A THRESHOLD MODEL OF CHOICE BEHAVIOUR

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Choice behaviour can give rise to a number of different questions. If a chick pecks more at a red stimulus than at a green one, we might ask questions about the physiological basis of the preference, about its survival value or its ontogeny. Some psychologists have investigated choice behaviour as it relates to outcome—'pay-off' or reward (Luce & Suppes 1965), in human gambling situations, or equivalents for animals (Logan 1965).

In this paper we are concerned with a different kind of question, which arises because the less preferred of a pair of stimuli is sometimes chosen. Whatever may be the overall colour preference of a chick, or the overall strategy of a gambler in relation to reward probability, there must be some internal mechanism which determines the actual sequence of individual choices. The purpose of this paper is to present a model, called the choice threshold model, to explain how this *decision-making* function might be performed. The model may be judged by the validity of the predictions which can be deduced from it. Only one of these, called Prediction 1, will be considered here. Others will be discussed in companion papers.

Ethologists attempting to explain short-term switching between alternative behaviour patterns have often made use of a threshold type of model (Lorenz 1950; Bastock & Manning 1955; van Iersel & Bol 1958; Andrew 1961; von Holst & von St. Paul 1963; Tugendhat Gardner 1964), in which the different items of behaviour are thought to be activated by the same 'drive', 'excitation' or equivalent, but at different threshold levels. These models were proposed to account for decision-making between alternative *motor patterns*. The present model uses the same principle to explain decisions between alternative *external stimuli* to which a given response may be directed.

A threshold model was plausible to Bastock & Manning for *Drosophila* courtship partly because of the way in which three behaviour patterns were *superimposed* on each other. Thus orientation, the 'low threshold' activity, could occur by itself but vibration only occurred if

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orientation also did; and licking, with the 'highest threshold', only occurred superimposed on vibration and orientation. If we are to make a similar model for choice, with the different stimuli having different thresholds, it is clearly impossible to consider an exactly parallel superimposition; a chick cannot peck simultaneously at two different targets. One could however imagine a probabilistic equivalent; instead of pecking simultaneously at the two targets the chick could go into a state of being *equally likely* to peck either of them. This is the basis of the choice threshold model now to be described.

There are three assumptions (Fig. 1).

1. There is a variable 'V' inside the animal, fluctuating in time, corresponding to the 'excitation' of Bastock and Manning.

2. In order that a response shall occur towards a particular stimulus, it is a necessary condition that V should exceed a threshold corresponding to that stimulus. The most preferred stimuli have the lowest thresholds. When V is below the thresholds of all available stimuli no response can occur.

3. When the thresholds of more than one available stimulus are exceeded, each of these stimuli has an equal chance of being chosen. In this state of 'suprathreshold indecision' the total chance of a response occurring is the same as if only one threshold were exceeded.

For example, if a chick consistently gave 80 per cent of its pecks to a red spot, and 20 per cent to a green one, the model would say that of the time in which V was above either threshold, 60 per cent was spent above red's but below green's and all the pecks were at red; in the remaining 40 per cent of the time V was above both thresholds and the two spots each received half the pecks.

Prediction 1

Prediction 1 (Table I) is that if any three stimuli, A, B and C, preferred in that order, are presented in all three possible pair combinations, the proportion of the responses which goes to A when it is presented with C, called P_{AC} should equal $2 (P_{AB} + P_{BC} - P_{AB} P_{BC}) - 1$, where P_{AB} and P_{BC} are the other two 'percentage preferences' ('percentage preference' is used loosely here as synonymous with proportion of responses, i.e. number of choices of preferred stimulus divided by total number of choices).

For example, if a chick presented with a blue and a red spot gives 70 per cent of its choices to blue, and when presented with red and green it gives 80 per cent of its choices to red, the model predicts that if the third possible pair combination, blue with green, is given, 88 per cent of the choices will be for blue.

Psychologists may recognize this as a prediction of 'strong stochastic transitivity' (Marschak 1960), and the formula itself may be familiar to them from an entirely different context, that of 'cue additivity' (Hara & Warren 1961; Sutherland & Holgate 1966; McGonigle 1967). Cue additivity, which is related to the ethologists' 'heterogeneous summation' (Seitz 1940; Tinbergen 1951) is not directly relevant here, though a modified version of the choice threshold model does make predictions about it (Dawkins 1969). It is mentioned now only with reference to the origins of the formula here called prediction 1. The choice threshold model originally emerged from the suspicion that the formula might have applicability outside the context of cue additivity.

The formula may be written in another way: if $Q = 1-P$, it becomes $Q_{AC} = 2 Q_{AB} Q_{BC}$. Though this version is mathematically simpler, I prefer to use the original because it seems biologically more interesting to think in terms of percentage preference rather than 'percentage avoidance'.

Miss V. Cane (pers. comm.) has shown that the prediction 1 formula is the only polynomial of second order or less which satisfies the following biologically reasonable conditions:

1. If $P_{AB} = \frac{1}{2}$, then $P_{BC} = P_{AC}$, and symmetrically if $P_{BC} = \frac{1}{2}$, $P_{AB} = P_{AC}$.

2. If $P_{AB} = P_{BC} = 1$, than $P_{AC} = 1$.

Only one other formula (McLaughlin & Luce 1965) has to my knowledge been used in this kind of situation, though other qualitative predictions have been made and tested by psychologists (Coombs 1964), and economists

(Papandreou 1957). This other formula (not a polynomial), called the Product Rule, is

$$P_{AC} = P_{AB} P_{BC} / (P_{AB} P_{BC} + Q_{AB} Q_{BC}),$$

using the same symbols as above. Luce (1959) derives it from his Axiom, which for present purposes can be abridged as follows: the percentage preference for one particular stimulus over another is not affected by any other stimuli which may happen to be around.

The choice threshold model does not obey Luce's Axiom: it predicts that if a third stimulus is superior to both others, it should depress the percentage preference; if it is inferior it should raise it; if it is intermediate the effect is undetermined. I intend to test these predictions soon. It might be thought that the presence of unavoidable extra stimuli, such as small pieces of dirt on the walls of the test cage, might affect prediction 1. However it can be shown that prediction 1 still follows from the model, provided that the extra stimuli are inferior to all the test stimuli. This is likely to be the case in all the experiments discussed in this paper.

For comparison with the choice threshold model, it is convenient to derive the Product Rule from a model which may be called the Set Releasing Value model. This model, which obeys Luce's Axiom, simply assumes that each stimulus possesses a fixed stimulating value for the animal, and the number of responses it elicits is always proportional to this value. Thus if a, b, and c are the releasing values of stimuli A, B, and C respectively,

$$P_{AB} = \frac{a}{a+b}, P_{BC} = \frac{b}{b+c}, P_{AC} = \frac{a}{a+c}, Q_{AB} = \frac{b}{a+b},$$
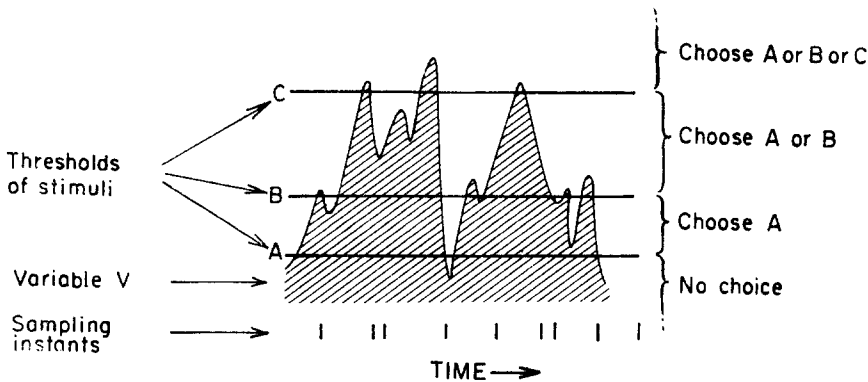

Fig. 1. The choice threshold model: three stimuli, A, B, and C, preferred in that order, are considered. Variable V, drawn arbitrarily, interacts with thresholds corresponding to the stimuli. At 'sampling instants' whose frequency is independent of V choices are made according to the rule that probability of being chosen is equally divided between all stimuli whose thresholds are at that instant exceeded by V.

Table I. The Deduction of Prediction 1

Stimuli presented	A with B	B with C	A with C
Threshold diagram	$\overset{z}{\text{------}}$ $\overset{y}{\text{------}}$ B $\overset{x}{\text{------}}$ A	$\overset{z}{\text{------}}$ C $\overset{y}{\text{------}}$ B ------	$\overset{z}{\text{------}}$ C $\overset{y}{\text{------}}$ ---- $\overset{x}{\text{------}}$ A
Pecks at	A: $x + \frac{1}{2}(y+z)$ B: $\frac{1}{2}(y+z)$	B: $y + \frac{1}{2}z$ C: $\frac{1}{2}z$	A: $x + y + \frac{1}{2}z$ C: $\frac{1}{2}z$
Percentage preference	$P_{AB} = \dfrac{2x+y+z}{2(x+y+z)}$	$P_{BC} = \dfrac{2y+z}{2(y+z)}$	$P_{AC} = \dfrac{2(x+y)+z}{2(x+y+z)}$

Prediction 1 Therefore, eliminating x, y and z, $P_{AC} = 2(P_{AB} + P_{BC} - P_{AB}P_{BC}) - 1$.

Three stimuli, A, B, and C are presented in all possible pair combinations. Time spent by variable V above A's threshold but below B's is x. Time spent by V above B's threshold but below C's is y. Time spent by V above C's threshold is z. When A is presented with B, A receives all the pecks during time x, since its threshold only is exceeded; during time y and time z both thresholds are exceeded and both stimuli receive half the pecks. Therefore number of pecks at A is proportional to $x+\frac{1}{2}(y+z)$, and number at B is proportional to $\frac{1}{2}(y+z)$. Therefore percentage preference $P_{AB} = \dfrac{2x+y+z}{2(x+y+z)}$. The other 2 percentage preferences are calculated in the same way. x, y and z are then eliminated, giving Prediction 1. This may be checked by substitution.

and $Q_{BC} = \dfrac{c}{b+c}$.

Eliminating a, b, and c therefore,
$P_{AC} = P_{AB}P_{BC} / (P_{AB}P_{BC} + Q_{AB}Q_{BC})$.

We shall use the Product Rule for comparison when we come to judge the success of prediction 1 in fitting observed data. It is unnecessary to test other known predictions separately, since the Product Rule fits the facts at least as well as them.

Audley (1960) does not explicitly derive a prediction for this situation from his model, but it can be shown, taking his k = 2, that it predicts a P_{AC} which is very close to, but slightly higher than that of the Product Rule. The same applies (Luce 1959) to Thurstone's (1927) Case V, assuming normal distributions of subjective values. E. Thomas (pers. comm.) has explored the interesting consequences of assuming other types of distribution in Thurstonian models. Flament's (1960) model obeys Luce's Axiom when only two stimuli are presented, and therefore predicts the Product Rule itself, as does Audley's model with k = 1.

The Product Rule predicts a P_{AC} which is nearly the same as, but consistently higher than prediction 1. It is therefore difficult, but possible, to decide which prediction is the better in practice. We shall attempt to arrive at a tentative decision about it. Quite apart from this we shall also be interested in whether the two predictions give an absolutely good fit to the data. Since they are so close in practice, if one of them is good the other one necessarily must be also.

I have done some experiments specifically to test prediction 1 on domestic chicks. In addition, several colleagues have kindly allowed me to use their unpublished data on a variety of species, and there are some published studies on human preference in which the data are presented fully enough for prediction 1 to be tested. One study on man has been carried out specifically (in part) to test the Product Rule (McLaughlin & Luce 1965).

Chick Pecking Preference Tests

Unfed white leghorn chicks, aged between 12 and 60 hr, were tested in groups of six together. Each group of six was placed for 5 min in one of three test chambers (Fig. 2) where their pecks
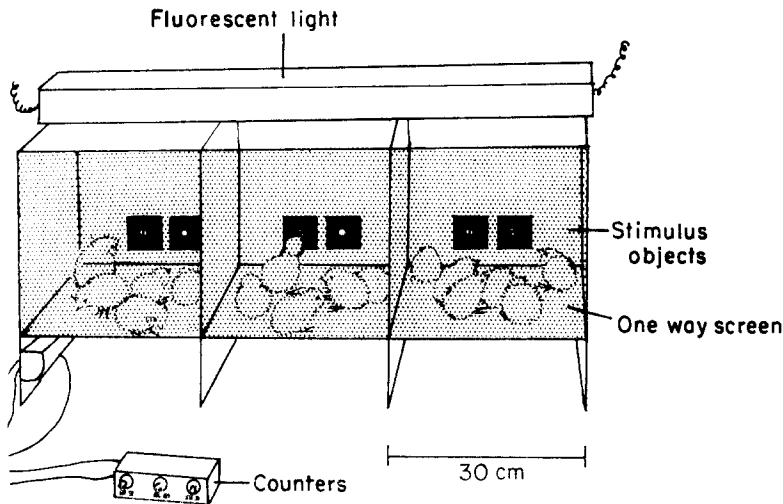
Fig. 2. Automatic peck-counting apparatus: each of the three chambers contained one pair of choice stimuli; at any one time each of the three possible pair combinations of the three stimuli was represented in one of the three chambers. Each stimulus was held in a hinged frame, behind which was a Bulgin Type M, S 530 microswitch with weakened springs, connected to a counter and a 48 V supply. Chicks were placed in darkness in the apparatus, and trials started when the light was switched on.

at each of two stimuli were automatically counted (Dawkins 1968). These chicks were then discarded.

Experiment 1 will be taken as an example for all eight experiments. The three stimuli presented in pairs were 6 mm diameter hemispheres, painted blue, red or green, mounted on a plain black background. Each of the three colour combinations, blue with red, red with green, and blue with green was presented twenty-four times, to a different group of six chicks in each case. There were thus seventy-two groups of chicks, making 432 chicks in all. Possible biasing effects of position or time of stimulus presentation were systematically eliminated by a predetermined schedule (Dawkins 1966).

The mean number of pecks per 5-min trial was 98·6, the median was 72, and the range was 0 to 570. Pecks were very non-independent, occurring in long runs at the same stimulus. This occurred to the non-preferred as well as the preferred stimulus. The apparent contradiction between this fact and the basic assumptions of the model is resolved if the unit of decision is not the single peck but the bout of pecks. More interestingly it can easily be explained, and indeed is positively expected, by the Attention Threshold Model, an extension of the present model (Dawkins 1969). The use of peck

data to test prediction 1 is still valid despite their non-independence, but possibilities for statistical treatment are limited. Blue was pecked more than red, which was pecked more than green (cf. Curtius 1954; Hess 1956). For each blue/red trial the percentage preference for blue over red was calculated as the number of pecks at blue divided by the total number of pecks at both. At the end of the experiment the mean of all these separate blue/red percentage preferences was the P_{AB} used to test the predictions. The standard deviation of the separate percentage preferences about the mean was 16·1: a large scatter such as this was typical. According to a predetermined rule, trials in which fewer than ten pecks were given, were rejected as inadequate to provide a meaningful percentage preference.

The mean percentage preference for red over green, and that for blue over green were calculated in the same way, and the three means used to test prediction 1 and the Product Rule. For purposes of statistical treatment, the individual percentage preferences from the three colour combinations were arbitrarily combined into triplets, i.e. each blue/red percentage preference was arbitrarily associated with one of the red/green ones, and one of the blue/green ones. This was so that prediction 1 could be calculated

independently many times, instead of only once as from the mean percentage preferences. In experiment 1, 19 separate tests of prediction 1 and the Product Rule could be obtained in this way. For each of these separate tests, the observed P_{AC} was subtracted from the predicted one; and then for each colour pair the standard deviation of these differences was calculated.

Learned Preferences in an Approach Response in Chicks

The methods of the three experiments in this category were somewhat different from each other, but the details are not important for the present purpose (Dawkins 1966, pp. 46–55). However because it may be of some interest to workers who need an efficient and trouble-free technique for training chicks, the method will be described for one of the experiments, experiment 10.

Fifty chicks were kept continuously for 5 days from the fifth day of life in an apparatus (Fig. 3) in which they could obtain food only by going into cubicles. Out of a total of twelve cubicles only six, three on each side of the apparatus, contained food at any one time; the others contained empty dishes. All the cubicles were illuminated with coloured light. On any one side of the apparatus at any one time, only two colours were to be seen, arranged in alternate cubicles, and only one of the two colours was associated with food. Thus during the whole period the chicks were rewarded for choosing, presumably on the basis of colour, which cubicles to enter. The positions of the colours (and the food) were changed several times during the training period, so that the chicks had plenty of experience on both sides of the apparatus with three colour combinations in different positional arrangements. These colour combinations were:

Blue with green, blue rewarded
Green with red, green rewarded
Blue with red, blue rewarded.

The purpose of the training was to build into the chicks the preference order blue–green–red, and in this it was very successful. One reason for this success may be that the coloured light, in addition to serving as the distance cue for the choice between cubicles, also completely bathed the food, which was the reward. It was also very fortunate that the chicks showed no tendency to position habits. Control tests suggested that colour not brightness was the important cue

After the 5-day training period, the chicks were given choice tests, having been deprived of food outside the apparatus. Each chick was released individually into one side of the apparatus from a start-box with two sliding doors, one of aluminium, the other of perspex.

In front of it were the six cubicles of that side of the apparatus, coloured alternately just as in the training phase, with, on any one trial, one
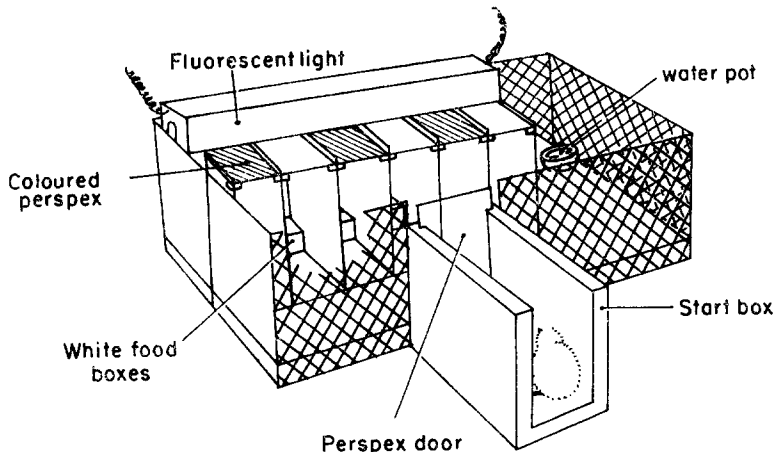

Fig. 3. Coloured light training apparatus. Living area of chicks contained twelve cubicles, six on each side of a central partitition (only one side visible in figure). Each cubicle was 9·5 cm wide by 20 cm long. Each cubicle had a coloured Perspex lid through which light shone, bathing the whole interior with coloured light. Food was consistently associated with colour. Except in cubicles there was a wire netting floor, so that spilt food could not be picked up outside. General illumination in room was low, so that coloured lights were more conspicuous. For choice tests as shown here individual chicks were used in only one side of the apparatus.

of the three possible pairs of colours presented. Each chick received six testing trials, two with each of the three colour pairs. Stimulus position and order of presentation were systematically varied so that no bias could enter in. Reward was available just as in the training phase.

After the aluminium door of the start-box was raised the chick had 5 sec in which to look at the coloured cubicles through the perspex door before that too was raised, and it was then allowed 2 min to make its choice. Most of them ran into one of the cubicles in a matter of seconds, and not one chick overran the time limit. A total of 300 choices was thus recorded, 100 for each colour pair combination. For each colour combination the proportion of choices of the 'correct' stimulus was the figure used to test prediction 1.

Experiment 11 was essentially similar, but differed mainly in that during the training phase only one pair of colours was seen, blue with red, blue being rewarded. In the testing phase the chicks were found to prefer red to green, and blue to green, as if due to spectral generalization. There was no reward in the testing phase.

Experiment 9 used a different apparatus, a normal Y-maze with feeding dishes of different colours as discriminanda. One chick was trained in the maze to prefer red to yellow, and yellow to green. It was then given ninety test trials, thirty with each of the three combinations, red with yellow, yellow with green, and red with green, the choice of the first named colour being rewarded in each case. Position and order effects were eliminated in the usual way. The proportions of choices of the 'correct' colour out of each pair combination were used to test prediction 1. Only one chick was tested in this way, before the method was superseded by the much more efficient coloured-light technique already described.

Other Sources of Data

A number of workers have studied preferences by presenting stimuli in all possible pair combinations. This 'method of paired comparisons' (Guilford 1954) is efficient and sensitive and it has the additional merit that it incidentally enables us to test prediction 1. For example Impekoven (Dawkins & Impekoven 1969, in press) presented black-headed gull chicks (*Larus ridibundus*) with stimuli of six different colours in pairs, and counted the pecks given to each colour when presented with each other colour. By taking the means of all the individual percentage preferences as described above for the

domestic chick, fifteen mean percentage preferences could be obtained, one from each of the possible pair combinations of the six colours. These fifteen were combined in the twenty possible triplet combinations, and prediction 1 calculated separately for each triplet. Thus for the triplet blue/yellow/green, P_{AB} is the mean percentage preference for blue over yellow; P_{BC} is that for yellow over green, and P_{AC} that for blue over green. Each percentage preference occurs in four different triplets, so the twenty separate tests of prediction 1 cannot be regarded as independent for statistical treatment. In this case it would be possible to publish all twenty tests of prediction 1. However for some of the human data treated in the same way the separate tests of prediction 1 approach 1000 in number and full presentation is not practicable. Though the individual results are heterogeneous, if there were any consistent deviation of predicted from observed P_{AC} this should show from their means, and these are the figures which will be given here.

Discussion of Results

Both predictions are quite well fulfilled (Tables II and III, and Fig. 4), especially with respect to the two species for which most information is available, the domestic chick and man. In these two species prediction 1 seems preferable, as the Product Rule rather consistently errs on one side (Fig. 4), but this is not the case for the other 'miscellaneous' species taken as a group.

It would be desirable to estimate whether the scatter of observed results about the predicted lines is acceptably low. The standard deviations of the predicted–observed differences given in the tables could in theory be compared with expected values computed from the variances of the original percentage preferences, but this depends heavily on assumptions of independence of data which are grossly violated in the present cases. However we can use a non-parametric test to compare, for each experiment, the standard deviation of the predicted–observed differences between the two predictions. The Product Rule is found to have a significantly larger scatter than prediction 1, if all independent experiments with all species are considered ($P<0\cdot001$), and this is also individually true of the domestic chick pecking data ($P<0\cdot01$) and the human data ($P<0\cdot001$, all Wilcoxon matched pairs tests, 2-tailed). This is what would be expected if

Table II. Domestic Chick Results

Experiment	Stimuli		P_{AB}	P_{BC}	P_{AC}	Pred. 1	S.D. (Pred. 1 — P_{AC})	Prod. Rule	S.D. (Prod. R. — P_{AC})	N. triplets
1	A	Light blue	54·6	73·8	77·5	76·2	25·3	77·2	25·9	19
	B	Orange								
	C	Light green								
2	A	Orange/yellow	75·9	65·0	83·5	83·1	19·8	85·4	21·7	15
	B	Light blue								
	C	Light green								
3	A	Orange/yellow	61·1	80·1	84·7	84·5	18·0	86·3	18·7	15
	B	Orange								
	C	Light green								
4	A	Light blue	71·2	87·8	91·5	93·0	9·8	93·0	14·5	24
	B	Orange								
	C	Orange disc 6 mm								
5	A	As 4	75·4	80·4	88·6	90·3	17·7	92·6	18·0	22
	B	,,								
	C	,,								
6	A	As 4	78·1	83·8	90·7	92·9	10·6	94·8	14·7	30
	B	,,								
	C	,,								
7	A	Light grey 5 mm hemisphere	70·9	69·9	84·0	82·5	24·5	85·0	27·8	27
	B	Photo 'Solid'								
	C	Photo 'Flat' (Dawkins 1968)								
8	A	Light blue	81·6	67·9	68·6	88·2	29·8	90·4	29·9	11
	B	Pottery blue (v. light)								
	C	Prussian blue (v. dark)								
9	A	Red dish	86·7	80·0	96·7	94·4		96·3		1
	B	Yellow dish								
	C	Green dish								
10	A	Blue light	81·0	75·0	88·0	90·6		92·7		1
	B	Green light								
	C	Red light								
11	A	As 10	84·2	61·2	89·3	87·0		89·4		1
	B	,,								
	C	,,								

Pecking experiments (1 to 8): percentage preferences are means from many trials, each involving 6 experimentally naive chicks. Prediction 1 and Product Rule calculated directly from these means. Standard Deviation of predicted minus observed P_{AC} obtained from multiple testing of predictions in N arbitrarily constructed triplets of original percentage preferences. Stimuli were all 6 mm diameter hemispheres unless otherwise stated, and colour names refer to Priosin Co. paints (except experiment 7—see Dawkins 1968).

Approach experiments (9 to 11): percentage preferences directly calculated from numbers of discrete choices as explained in text.

prediction 1 were more accurate than the Product Rule.

Furthermore, as indicated already, the predicted P_{AC} of the Product Rule tends to be higher than the observed one. This is just significant if the mean observed and predicted results from the domestic chick experiments are compared ($P<0·05$), and is significant if all the

Table III. Results from Other Workers

Author	Subjects	Choice	Mean P_{AC}	Mean Pred. 1	S.D. (Pred. 1 $- P_{AC}$)	Mean Prod. Rule	S.D. (Prod.R. $- P_{AC}$)	N. triplets
Impekoven	Gull chicks (*Larus ridibundus*)	Colour pecking	89·8	89·4	2·7	90·6	2·7	20
,,	,,	Colour approach	87·0	84·4	12·5	85·3	12·5	20
,,	,,	,,	90·0	87·9	11·7	89·2	11·9	20
,,	,,	,,	88·9	87·7	9·7	88·9	9·4	20
Kear	Ducklings (*Anas platyrhynchos*)	Colour pecking	85·1	80·9	7·0	81·6	7·2	20
,,	Young moorhen (*Gallinula chloropus*)	,,	94·2	94·2	5·0	95·6	5·2	20
,,	Young coot (*Fulica atra*)	,,	81·0	79·9	14·7	80·7	14·8	20
,,	Gull chicks (*Larus argentatus*)	,,	87·4	86·1	8·3	87·5	8·6	20
,,	,, (*Larus fuscus*)	,,	89·4	83·3	9·9	84·2	9·6	20
,,	Goslings (*Anser canagicus*)	,,	86·6	90·3	10·2	91·9	10·0	20
,,	Ducklings (*Aix sponsa*)	,,	80·4	79·8	10·7	79·8	10·8	20
Muntz	Frog (*Rana temporaria*)	Colour jumping	78·0	75·5	12·8	75·5	13·4	35
Rees	Beetle (*Phyllobius urticae*)	Airstream humidity	78·3	77·9	7·7	79·0	7·6	35
Folgmann	Boston Symphony Orchestra	Composers	85·5	85·5	5·8	86·7	6·0	969
,,	N.Y. Philharmonic Orchestra	,,	87·1	87·2	6·1	88·4	6·3	969
,,	Minneapolis Symphony Orchestra	,,	86·1	85·1	6·2	86·2	6·5	969
,,	Philadelphia Orchestra	,,	90·2	90·3	4·1	91·3	4·2	969
Hevner	American students	Handwriting	95·0	95·8	4·8	95·3	4·1	1140
Guilford	American students	Vegetables	80·2	80·3	5·8	81·8	6·0	84
Shen	Chinese students	Colour	72·0	74·1	3·9	75·5	4·0	35
Dorcus	Various human (means from 24 small experiments)	Colour	65·7	63·7	15·6	63·5	16·6	24 × 20
McLaughlin & Luce	American student (all triplets truly independent)	Taste bitter/sweet	73·9	76·4	7·1	77·7	7·7	9
,,	,,	,,	64·3	61·8	5·9	62·3	6·1	9
,,	,,	,,	61·0	62·5	5·4	63·0	5·8	9

Observed and predicted P_{AC} values are means from N non-independent (except McLaughlin & Luce) tests of the predictions. Standard deviations of predicted minus observed values are therefore not valid absolutely, but valid for non-parametric comparison between the two predictions. Dorcus did 24 small experiments whose individual results are not separated here, though they are separated for statistical treatment in text.
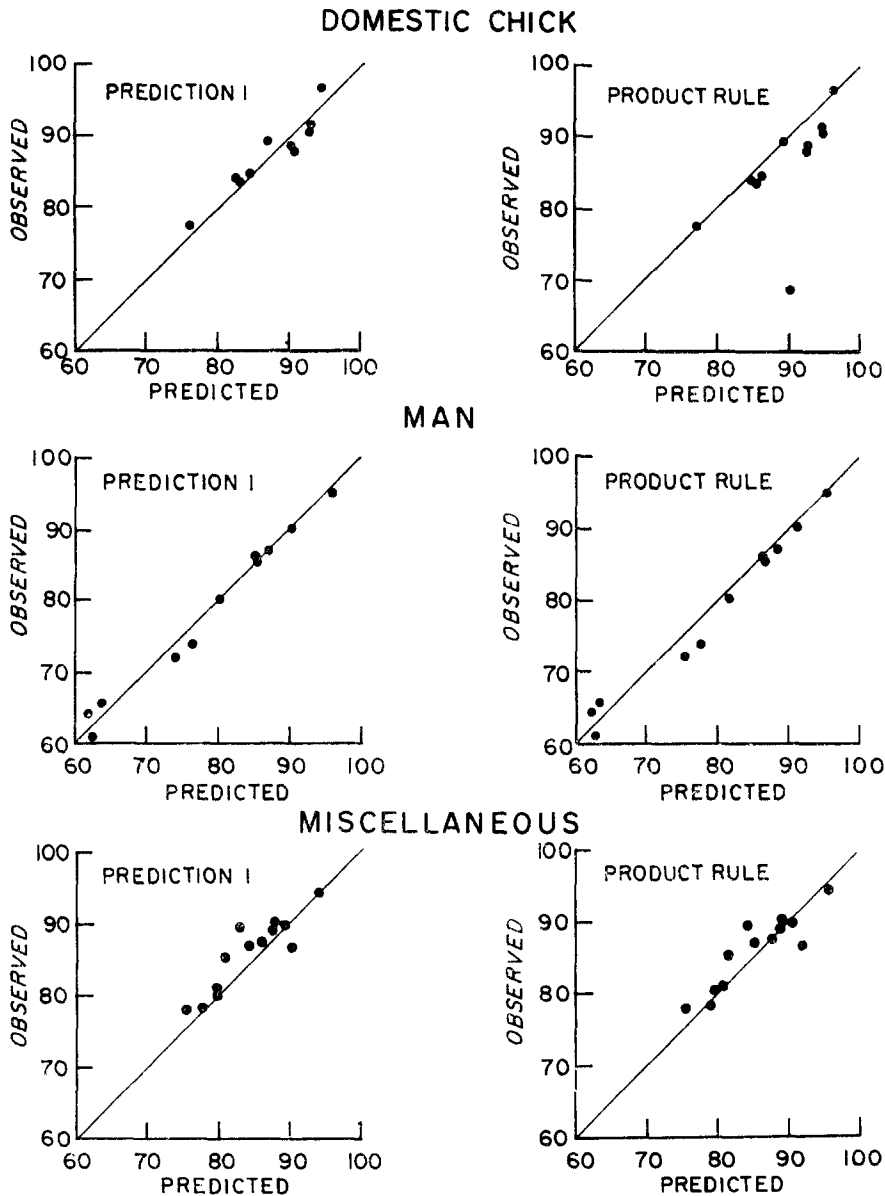
Fig. 4. Scatter diagrams of mean observed against predicted values of P_{AC} for prediction 1 and the Product Rule, divided for convenience into three groups according to species. Ideally, according to the predictions, the points should lie along the 45° line on the respective graphs.

independent tests of the prediction from all the data are considered ($P<0.006$, N = 236); prediction 1 results, on the other hand do not differ significantly from observed ($P<0.05$; N = 234, all Wilcoxon matched pairs tests, 2-tailed). This failure to disprove prediction 1 is encouraging, especially since N is large, and also since the Product Rule, which is inevitably very close to it in practice, is apparently disproved.

One prediction cannot validate a model. This is partly because a prediction cannot be proved correct—we can only fail to disprove it—and

partly because the same prediction may be derivable from other models. However the success of a precise prediction such as prediction 1 is at least a powerful encouragement to testing further predictions of the model. Some others have already been tested (Dawkins 1969; Dawkins & Impekoven 1969) but many remain (see example p. 122). To state but one more, a quantitatively precise one which seems therefore temptingly easy to disprove, the percentage preference for A when presented with both B and C together should be given by

$$P_{AB} + \tfrac{1}{3} P_{AC} + \tfrac{1}{3}.$$

A good model is one whose predictions are vulnerable to disproof.

General Discussion

What other models are equivalent or analogous to the threshold model as discussed above, and are any of them physiologically plausible?

The essential features of the model can be expressed in terms of states, without any mention of 'thresholds', or 'variable V'. Thus if there are a number of stimuli, A, B, C, D, preferred in alphabetical order, the states which the animal can be in are:

1. Choosing nothing
2. Choosing A only
3. Choosing A or B with equal probability,
4. Choosing A or B or C with equal probability
5. Choosing A or B or C or D with equal probability.

It is assumed that, with the exception of state 1, the overall response rate is the same for all states. Examples of states which are not possible according to the model are choosing B without being equally likely to choose A, or choosing D without being equally likely to choose A or B or C.

The conditions specified for the state model can be realized in a number of different hypothetical ways, of which the threshold model as described in the introduction to the article is only one (and a restricted one, in that only certain transitions between states can occur). Another may be called the 'inverted threshold model' (Fig. 5).

It is hoped that other, more neurological analogues of the basic state model may be devised by other people. It may be helpful to summarize the main functions which would have to be performed by such models, or in association with them.

1. There must be some means of stimulus evaluation (to determine whether stimuli should have high or low thresholds). It is of course perfectly legitimate to ignore the details of this function as has been done in this paper. It is a
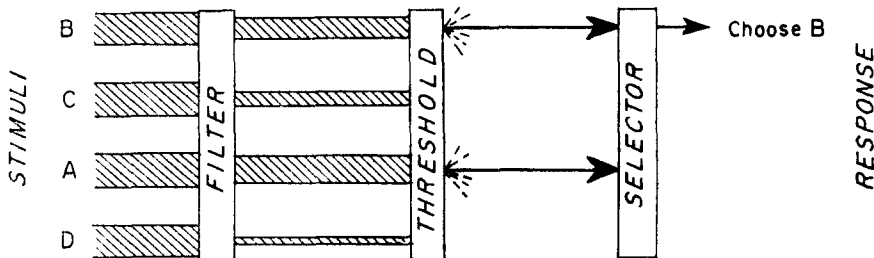

Fig. 5. Inverted threshold model: four stimuli, A, B, C and D are considered. They are evaluated by a *filter*. Thickness of the hatched area leaving the *filter* denotes the preference *value* of the corresponding stimulus. Thus here preference order is alphabetical. The preference *value* has to exceed a fluctuating *threshold* level in order for the corresponding stimulus to be eligible to be chosen. Any preference *value* which penetrates the *threshold barrier* gives rise to a standard all-or-none output from the *threshold barrier*. If at a particular *sampling instant* only one *value* penetrates the *threshold barrier*, that stimulus will be chosen by the *selector*. If more than one penetrate at a given *sampling instant* both will give rise to an identical all-or-none output from the *threshold barrier*, but random noise will ensure that one of these is slightly larger than the other when they reach the *selector*, and the corresponding stimulus will be chosen. It is assumed that the effect of noise before the *threshold barrier* is negligible compared with the variation in preference *value*.

At the sampling instant shown here, the two best stimuli, A and B, penetrate the *threshold barrier*, and of these B, the second best, is actually chosen.

subject much discussed in the ethological literature ('Releasing Mechanisms', Schleidt, 1962; 'Stimulus Filtering', Marler 1961; 'Selective Responsiveness', Quine & Cullen 1964).

2. There must be some source of variation (V) in the system, so that the animal can change from one state to another. This might be thermal noise in the nervous system (Pringle 1951).

By analogy with earlier threshold models V might be associated with motivational variables such as hunger and thirst. I have verified with pecking in chicks, the prediction from this that percentage preference in choice tests should be

controlled by the same nerve supply. At low firing rates only Sach's organ responds. At higher firing rates both organs respond (Bennett, pers. comm.; Bennett, Giménez, Nakajima & Pappas 1964).

4. The model involves states of equal probability of choice of stimuli, i.e. states of 'suprathreshold indecision'. The original version of the model included no specific suggestion of how this might come about. The 'inverted' version (Fig. 5) involved an indecision mechanism which could be adapted to the original model. Another possibility would be response alternation or some

Table IV. Effects of Hunger and Thirst on Percentage Preference for Blue over Green

	Both hungry			Both thirsty		
	Thirsty	Not thirsty	P Mann-Whitney	Hungry	Not hungry	P Mann-Whitney
No. of groups of 6 chicks	35	35		30	30	
Mean no. of pecks per trial	41·7	4·7	<0·00006	72·3	109·0	<0·05
Mean percentage preference blue over green	82·4	87·0	<0·01	61·8	74·3	<0·01

The automatic peck-counting apparatus was used as described earlier. Deprivation in all cases was for 2 to 3 days. The non-deprived groups had continuous ad lib access to food or water as the case might be. The chicks were 3 days old at the time of testing. Both hunger and thirst had the predicted effects on percentage preference, decreasing them, but the paradoxical effect of hunger on overall peck rate makes the results difficult to interpret.

lowered by deprivation of food or water (Table IV). Alternatively V might be associated with fluctuations in the reticular activating system (Livingston 1960).

3. The model is one of discrete states with no intermediates, and involves some kind of all-or-none function (interaction between V and thresholds). Of these discrete states, not all of the possible ones are allowed by the model (p. 129). Some kind of hierarchy of states is indicated.

Systems with somewhat analogous properties are known to neurophysiologists. Thus the dorso-ventral flight muscles of field crickets (Gryllus sp.) have one to three separate units, each unit consisting of a motor axon and the muscle fibres which it innervates. In a muscle with two units, there is a threshold difference between them such that although the low threshold unit can fire by itself, the high threshold one never fires without the low threshold one firing as well (Bentley, pers. comm.; Bentley & Kutsch 1966).

In the electric eel Electrophorus the two electric organs, Sach's organ and the main organ, are

more complex consequence of stimulus satiation (Glanzer 1953).

An interesting possible indecision mechanism is inspired by the concept of selective attention to particular stimulus dimensions or cues (Sutherland 1964; Mackintosh 1965). Briefly the suggestion is that, in states of suprathreshold indecision when animals are choosing 'indiscriminately', they are really attending to an irrelevant cue, and showing a definite preference for one stimulus or the other. For example in a colour choice test, it is suggested that when in the state of suprathreshold indecision the animal switches its attention to another cue, perhaps stimulus position, and consistently chooses say the left-hand stimulus. The experimenter will of course be randomizing the positions of his two coloured stimuli in successive trials, with the result that during these periods of position preference the overall choice of each colour will be 50 per cent. This idea gave rise to a more elaborate and powerful version of the model, which will be discussed in a companion paper (Dawkins 1969), under the name 'attention threshold model'.

5. There must be some means of deciding the moment at which each choice is made. Evidence that this function is performed by an independent 'go/no-go decision-making mechanism' for pecking in the black-headed gull chick will be presented elsewhere (Dawkins & Impekoven 1969).

6. Finally, the decisions as to which stimulus to choose and when, must be executed by motor machinery, and a response steered towards the chosen target. This is an orientation problem with which we are not here directly concerned, but it is mentioned in order to emphasize its distinctness from the other problems of stimulus evaluation and decision-making.

The basic properties of a model such as the choice threshold model can be realized in a number of different ways, some of which may have the merit of aesthetic appeal and the power to stimulate further ideas; others may be closer to physiological feasibility. When we draw conclusions from any success the predictions of a model may have had it is important to attribute the success only to the basic essentials of the model necessary to the deduction of the predictions, and not to the superficial pictorial qualities in terms of which we happen to have expressed it and thought about it.

The possible usefulness of a model such as this one can be illustrated by analogy with comparative studies between different animals. If chicks, beetles and the Boston Symphony Orchestra behave in the same way with respect to prediction 1, we might cautiously suggest the existence of similarities in their decision-making mechanisms. We might well be wrong. In the same way we could suggest, and again we might be wrong, that the similarity between the behaviour of chicks and that of the artificial machine called the choice threshold model is also due to a similarity of internal mechanism.

A comparative approach may be useful to the physiologist if, for example, it happens to be easier to work with certain species than with others. Much medical research is conducted in the hope that information obtained from other animals may be generalized to man. Comparative studies between models and animals have a special usefulness insofar as, having made them ourselves, we know exactly how the models work. It is not very helpful to conclude that chicks and beetles have similar decision-making mechanisms if we do not know how either of these mechanisms works. But it could be helpful to conclude that chicks have a similar decision-making mechanism to the machine called the choice threshold model, because the workings of the latter are precisely known.

There remains the difficult question of what is meant by 'similar'. In comparing bird and insect, if we concluded that they had a similar decision-making mechanism we should not be thinking of identical neural structures. We should hope however that detailed knowledge of the underlying mechanisms in one animal might provide enough fruitful ideas to shorten the labour of an investigation into the corresponding nervous mechanisms of the other. It is my hope that the choice threshold model, through a cautious comparative approach, might eventually in a modest way make this kind of contribution to physiology.

Summary

1. Among the problems raised by choice behaviour is that of the mechanism of decision-making. Given that a chick pecks more often at a red spot than at a green one, but nevertheless sometimes pecks at the green one, what mechanism determines each individual choice? This paper presents a model called the choice threshold model to help answer this type of question.

2. The model is initially expressed in terms, familiar from the ethological literature, of a fluctuating variable (cf. 'drive'), interacting with thresholds. Whether expressed in this pictorial way or not, the important assumption of the model is that for any two stimuli presented together, an animal either chooses the preferred one or chooses completely indiscriminately; the less preferred stimulus can only be chosen during periods of non-discrimination.

3. A precise quantitative prediction (of what psychologists call 'strong stochastic transitivity') is deduced from the model and named prediction 1. If any three stimuli are presented in all three possible pair combinations, and if the percentage preference for the best over the worst is called P_{AC}, the other two percentage preferences being P_{AB} and P_{BC}, prediction 1 is that P_{AC} should equal

$$2 (P_{AB} + P_{BC} - P_{AB} P_{BC}) - 1.$$

4. Experiments on domestic chicks, and data from other workers on a variety of species including man tend to confirm prediction 1. Other predictions will be discussed elsewhere.

5. Some general properties of the model, and alternative ways in which they might be realized are discussed.

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