sensitizing and long-term organizing effects of external factors. External stimulation can have three types of effect upon a behavioural system: (1) it can induce structural (irreversible) changes, (2) alter the internal state of the system, and (3) have relatively rapid direct effects upon behaviour (see McFarland 1971 for further discussion). We are concerned here with (2) and (3) only. That is, we are ignoring changes due to learning, maturation or injury.

Attempts to find a global recipe for the interaction of internal and external factors controlling behaviour have been singularly unsuccessful (McFarland 1971). We make no such attempt here, but are concerned to show how the problem can be formulated without making too many special assumptions.

Internal factors

As the problem of mathematical representation of the internal state of the animal has been discussed at length elsewhere, only a brief outline will be given here.

Provided that the animal is adapted to its environment, and the relation between behaviour and its consequences is known, the internal state can be represented in a *command space* (a subspace of causal factor space), the axes of which can be specified directly in relation to the consequences of the behaviour. In reaching this conclusion Sibly & McFarland (1974) claim that motivational state can be represented in a unique space of minimal dimensionality. To uphold this claim they assume that there exists a finite space (the 'ideal command space') in terms of which every internal causal factor can be completely represented. The smallest subspace of the ideal command space that can be attained in a particular environment is the 'command space'. Knowledge of the relevant aspects of the environment is sufficient to determine the dimensionality of the command space. Note that the command space is an abstract construction, and is not intended to correspond to any neurological structure. Although some animals may not have their internal state represented in the brain in a minimal from, a minimal form is all that is required in considering the control of behaviour (McFarland 1971).

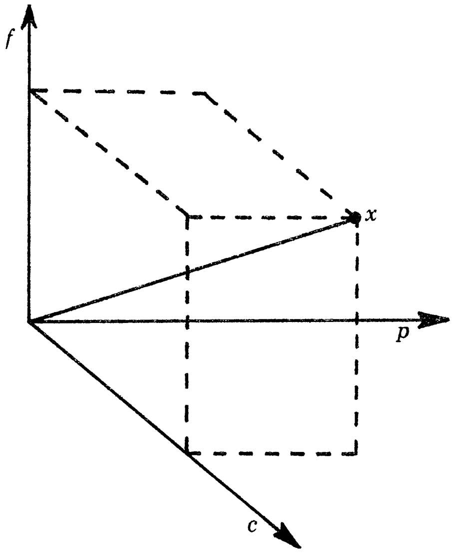

FIGURE 7. Representation of a hunger command in a three dimensional space. Axes indicate carbohydrate (c), protein (p) and fat (f) requirements. The hunger state is represented by the point x, and satiation is achieved when this point reaches 0. (From McFarland & Sibly 1972.)

The axes of the command space correspond to the primary motivational state variables, which in turn correspond to the degrees of freedom in the consequences of the behaviour. For example, if the consequences of eating were expressible in terms of quantities of carbohydrate, protein and fat consumed, then a maximum of three axes would be necessary to represent the hunger command in vectorial form. However, if the constitution of the food were always homogeneous, and feeding had no consequences in common with other activities, then a single hunger axis would be required. The relation between command space and consequences of behaviour is discussed at length by McFarland & Sibly (1972). For the present purposes it is sufficient to note that the command state arises as a result of all the complex interactions of relevant internal states, including those resulting from both short-term and long-term consequences of ongoing behaviour. It can be thought of as a set of instructions to the mechanism controlling behaviour. In terms of our simple example (figure 4), the command state might correspond to the amounts of carbohydrate, protein and fat required by the animal. This state would be represented by a point in a three-dimensional command space, as shown in figure 7.

External factors

External factors can be divided into those which directly alter internal state and those stimuli which can be ranked in order of their effectiveness in releasing a particular response. The strength of the response depends in some cases upon the summated value of all the stimuli relevant to the response, which are present. This is the rule of heterogeneous summation (Seitz 1940). There have been a number of empirical demonstrations of this rule, and a recent example comes from a study reported by Baerends & Kruijt (1973).

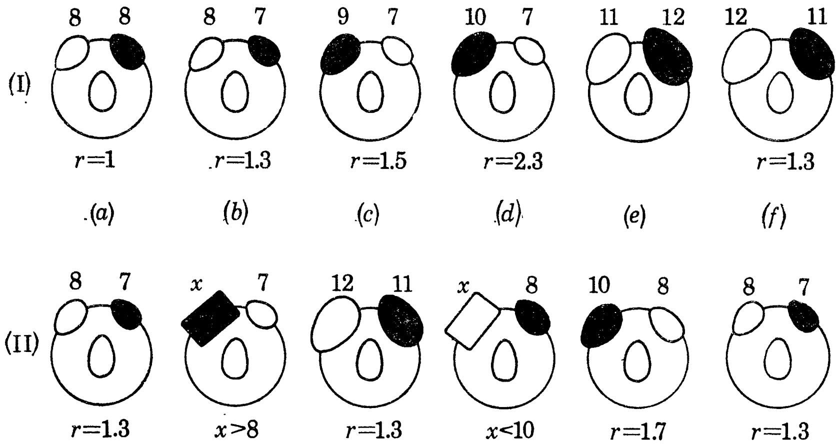

FIGURE 8. The 'titration' method for determining the value of an egg dummy. The circle represents the nest with one egg in the nest bowl and two dummies on the rim. The code numbers 7, 8, 9, 10, 11, 12 refer to the dummies of the size series (R) shown in figure 9; x is the model to be measured; r is a way of indexing the R series and is defined as the ratio between maximal projection surfaces of the dummies on the nest rim. The black dummy is always the preferred one.

(I) Determination of the value of the position preference. I*a* shows that the right site is preferred. This preference remains when dummy 8 is replaced by the smaller dummy 7 (I*b*) but can then be overcome by replacing 8 by 9 (I*c*); this sequence shows that the value of the position preference lies between $r = 1.3$ and $r = 1.5$: this conclusion holds when another pair of dummies with the same ratio is used (I*f*). Control test I*e* shows that the size optimum for this gull exceeds size 11.

(II) (*b*) Determination of the r-value of model x. Tests II*a*, II*c* and II*f* show that the position preference has remained unchanged. Tests II*b* and II*d* indicate, in combination with the preceding and succeeding tests, that the r-value of x is between those of the models 8 and 10 of the reference size series. (From Baerends & Kruijt 1973.)

Baerends and his co-workers, working with the herring gull (*Larus argentatus*), studied the effectiveness of various dummy eggs in eliciting the response of retrieving an egg placed on the nest rim. They used a 'titration' method for quantifying egg preference, which is illustrated in figure 8. A summary of the results is depicted in figure 9. This shows how the value of a dummy with respect to a standard size-ranking series is affected by certain changes in features, namely (*a*) changing the egg shape to rounded-edge block shapes; (*b*) omitting the spotted pattern on standard brown dummies; (*c*) changing the standard brown background for a green one; (*d*) adding a speckled pattern to the green dummies. All changes were carried out on dummies of different sizes. It is clear that the various features of the dummy combine in their effect upon the response. The quantitative effect of a combination on the response depends on which features are present and to what extent. Each feature adds a specific quantitative contribution which is independent of the contribution of other features. Therefore, the rule of heterogeneous summation applies.

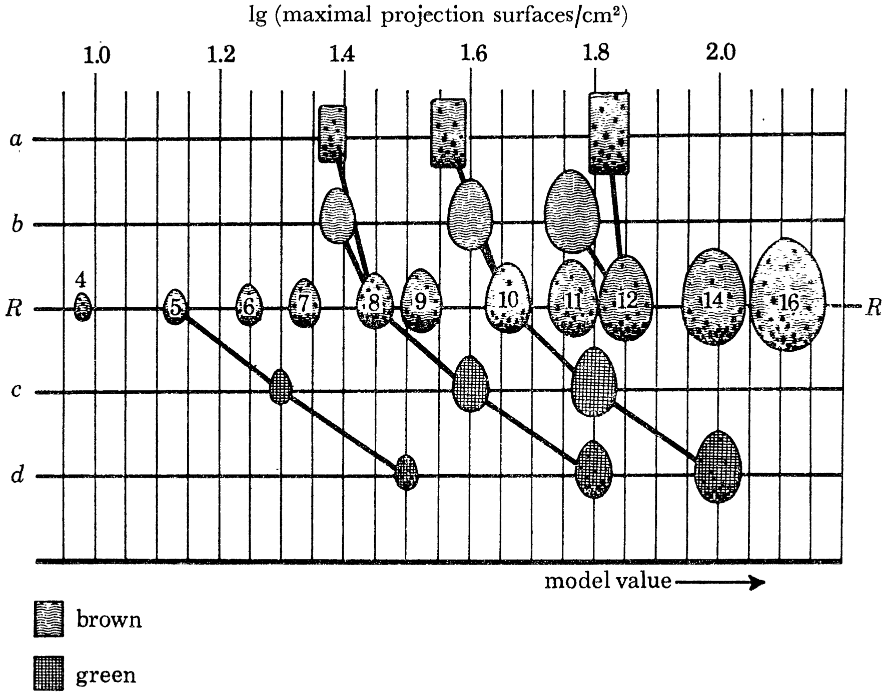

FIGURE 9. The average values found for various dummies with respect to the reference size series R. The position of different types of dummies (brown, speckled, block-shaped; brown, unspeckled, egg-shaped; green, unspeckled, egg-shaped; green, speckled, egg-shaped) each in different sizes was determined with the method described in the legend of figure 8. The code numbers 4–16 in the R series stand for, respectively, 4/8 to 16/8 of the linear dimensions of the normal egg size (8 = 8/8). The maximal projection surfaces (cm²) of the eggs of the reference series have been plotted (egg centres) along the logarithmic scale of the abscissa. Equal distances between points on this scale imply equal ratio values. (From Baerends & Kruijt 1973.)

Quantitative verification of the rule of heterogeneous summation implies, not only that external cues summate, but that they are evaluated by the animal in a quantitative manner. It is the results of such evaluation that we term *cue strength*. We can imagine that for each particular response there is an overall cue strength, and that this somehow combines with the command state to produce a motivational state. If the rule of heterogeneous summation were a universal rule, then we would require a single dimension along which to measure the cue strength relevant to any particular response. Since we cannot assume that this is so, we have to allow the possibility of more than one dimension, giving a *cue space*, somewhat analogous to the command space. A point in the cue space represents the *cue state* associated with a particular environment.

Motivational state

We represent the motivational state of an animal in a Euclidian causal factor space of n dimensions. Each axis of the space is independent, and axes relevant to the command space are combined in a Cartesian product with those of the cue space. In combining external and internal factors in this way we are making no assumptions about the particular mathematical functions by which the internal and external factors relevant to a particular response are related. We regard this question as an entirely empirical matter, and none of our conclusions depend on any particular formulation of this combination function. We can perhaps best illustrate our approach by reference to some particular examples.

Quantitative data on the effect of external stimuli on motivational state are provided by Heiligenberg's (1965) study of attack readiness of the cichlid fish *Pelmatochromis subocellatus*. The strength of the attack readiness may be defined by the number of attacks the fish delivers per unit time in a standard situation. Specifically:

> 'An adult male fish is placed together with a group of young fish for several weeks. The male can attack the young fish at will. However, the young fish always escape before being seriously bitten, so that a real fight – which might exhaust the male – never occurs. The behaviour of the male is recorded for 15 min; then a dummy of another male is presented behind a glass pane for half a minute, and the behaviour of the male is again recorded for the next 30 min. During the presentation of the dummy the male watches it, very rarely doing anything else than standing quietly in its place. Immediately after the removal of the dummy the male attacks the young fish much more than before and then returns slowly to his previous level of aggression.' (Heiligenberg 1965.)

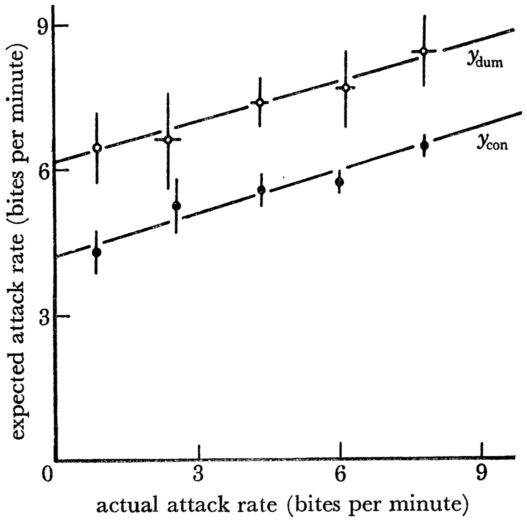

FIGURE 10. Expected values of attack rate y_{con} (ordinate) within a subsequent 400 s interval as a function of the attack rate x (abscissa) observed with a given 400 s interval (black circles). The expected value y_{dum} is additively increased if a dummy is presented between the given and subsequent 400 s interval (○). Data were divided into classes according to different levels of attack rate within the first 400 s interval. Within each group, average values (●) and variances of the mean (bars) were calculated with respect to both coordinates. (From Leong 1969.)

Because the attack rate of the fish fluctuates considerably it is impossible to predict, from knowledge of its value in a given time interval, the exact rate for the subsequent interval. However, the expected value y, of attack rate within a specific interval, can be estimated as a function of the observed attack rate x in the preceding interval. The attack rates observed within pairs of successive standardized time intervals, separated by a short intervening interval, were separated into classes on the basis of the level of attack observed in the first interval. Within each class the average values and variances were calculated for the attack rate within the first interval x and within the following interval y. As can be seen from figure 10, the relation between the two is linear. The same procedure is applied when a dummy is presented in the short intervening interval. Presentation of the dummy always alters the relation between x and y by a constant amount (figure 10). In other words, the increment in attack rate caused by presentation of a dummy is independent of the pre-stimulatory attack rate and the presentation is additive in its effect on the stimuli already existing.

Using Heiligenberg's method with the cichlid fish *Haplochromis burtoni*, Leong (1969) found that different components of the colour patterns of territorial males, painted on dummies, were additive in their effects upon attack rate. Similarly, Heiligenberg, Kramer & Schulz (1972) showed that different angular orientations of the black eye-bar of *H. burtoni* (figure 11) were additive in their effects upon attack rate. Both these findings are in agreement with the rule of heterogeneous summation.

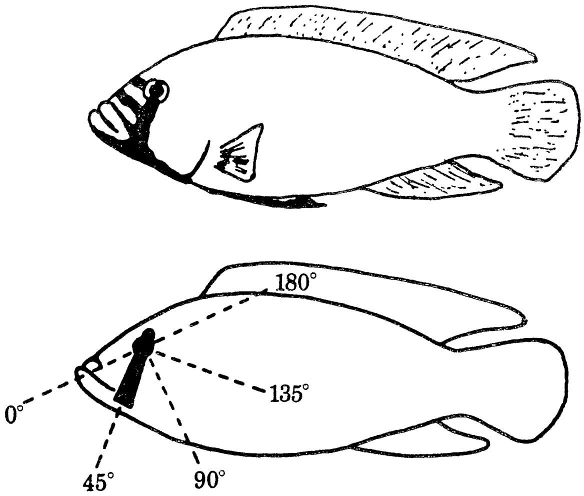

FIGURE 11. Black pattern marking head of territorial male (top) and dummy (bottom) showing only the black eye-bar represented by a piece of metal foil rotatable around the centre of the eye. The five eye-bar positions chosen in the experiments are indicated by dotted lines, the angle between the eye-bar and the eye-snout axis being 0, 45, 90, 135, and 180° respectively – the second position represents the natural location of the eye-bar. The body coloration of the dummy is yellowish grey matching the natural ground coloration of territorial males. All additional colour patterns are omitted. (From Heiligenberg *et al.* 1972.)

The pre-stimulatory attack rate is presumably the result of the combined effect of the internal and external factors. The results of these and subsequent (Heiligenberg 1973), experiments indicate that various external stimuli can increase, or reduce, attack rate in an additive manner. At first sight, this seems to imply that internal and external factors combine in an additive manner, but this is not necessarily so. What is achieved, however, is a constraint on the possible shapes of the isoclines. On a plot of external stimulation (cue strength) against internal state, a motivational isocline connects points which produce a particular action (attack rate). Heiligenberg's result shows that whatever the animal's position in this space, a given change in external stimulation produces the same shift between isoclines. Thus if it starts on isocline A, it always shifts to isocline B whatever its initial position on isocline A. Although this places an important constraint on the possible shapes of the isoclines, it does not show that they are necessarily straight (i.e. that internal and external factors combine in an additive manner).

Another example is provided by the work of Baerends, Brouwer & Waterbolk (1955) on the courtship of the male guppy *Lebistes reticulatus*. The tendency of the male to attack, flee from, and behave sexually towards the female can be gauged from the colour patterns characteristic of each motivational state. In figure 12 increasing sexual motivation is plotted as an index of colour change along the abscissa. The effectiveness of the female in eliciting courtship increases with her size and is plotted on the ordinate. The points plotted on the graph represent the relation between the measures of internal state and external stimulation at which particular patterns of behaviour are observed. If the patterns, p, si, and s are taken to represent increasing values of response strength, and the scaling of the ordinate is taken at face value, then the isoclines obtained represent closely those that would result from multiplication of internal and external factors. In practice the method of quantification is somewhat arbitrary, the scaling on the abscissa depending on the association of the different colour patterns with the relative frequency of activities characteristic of sexual tendency. Nevertheless, figure 12 is a good example of the type of representation that we have in mind.

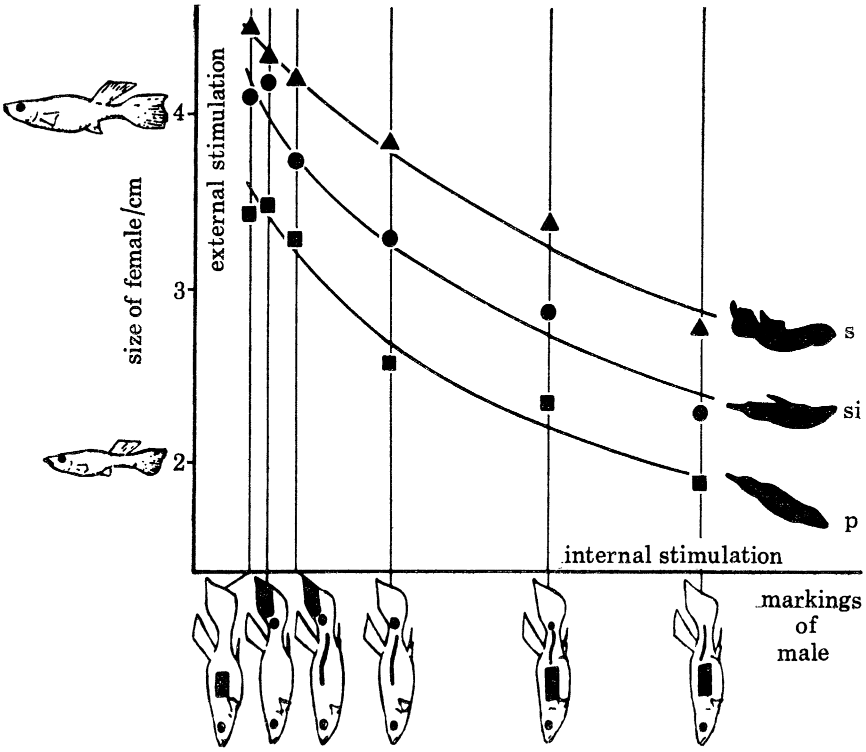

Figure 12. The influence of the strength of external stimulation (measured by the size of the female) and the internal state (measured by the colour pattern of the male) in determining the courtship behaviour of male guppies. Each curve represents the combination of external stimulus and internal state producing posturing (p), sigmoid intention movements (si), and the fully developed sigmoid (s), respectively. (From Baerends *et al.* 1955.)

Empirical determination of motivational isoclines

The behavioural final common path provides a point of convergence in a complex net of interacting variables. A set of points in causal factor space, constituting a motivational isocline, correspond to a single point in candidate space (theorem 1). This principle applies whatever the particular relation between causal factors and behaviour. The problem of determining any such relations empirically is the same as the problem of determining the shape of the relevant motivational isocline.

One of the main difficulties in the empirical determination of motivational isoclines is the confusion arising from the large number of causal factors involved. In order to discount the effect of most of them, it is sensible to look for a phenomenon which is independent of particular consequences of behaviour, and therefore of the particular route followed by the changing motivational state (trajectory). McFarland (1974*a*) has suggested that such a phenomenon be called a landmark. A simple example of a landmark is the satiation point. The true satiation point is independent of the particular behavioural route taken to reach satiation. However, in practice the satiation point is not very suitable as a landmark as it is easily bypassed by the trajectory, and the experimenter can therefore never be sure whether the satiation point has been reached or not. A better form of landmark would be a boundary line that the trajectory would be less likely to miss. The axes themselves provide such boundaries, but it is not always clear from observation of behaviour when this line has been crossed. In schedule-induced polydipsia (Falk 1969, 1971), for example, the animal readily becomes overhydrated, but it is not possible to say at what precise point this occurs. A more useful type of boundary is the switching-line in candidate space.

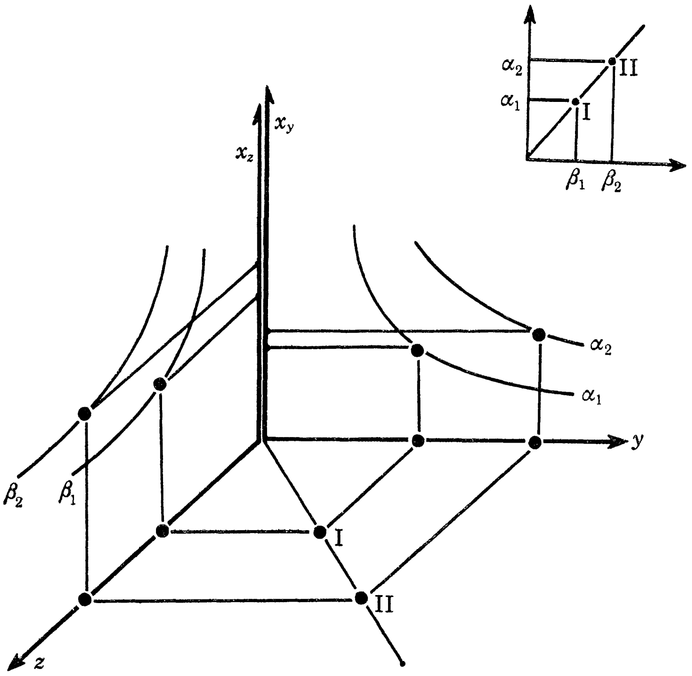

FIGURE 13. Two planes ($x_y y$ and $x_z z$) in causal factor space, showing points on isoclines where changes between activities α and β occur. These points (I and II) fall on a straight line when projected in the yz plane. This line corresponds to the switching-line in candidate space (inset).

Suppose we consider two planes in the causal factor space, which are relevant to different activities α and β. Suppose we have the ability to make accurate measurements along one axis in each of these planes: call these axes y and z. We also have the ability to make directional manipulations in the states corresponding to the other two axes, x_y and x_z, which are relevant to axes y and z respectively as illustrated in figure 13. For example, x_y and x_z might represent external stimuli relevant to internal states y and z. Activities α and β are mutually exclusive, so that only one can be observed at a time. However, if by manipulating the values of x_z and x_y, we can cause changes in behaviour, then we can identify the switching-line in candidate space. For example, if at known values of y and z, we observe a change in behaviour, when x_z and x_y are held constant, then we can identify a point I in a plot of z against y (figure 13), which corresponds to a point on the switching line in candidate space (figure 13 inset). Similarly, at other known values of y and z we can identify another switching point II. We do not know what values of x_z and x_y correspond to these points, but it is evident that I and II must lie along a single line in the yz plane, and that these points correspond to points on motivational isoclines, as illustrated in figure 13. In other words, if we can find one measurable axis in causal factor space that is relevant to each of the activities in which we are interested, then we can identify the 'shadow' of the switching-line in candidate space.

Let us now consider a hypothetical experiment. We take an animal with measurable values along axes y, z, and a manipulable state x. We start the experiment with the animal at a point p in the yz plane, and at a constant value x_1 of X, as illustrated in figure 14. Suppose we observe activity α which implies that the value of y is progressively reduced. The point p in the yz plane moves towards the z axis, and in the xy plane it moves correspondingly until it hits the isocline z_1. At this point, according to the theory, a change in behaviour is observed, and this implies that the switching-line in the yz plane is crossed. For ease of illustration, and to simplify the argument, we can suppose that there is a little overshoot,† so that the animal does not start activity β until the switching-line is passed. Activity β results in a trajectory parallel to the z axis of the yz plane, and we can suppose that a situation similar to that in the xy plane (but not illustrated in figure 14) holds for the case of activity β. If the trajectory crossed the switching line at a point corresponding to z_1 on the z axis, it will now recross at z_2 in the xy plane, but may overshoot. If the points at which the switching-line is crossed can be identified, in the yz plane, then the position of the switching-line will now begin to become evident.

Suppose we now introduce an experimental change in x, from x_1 to x_2 which we cannot measure. We can use the switching-line as a landmark to find the shape of the isoclines. The point at which the experimental manipulation is made is marked by an arrow in the yz plane, and a corresponding arrow in the xy plane. After the manipulation, the trajectory has to travel much further in the direction parallel to the y axis before it hits the z_3 isocline. When this trajectory is portrayed in the yz plane, the point at which the z_3 isocline is crossed no longer lies on the previously defined switching-line. In fact if the observations were carried to their conclusion with x held constant at x_2, the switching-line would appear to have rotated through an angle α.

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† Note that by definition there cannot be overshoot of the switching line in *candidate* space, because when one candidate becomes stronger than another ('overshoots the switching line') it assumes control of ongoing behaviour. The sophisticated reader may fairly object to this apparent inconsistency, our reply is to extend the exposition. The causal factor space depicted in figure 14 is a simplification of the true causal factor space because it leaves out many of the causal factors involved in the control of activities α and β. In fact it only represents the major determinants of behaviour in the hypothetical experiment, namely x, y, and z. They cannot account for the finer detail of behaviour, since if they were the only determinants of behaviour the animal would perpetually dither at the point at which it first reached the switching line. Thus there must exist at least one further causal factor which causes overshoot of the switching line in the xyz space. Of course, it does not cause overshoot of the switching line in the candidate space, instead it 'artificially' increases the strength of the candidate controlling ongoing behaviour. When that candidate relinquishes control the artificial boost is removed, so that the candidate's strength is by that amount less than that of its competitor.

A number of authors have suggested that overshoot of this type is necessary to avoid 'dithering' in the decision-making system (e.g. Atkinson & Birch 1970; McFarland 1971). Various mechanisms, such as hysteresis (Toates & Oatley 1970) and positive feedback (McFarland 1970; Wiepkema 1971) have been suggested. It is worth noting that a different account of the phenomenon has been suggested by Zeeman (1971, 1972) in terms of Thom's (1972, 1974) catastrophe theory, according to which the behaviour is not determined only by the current values of the state variables, but also by the manner in which this set of values was approached.

Now if this experiment were repeated many times with different values of x, from the values of the angle α that would be obtained, it should be possible to calculate the shape of the z isoclines.

Experimental methods

We have so far regarded the shadow in causal factor space of the switching-line in candidate space as a suitable motivational landmark. The variability of animal behaviour makes direct observational estimation of the position of motivational landmarks difficult. However, much of this variability can be masked by means of a particular experimental method, which is based on the concept of dominant behaviour.

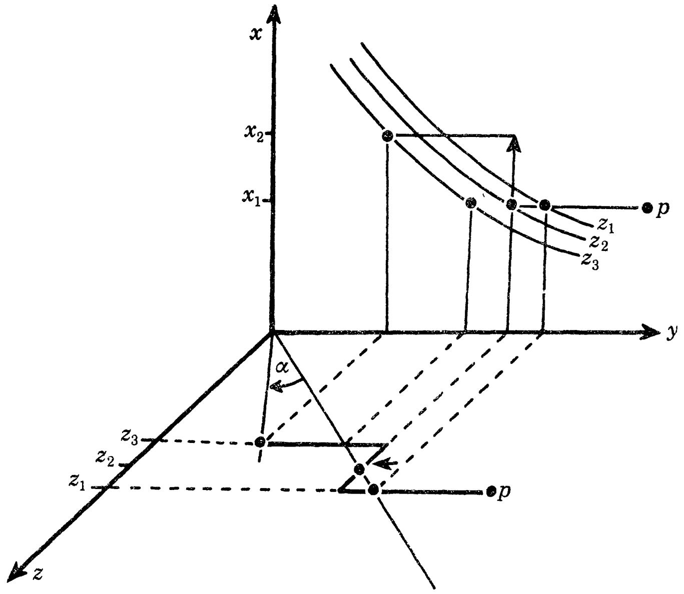

FIGURE 14. Positions on isoclines in a plane (xy) in causal factor space are projected in the yz plane. The position of the switching-line in the yz plane appears to rotate through angle α when an experimental manipulation (arrowed) is performed, such that the value of x is raised from x_1 to x_2.

Dominant behaviour can be defined as that behaviour which is always resumed following interruption (McFarland 1974*b*). Behaviour which is not always resumed is called subdominant. In practice, the interruption must be neutral, in the sense that it does not alter the animal's motivational state. For accurate identification of subdominant behaviour, the interruption must also be of sufficient duration to permit a re-establishment of the dominant behaviour. For example, McFarland (1974*b*) found that in a situation where the male three-spined stickleback (*Gasterosteus aculeatus*) alternates between courting a female and visiting his nest, interruption of courtship is nearly always followed by continuation of courtship, indicating that courtship is dominant. Interruption of nest-visits is followed by continuation of nest-visits only when the interruption is short (0–15 s). Longer interruptions (15–20 s) are generally followed by courtship, and nest-visit behaviour must therefore be classified as subdominant under these conditions. McFarland & Lloyd (1973) found that a similar type of 'time-sharing' occurs during feeding and drinking in the Barbary dove (*Streptopelia risoria*). Barbary doves were tested in an operant situation in which they characteristically alternate between feeding and drinking. When primarily hungry doves were interrupted while feeding, or primarily thirsty animals while drinking, the behaviour was resumed after the interruption and was thus classified as dominant.

When primarily hungry doves were interrupted while drinking, or primarily thirsty doves while feeding, the behaviour was resumed after a short interruption, but changes to the alternative behaviour followed a long interruption. McFarland & Lloyd found that it is possible to identify a dominance boundary in the motivational state plane, on one side of which feeding is dominant, while drinking is dominant on the other side. Such a boundary is readily detectable by simple experimentation, and it is detection of this type of boundary that forms the basis of the method described below.

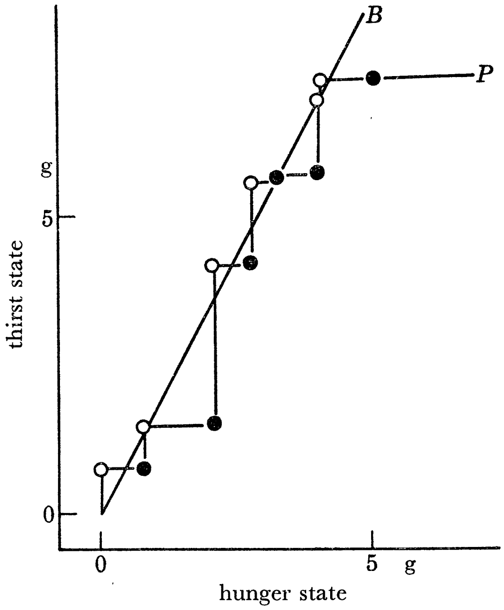

Figure 15. Trajectory in the hunger–thirst state plane resulting from the use of a double-interruption test on a hungry and thirsty dove. From the initial state P the bird feeds, thus reducing its hunger state. On changing from feeding to drinking it is interrupted for one minute, and resumes feeding after the interruption, showing that hunger is dominant (●). On being interrupted the second time it changed from feeding to drinking, the bird drinks showing that thirst is now dominant (○). This procedure is continued until the satiation point is reached. The black circles tend to fall on one side of the boundary line B, while white circles fall on the other side.

The basis of the method is to interrupt both feeding and drinking following a transition from feeding to drinking, and vice versa. The subject is allowed to work for both food and water in an operant situation, following some combination of food and water deprivation. Under such conditions doves alternate between feeding and drinking until satiated. The interruption procedure is to turn off all key-illumination and reward mechanisms. The doves soon adjust to this procedure, and cease to peck when the keys are unilluminated. The experiments are run under the control of a digital computer, which records all key-pecks and delivers a food or water reward for each peck, and determines the duration of interruptions following transition from feeding to drinking and vice versa.

Provided that the interruption is sufficiently long, it will either postpone the interrupted activity, or mask it. In the former case the interrupted behaviour must be classified as dominant, in the latter case it is subdominant. Therefore, if every transition is interrupted for a standard period, the behaviour is dominant if it is resumed following the interruption, and subdominant otherwise. For example, suppose hunger is dominant and the bird changes from feeding to drinking; it is interrupted and continues feeding, showing that hunger is still dominant. When it changes to drinking following such an interruption, thirst has become dominant. This method has the virtue of being simple and accurate. The complete masking of subdominant behaviour pushes the trajectory quickly towards the boundary, and the role of the interruption is automatically reversed when the boundary is crossed. Figure 15 illustrates an example of a result obtained using this technique. The effectiveness and reliability of this technique has been proven in a long series of repeated experiments (Sibly & McCleery 1975); which have also been used to confirm that the position of the boundary is reasonably consistent from one trial to the next.

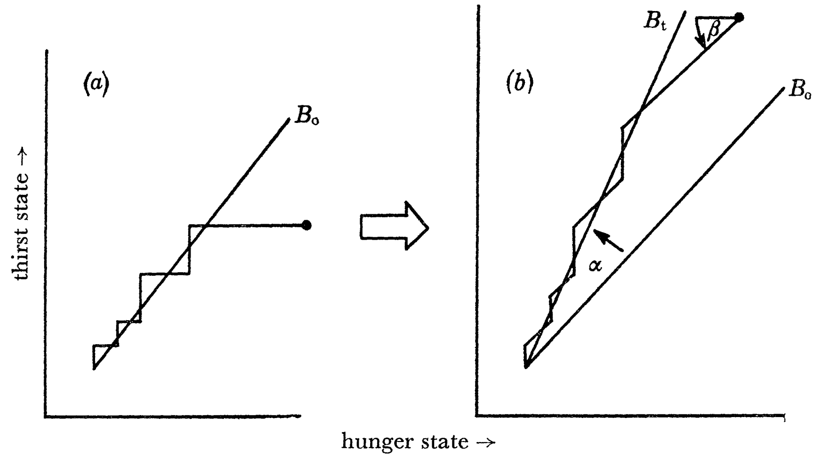

FIGURE 16. (*a*) Hypothetical trajectory and boundary B_0, based upon orthogonal feeding and drinking vectors. (*b*) Transposition of (*a*) resulting from rotation of feeding vector through angle β, giving the transposed boundary B_t, which has apparently rotated through angle α from position B_0.

The establishment of the dominance boundary as a landmark in motivational space is only the first step in the determination of a motivational trajectory. It is an important step because it provides a means of identification of motivational state that is independent of the particular behaviour of the subject. Just as a landmark can be viewed from many directions, so the boundary can be found by different trajectories. Just as apparent motion of a landmark must be interpreted in terms of the motion of the observer, so apparent motion of the dominance boundary must be interpreted as changes in the direction of the trajectory. This apparent motion of the boundary forms the basis of a further step in the determination of motivational trajectories.

When the trajectory in the hunger–thirst state plane is composed of orthogonal vectors, there is a tacit assumption that the consequences of feeding affect only hunger, and those of drinking affect only thirst. This will not always be a correct representation of the true state of affairs. However, the direction of the vector representing the consequences of behaviour depends not only on its components but also the scaling of the hunger and thirst axes. Since the scaling is an arbitrary matter, no great importance can be attached to the absolute direction of a vector, but relative differences between vectors are meaningful. In these circumstances, it is useful to represent a standard situation by orthogonal vectors, as has been done above.

Suppose we introduce an experimental manipulation which we know will alter the direction of the vector consequent upon a particular behaviour. For example, if food had a high water content, feeding might be expected to affect the animal's state of thirst as well as its state of hunger. In such a case we would initially represent the trajectory of a boundary-finding experiment in terms of orthogonal vectors, as illustrated in figure 16*a*. However, if we knew the effect of wet food compared to that of dry food, we could rotate the feeding trajectory through an angle β to represent the contribution of feeding to the reduction of thirst. This would have the effect of transforming the original trajectory (figure 16*a*) into a new trajectory (figure 16*b*). A corollary of this line of reasoning is that an apparent rotation of the boundary, induced by some experimental manipulation, can be used as evidence for transforming the trajectory. A simple experiment will serve to illustrate this phenomenon.

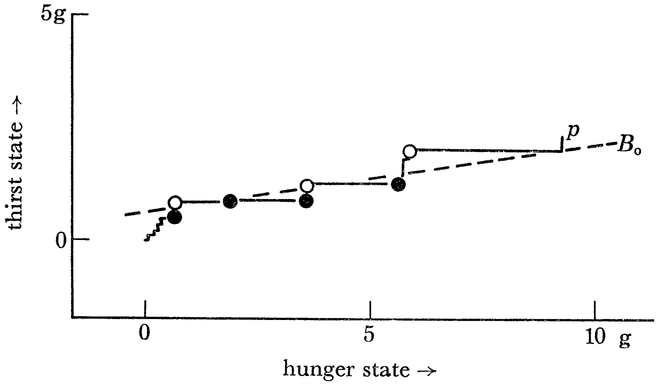

FIGURE 17. Orthogonal trajectory (double interruption procedure) from an experiment in which a fistulated animal received 0.1 g water per food reward. B_o is the observed boundary.

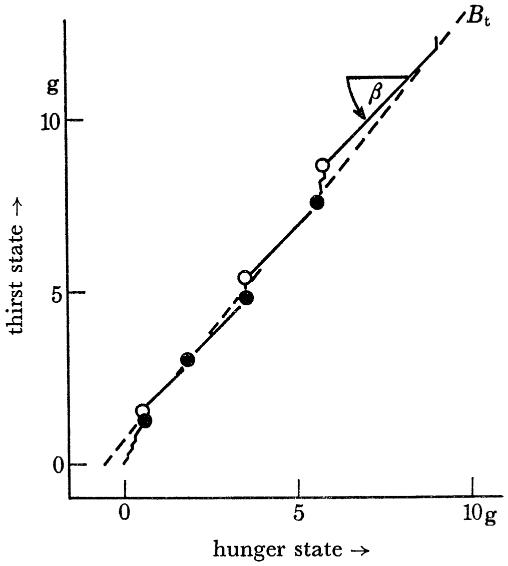

FIGURE 18. Transposition of figure 17 trajectory by rotating feeding vector through known angle β to account for water intake during feeding. B_t is the transposed boundary.

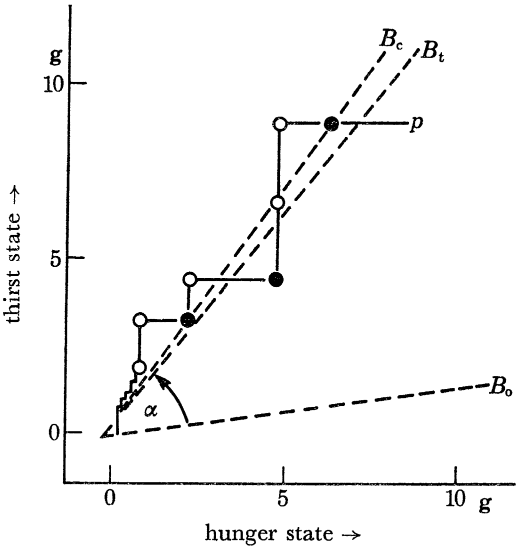

FIGURE 19. Orthogonal trajectory from control experiment (no water injection), giving boundary B_o. Observed B_o and transposed B_t boundaries are shown for comparison.

Sibly & McCleery (1975) implanted a number of doves with oesophageal fistulae by means of a previously well-tried technique (McFarland 1969). These fistulae permit water to be injected directly into the crop. When the animals had recovered from the operation they were run in a series of boundary-finding experiments using the double-interruption technique. Each animal was run under three conditions. (1) Each time the bird received a food reward, 0.1 cm^3 water was injected directly into the crop, oral water presentation remaining normal.

(2) Each time the bird received a water reward, 0.1 cm^3 of water was injected directly into the crop, oral food presentation remaining normal. (3) Both food and water rewards remained normal, no water being injected into the crop. Figure 17 shows the orthogonal trajectory obtained from an animal run under condition 1. Clearly, it is not difficult to calculate the angle β through which the feeding vector should be rotated. The result of applying this transformation is illustrated in figure 18, giving a new boundary position B_t. Is this boundary in the position that would be expected from previous experiments? The question can be answered by looking at the results of the subsequent control run (condition 3) for the same animal (figure 19). The control run gives a boundary B_c not very different from that (B_t) obtained from transformation of the results of the experimental run. The results from animals tested under condition (2) showed similar apparent rotation of the boundary. These results confirm earlier findings (McFarland 1969), that doves are quantitatively sensitive to water injected directly into the crop, and that this information contributes additively to the satiation feedback.

So far, we have considered trajectories as a direct reflection of the primary motivational state of the animal. The primary motivational state represents the potentiality of the animal to perform certain types of behaviour. However, there are also motivational effects dependent upon the ongoing behaviour itself. These aspects of motivation can be identified with a type of motivational state analogous to momentum (McFarland 1970, 1971). If this view is correct we might expect such effects to influence the form of motivational trajectories.

Momentum could be provided by positive feedback from the consequences of behaviour so that animals will tend to accelerate their behaviour, when the 'going is good' (Wiepkema 1971). McFarland & McFarland (1968) argued that such positive feedback must have a built-in decay mechanism, so that the state induced by positive feedback would decay if the feedback were interrupted. They obtained some evidence for this effect in doves, and this has since been confirmed for both feeding and drinking behaviour (Dantzer & McFarland 1975).

Each reward received by a dove, in the type of feeding-drinking experiment described above, reduces hunger and/or thirst by a given amount by virtue of the negative feedback involved in satiation. The magnitude of the reduction will depend upon the size of the reward in terms of its satiating characteristics as learned by the animal. This magnitude will also be offset by any positive feedback resulting from the ingestive behaviour. Thus the size of the decrement in hunger and/or thirst resulting from each reward will be an inverse function of the reward rate. When reward rate is high, more reward 'steps' in a given direction will be required to reach the dominance boundary. To the naive observer, counting all steps as equal, the position of the dominance boundary will appear to shift. The magnitude of this apparent shift should be a function of the reward rate differential. Our method is to start the animal with a low reward rate for both feeding and drinking, and use the double-interruption method to determine the position of the dominance boundary. As soon as the boundary has been crossed twice (i.e. crossed and recrossed) the reward rate for feeding or drinking is increased, and the boundary is again 'searched' for. A typical result is illustrated in figure 20. Here the position of the boundary has clearly shifted following the change in reward rate. This result is consistent with the view that the degree of positive feedback is increased when the reward rate is increased.

We have carried out a number of experiments using this technique, and these are reported in detail elsewhere (McFarland 1974*a*; Sibly 1975). A variety of combinations of reward rates were employed in these experiments. The manner in which the results of these tests are evaluated is illustrated in figure 21 and a summary of the results obtained is given in figure 22.

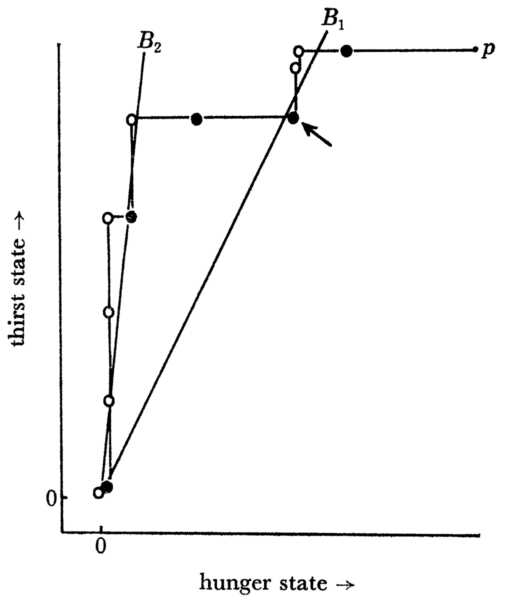

FIGURE 20. Apparent boundary rotation due to increased food reward rate. The boundary B_1 is initially found by the double-interruption method, then (arrow) the feeding reward rate is increased and the boundary B_2 found again.

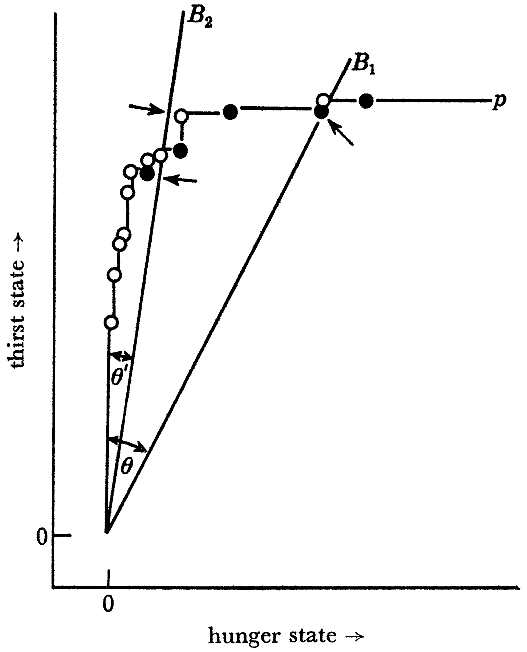

FIGURE 21. Method of measuring boundary rotation. The initial position of the boundary (B_1) is measured as θ, and the rotated position (B_2) as θ'. Boundary lines are drawn so that discrepancies (marked by solid arrows) are balanced. Other symbols as in figure 20.

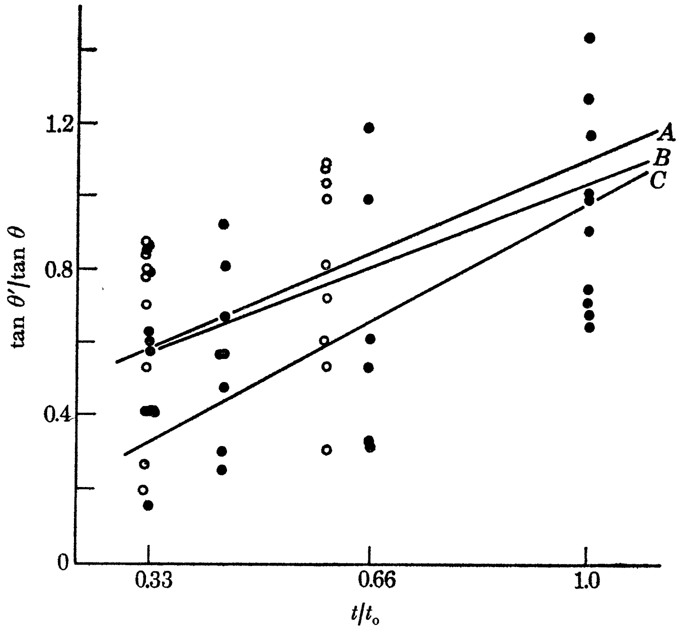

FIGURE 22. Results from a series of momentum tests. Each point represents the result obtained from a single test. Each animal was tested once under each condition. Black points are from one group of birds (I), and white points from another group (II). Line A is the regression line obtained for the group I data, line B that for the group II data. Line C is theoretically derived (see text). t_0 is the initial inter-reward interval, and t the subsequent interval in each test employed.

These results can be interpreted directly in terms of a motivational isocline. Suppose we consider a two dimensional causal factor space with axes corresponding to primary hunger q_h (amount of food needed) and rate of obtaining food $\dot{q}_h$ (amount of food/unit time). An isocline in this space would join all those points which map to a single point on the feeding axis in candidate space. The theoretical line C in figure 22 corresponds to a set of hyperbolic isoclines in the causal factor space (i.e. isoclines of constant $q_h \dot{q}_h$). This may be shown as follows:

Let the point on the feeding axis of candidate space be $F = q_h \dot{q}_h$. On the graphs of our results (figure 21), $q_h = q_t \tan\theta$ for points on the dominance boundary, therefore

$$q_t \tan\theta\, \dot{q}_h = F. \tag{1}$$

If $\dot{q}_h$ is changed to $\dot{q}'_h$ inducing a change in θ to θ', then for points on the new dominance boundary

$$q_t \tan\theta'\, \dot{q}'_h = F$$

therefore

$$q_t \tan\theta\, \dot{q}_h = q_t \tan\theta'\, \dot{q}'_h$$

or

$$\frac{\dot{q}'_h}{\dot{q}_h} = \frac{\tan\theta}{\tan\theta'} = \frac{t_0}{t},$$

which is line C in figure 22.

A more intuitive understanding of the situation can be gained from figure 23. Suppose the state approaches a dominance boundary (B_1) at reward rate a and thirst x (figure 23). The boundary is crossed at point A on the hunger (q_h) axis, and the reward rate is then changed to b, or to c. In the former case the boundary (B_2) will be crossed again at $q_h = B$: in the latter case the boundary (B_3) will be crossed again at $q_h = C$. In the causal factor space (figure 23*b*), the points A, B and C correspond to points on a hyperbolic isocline. Now compare an animal at thirst x, reward rate a, crossing the boundary at $q_h = A$; changing to reward rate b and crossing again at $q_h = B$, giving isocline x in figure 24*b*. Compare this with the same animal at thirst y, and reward rate a, crossing B_1 at $q_h = X$, then changing to reward rate b and crossing B_2 at $q_h = Y$. This gives two points on a new isocline y in the causal factor space (figure 24). Clearly we have a set of nested isoclines, each corresponding to a different degree of thirst (q_t), at which there is a change from hunger to thirst dominance. As each isocline must correspond to a point on the feeding axis of candidate space, it is clear that there must be a corresponding point on the drinking axis at which thirst becomes dominant. This situation is summarized in figure 25. Since we know that there must be a boundary in the candidate space (figure 3), namely the switching line, it is evident that the dominance boundary in causal factor space is merely a reflexion of the boundary in candidate space.

A further example may serve to illustrate this point. Reynier & McFarland (1974) trained doves to obtain food and water by pecking at red and green keys respectively, as described above. They then trained the birds in sessions in which the colour of the food key was changed from red to orange, and the birds were not rewarded for pecking when the key was orange. At intervals throughout this training, the birds were given a double-interruption test, in which the food key was changed from red to orange following detection of the dominance boundary. In these tests pecks at the orange key were rewarded. We can represent this situation in a two-dimensional causal factor space, in which cue strength is plotted against hunger q_h (figure 26*b*). In these experiments, the trajectory approaches the boundary from the hunger side, and must cross twice (i.e. back to the hunger side) before the food cue is changed. As illustrated in figure 26*b* the boundary (B_1) is crossed at $q_h = A$, and this corresponds to a point on an

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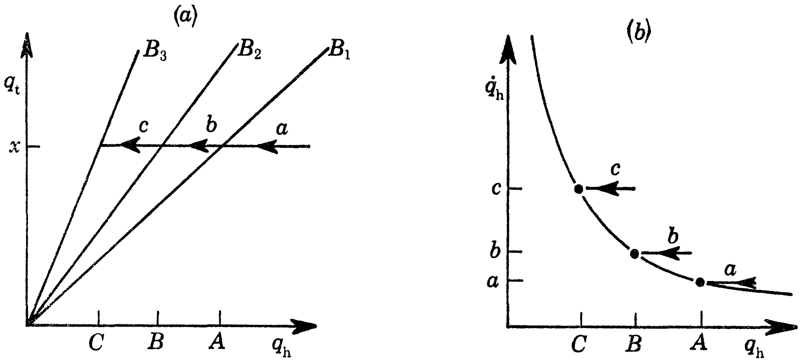

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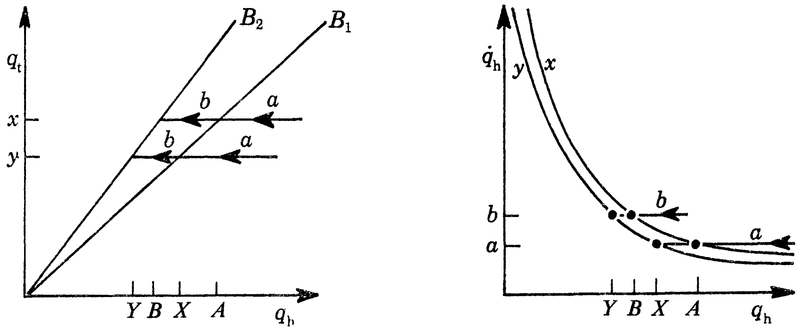
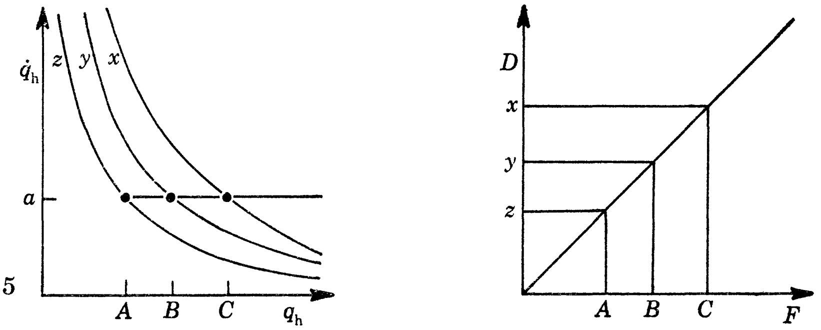


25


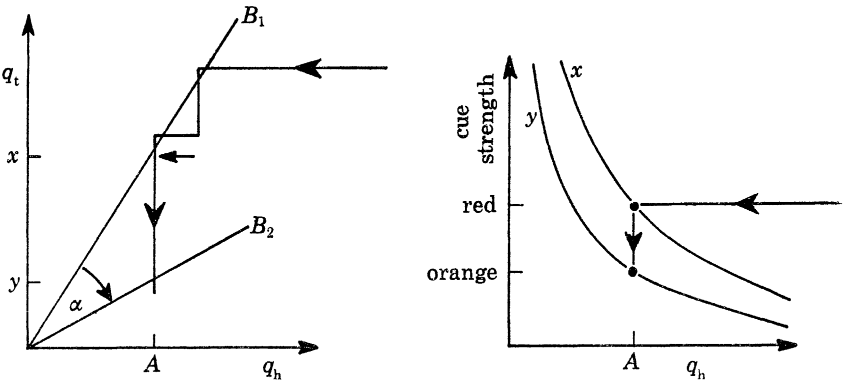
26


FIGURE 23. (*a*) Hypothetical situation in hunger–thirst state plane, showing where the boundary would appear to be at reward rates *a*, *b* and *c* (see text). (*b*) the same situation portrayed in causal factor space. q_t, thirst state; q_h, hunger state; $\dot{q}_h$, rate of change of hunger state.

FIGURE 24. Hypothetical situation in hunger–thirst state plane (*a*), and (*b*) corresponding causal factor space (see text). Symbols as in figure 23.

FIGURE 25. Hypothetical situation in causal factor space (*a*), and (*b*) corresponding candidate space. Symbols as in figure 23.

FIGURE 26. Hypothetical situation in hunger–thirst state plane (*a*) resulting from manipulation of cue strength, as portrayed in causal factor space (*b*). See text for details.

isocline x (figure 26*b*). The change from a red to orange key, presumably corresponds to a reduction in cue strength, so that hunger dominance is lost, and the animal drinks until the boundary (B_2) is again crossed at a point corresponding to a new isocline y (figure 26*b*). Thus there is, according to the theory, an apparent rotation of the boundary through an angle α. In practice, Reynier & McFarland found a correlation between the observed angle α, and the degree to which each individual bird had learned not to peck the orange key (as assessed in separate tests). In four sequential tests, interspersed by retraining on food alone, the correlations between degree of learning and the angle α obtained in double interruptions tests was as follows: Kendal Rank correlation coefficients = 0.60, 0.66, 0.75, 1.0, giving p values of 0.771, 0.167, 0.028, 0.0014, respectively. These results support the view that the magnitude of apparent boundary rotation in a double-interruption test is correlated with the magnitude of reduction in cue strength. This view is consistent with the idea that the apparent boundary position observed in experiments is a reflexion of the boundary in candidate space.

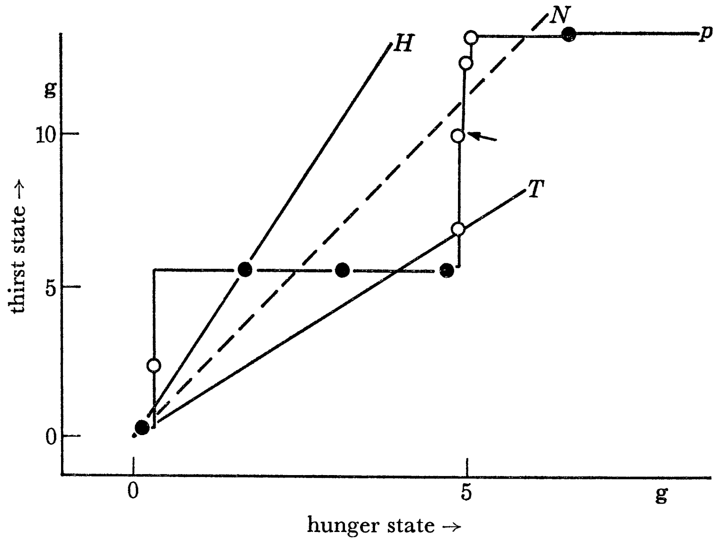


FIGURE 27. Example of split boundary obtained by increasing reward rate for both feeding and drinking. The position of the boundary (dotted) is initially determined for a low reward rate (N), then the rate is increased. Boundary T has all white points to its left, and boundary H has all black points to its right. Other symbols as in figure 15.

A further test of the theory can be devised by reference to figure 14. Here we see that an experimental manipulation in the xy plane induces an angular shift, towards the z axis, of the switching-line in the yz plane. Suppose the x axis were relevant to the z axis as well as the y axis (alternatively we can imagine an independent x_z axis relevant to the z axis). If the experimental manipulation $x_1 \rightarrow x_2$ were relevant to both y and z axes, then a situation similar to that portrayed in the xy plane (figure 14) would occur in the xz plane. A consequence of this experiment would be to rotate the switching line in one direction for $y \rightarrow z$ behaviour changes, as illustrated in figure 14, and in the opposite direction following $z \rightarrow y$ behaviour changes. In other words, there would appear to be two switching lines following the experimental manipulation.

This phenomenon can be illustrated with respect to the dominance boundary in the hunger–thirst plane in the type of double-interruption experiment described above. Figure 27 illustrates a typical result obtained when the reward rates for food and water are simultaneously increased at the point marked by an arrow.

Discussion

In this paper we have concentrated on one aspect of motivational organization, the behavioural final common path. In this final section we attempt to show how the behavioural final common path is related to motivational systems in general.

A motivational system is usually envisaged as a system controlling a group of functionally related behaviours (McFarland 1971). It is convenient to refer to such systems in general terms, as 'feeding system' or 'aggression system'. The variables of a motivational system relate to behaviour as a function of time, examples being 'hunger', 'frustration' and other typically 'motivational' variables. This view of a motivational system is largely a matter of convenience, and interactions between such systems can occur at many levels (McFarland 1971). Indeed, division into different systems is not strictly necessary, and the system as a whole can be represented as a causal factor space, as has been done in this paper.

An animal cannot always satisfy its needs in the face of environmental ambivalence. For example, if an animal has to expose itself to the hot sun in order to obtain food, then hyperthermia may become a consequence of feeding behaviour. If the animal cannot satisfy both hunger and thermal requirements, it has somehow to be able to compare the merits of reducing hunger with those of reducing hyperthermia, and choose an optimal compromise solution.

Our argument is that decisions among different courses of action must be made in terms of a common currency, and weighed among a common set of criteria. The necessity for comparing the merits of different courses of action implied that there must be some 'trade-off' mechanism built into the motivational control system. Since the trade-off process must take into account all relevant motivational variables, it is clear that the mechanism responsible must be located at a point of convergence in the motivational organization. This point is provided by the behavioural common path, and the description of the structure of the common path in terms of motivational isoclines is merely an expression of the necessity for some trade-off mechanism. In other words, whatever the mechanism, it can always be described in terms of motivational isoclines.

Appendix 1

Axiom 1. We do not allow the possibility that two candidates exist such that each displaces the other, without any change in causal factors. The symbol $>$ will be used when transference of behavioural control occurs between two candidates. A displaces B is written $A > B$. The relation is said to be transitive if $A > B$ and $B > C$ implies that $A > C$.

Lemma 1. The relation $>$ is transitive when applied to candidates on different axes.

Proof. If this were not so than there would exist candidates A, B, C, $D\ldots$ such that $A > B > C > D > \ldots > A$. If these candidates were simultaneously present they would form the components of the candidate state and each would displace the other, which is impossible by axiom 1, proving the lemma.

Axiom 2. If A_1 and A_2 are candidates on the same axis, and B is a candidate on another axis such that $A_1 > B > A_2$, then there exists at least one candidate C on a third axis such that $A_1 > C > A_2$.

Lemma 2. There do not exist two candidates B_1 and B_2 on the same axis such that $A_1 > B_1 > A_2$ and $A_2 > B_2 > A_1$.

Proof. Suppose the contrary. Then by axiom 2 there exists a candidate C on a third axis such that $A_1 > C > A_2$. Without loss of generality suppose $C > B_1$. Thus $A_1 > C > B_1$.

If $B_2 > C$ then $C > B_2 > A_1 > C$, contradicting lemma 1.

If $B_2 > C$ then $A_2 > B_2 > C$ and $C > B_1 > A_2$, so $A_2 > C$ and $C > A_2$ (lemma 1) contradicting axiom 1.

Thus it is possible to apply the relation $>$ to candidates on the same axis. If $A_1 > B_1$ and $B_1 > A_2$ we can write $A_1 > A_2$.

Similarly it is possible to prove

Lemma 3. The relation $>$ is transitive when applied to candidates on the same axis.

Lemma 4. The relation $>$ is transitive on the set of all candidates.

Proof. If this were not so there would exist candidates $A, B, C\ldots$ such that $A > B > C \ldots > A$. Those parts of the sequence that involve candidates on different axes can be simplified by using lemma 1. Those parts that involve candidates on the same axis can be simplified by lemma 3. Whenever $K > L > M$ with K and M on the same axis it follows that $K > M$ as shown above. Hence the sequence must simplify to $A > L > A$ for some L, which contradicts our assumptions.

Appendix 2

For the sake of simplicity, suppose that candidate space is the positive cone of a Euclidean space E. Thus the axes represent the candidates for the different activities, labelled from 1 to n. In general, when A displaces B we shall write $A \succ B$, and $A \doteq B$ whenever they are equal (defined in the obvious way): these relations have not been shown to be equivalent to $>$ and $=$. Axiom 1 of appendix 1 implies that the relation between any two candidates does not depend on the strengths of the others.

Lemma 1. If

$$x_{i1} \doteq x_{j1}, \quad x_{i2} \doteq x_{j2} \quad \text{and} \quad x_{i1} < x_{i2}$$

then

$$x_{j1} < x_{j2} \quad \text{for all} \quad x_{i1}, x_{i2}, x_{j1}, x_{j2}.$$

Proof. Else $x_{j1} > x_{j2}$ implying simultaneously

$$x_{i2} \succ x_{i1} \doteq x_{j1} \Rightarrow x_{i2} \succ x_{j1},$$

$$x_{j1} \succ x_{j2} \doteq x_{i2} \Rightarrow x_{i2} \prec x_{j1},$$

contradicting axiom 1.

This shows that the relation $\doteq$ has a property analogous to that of a function which is increasing. To proceed we must assume that the relation is a function and not only increasing but monotonic increasing, and therefore one-to-one. (Such a function can always be constructed when the original candidate space is discrete.) Choosing x_1 arbitrarily as parameter, we can now define the switching line by $n-1$ equations.

$$
\begin{aligned}
x_2 &= f_2\,(x_1)\\
&\;\;\vdots\\
x_n &= f_n\,(x_1),
\end{aligned}
$$

where each f_i is one-to-one and $x_i = f_i\,(x_1)$ if and only if $x_i = x_1$.

THEOREM 1. The map $f^{-1}\colon E \rightarrow E$ defined by

$$
f^{-1}\begin{bmatrix} x_1 \\ x_2 \\ \cdot \\ \cdot \\ \cdot \\ x_n \end{bmatrix} \begin{bmatrix} x_1 \\ f_2^{-1}\,(x_2) \\ \cdot \\ \cdot \\ \cdot \\ f_n^{-1}\,(x_n) \end{bmatrix}
$$

maps the switching line to a straight line and makes the relations $>$ and $\mathrel{\scriptstyle >}$ equivalent.

Proof. The first part is trivial. To show the second part suppose that A and B such that $A > B$, and let the candidates of equal strength on the x_1 axis be x_{1a} and x_{1b}, i.e. $A = x_{1a}$ and $B = x_{1b}$ or equivalently $x_{1a} = f^{-1}(A)$ and $x_{1b} = f^{-1}(B)$. Then

$$
\begin{aligned}
A > B &\Leftrightarrow x_{1a} > x_{1b} \quad \text{by lemma 1,}\\
&\Leftrightarrow x_{1a} \mathrel{\scriptstyle >} x_{1b}
\end{aligned}
$$

by assumption, since they are candidates on the same axis

$$
\Leftrightarrow f^{-1}(A) > f^{-1}(B),
$$

APPENDIX 3

THEOREM 1. Corresponding to every state in causal factor space there is one and only one candidate state.

Proof. The candidate state is a point in candidate space with coordinates the candidates for each activity. We have not hitherto formally excluded the possibility that two candidates exist for the same activity, we do that now and refer only to the stronger of the two as the candidate for that activity. Thus the coordinates of the candidate state are uniquely determined by the state of the causal factors.

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