SELECTIVE PECKING IN THE DOMESTIC CHICK

C. R. Dawkins

Balliol College Oxford

Thesis
submitted for the degree of
Doctor of Philosophy

June 1966

C O N T E N T S

	Page
Abstract	1
Acknowledgements	7
Chapter:	
1. A model for choice	8
Introduction	8
The control of pecking in chicks (Postulation of four functional units controlling pecking.)	11
The Threshold Model: Introduction	16
Basic assumptions	18
Symbols used	20
Deduction of Prediction 1	23
A simpler equivalent to Prediction 1	27
Alternative ("Set Releasing Value") Model Prediction 1A	28
Previous work	30
2. Methods and Prediction 1 results	32
Introduction	32
Recapitulation: Predictions 1 and 1A	33
Rejection of non-significant preferences	34
Domestic chick pecking preference tests (Apparatus; methods; results Experiments 1 to 8.)	36
Experiments with domestic chicks, using learned preferences in an approach response (Y-maze; coloured light training apparatus; results Experiments 9 to 11.)	46
Dr. M. Impekoven's experiments on pecking and approach colour preferences in the black-headed gull chick (*Larus ridibundus*)	56
Dr. J. Kear's experiments on pecking preferences in young birds	60
Dr. W. R. A. Muntz's experiments on frog colour preferences	62
Dr. C. J. C. Rees's experiments on humidity preferences in the beetle Phyllobius	63
Discussion of tests of Prediction 1	65
Conclusion	70
3. The "Go/No go" decision-making mechanism.	
Deduction of Predictions 2 to 6	73
Introduction	73

The Set Releasing Value Model and the Go/No go decision-maker 79
Predictions 2 to 6 and 2A to 6A 79
Conclusion 84

4. The Go/No go decision-maker in the domestic chick 85
Tests of Prediction 2 to 6 85
Discussion 94
(Including deduction and test of "composite prediction", equivalent to Prediction 1)

5. The Go/No go decision-maker in the black-headed gull chick (All data from Dr. M. Impekoven) 98
Predictions 2 to 5 100
Discussion 105
(Hypothesis about the determination of K)
Prediction 6 106
Discussion 110
("Composite prediction")
Calculation of threshold values and K values 113

6. Factors affecting the function units postulated; Relationships between them; Related models 122
Introduction 122
The Go/No go decision-maker 123
The Stimulus Evaluator 127
The Left/Right decision-maker 128
(Different forms of Threshold Model; more general form; inverted form; source of variation in model; mechanism of "50/50 behaviour"; Attention Threshold Model.)
The Executive Mechanism or "Pecker" 136
Influences on the functional units proposed 137
(Interactions between functional units; learning; motivational state; experiments on hunger and thirst.)

7. Interactions between stimulus dimensions 146
Introduction 146
(Type of experimental situation involved; definitions.)
Attention Threshold Models 149
(Assumptions; first stage in deducing predictions.)
Predictions of the Attention Threshold Model 158
(Effect of changes in irrelevant cues; cue additivity; cue opposition; decision-latencies; function; interpretation of preferences.)

Conclusion 176

8. Conclusion 177

Predictions 178
(Evaluation of model according to information content of predictions; success of predictions.)
Other aspects not directly concerned with predictions 183
(Aesthetic appeal; representation of reality.)

Appendix 1 Testing Prediction 1 with data on human preference 186

Introduction 186
Brief remarks about studies used 187
Results 189
Discussion 190

Appendix 2 The ontogeny of a pecking preference in domestic chicks 192

Introduction 192
The ontogeny of the solidity preference 194
(Changes in preference; cause of change; stimulus-specific waning; flatness generalisation; dark-reared chicks.)
The ontogeny of the use of surface-shading cues of solidity 208
(Experiments with photographs of solid and flat objects; chicks reared in darkness and with underfloor lighting.)
General discussion 219
(Functional approach to ontogeny.)

References 226

ABSTRACT

When a chick pecks at one of a number of alternative stimuli, two questions about mechanisms of decision-making arise. One of these concerns the timing of the peck - this will be discussed later - and the other is about its orientation. In an attempt to answer the second of these questions, a model is proposed, called the Threshold Model. This model then is a possible analogue of the mechanism in a chick which determines at which of the available stimuli each individual peck is directed.

The Threshold Model embodies the following assumptions. There is a fluctuating variable of unknown nature called Variable X, which interacts with thresholds corresponding to the external stimuli. A stimulus cannot be pecked unless Variable X exceeds its threshold. Some stimuli have lower thresholds than others and are therefore more likely to be pecked - they are "preferred". If the thresholds of more than one available stimulus are exceeded at any one time, they are equally likely to be pecked.

From these assumptions it is possible to deduce a prediction about the precise relationship between the three percentage preferences obtained when any three stimuli are presented to animals in all possible pair combinations.

This prediction, called Prediction 1, was tested on domestic chicks, by counting the numbers of pecks given to small hemispherical spots presented in pairs, and differing in colour or some other quality.

In general it was well confirmed. The model need not be confined to the pecking response, nor indeed to the domestic chick. Prediction 1 also gave a good fit to the findings in experiments again on demestic chicks involving learned preferences in approach situations. Also, M. Impekoven, J. Kear, W. Muntz, and C. Rees allowed me to test and fairly well confirm Prediction 1 using their data from choice experiments on a number of different species.

To assist in evaluating the success of Prediction 1, an alternative prediction for the same situation, called Prediction 1A, was deduced from a simpler model, called the Set Releasing Value Model, the basic assumption of which is that the number of responses each stimulus receives should be proportional to a constant, specific to that stimulus, regardless of what it is paired with. Prediction 1A, or something closely similar to it, can also be deduced from other, published models. Prediction 1A always gives a fairly similar result to Prediction 1, but nevertheless it seems possible to say that Prediction 1 gives the closer fit to the facts, at least in the domestic chick and the black-headed gull chick (Impekoven), which are the two species for which most information is available.

The Threshold Model, in addition to determining the orientation of pecks or other responses, might also be responsible in for determing when they occur. On the other hand the latter role might be filled by a separate "Go/No go" decision-making mechanism. On the former assumption, or on the latter assumption with the proviso

that Go/No go decisions are not influenced by the stimulus situation, it is possible to deduce a number of further predictions from the Threshold Model, and equivalent ones from the Set Releasing Value Model. Some of these additional predictions were tested using pecking data from domestic and black-headed gull chicks.

In the case of the domestic chick, all the predictions were disproved, suggesting that the condition or assumption on which they were based was false: a separate Go/no go decision-maker must indeed be postulated, and its activity, represented by the symbol K, must be influenced by the stimulus situation. If K varies, the Threshold Model is able to account for the results, but the Set Releasing Value Model is not.

Numbers of pecks given by black-headed gull chicks (Impekoven) at 6 different coloured stimuli presented in all possible pair combinations, also disproved most of the additional predictions, with one important exception which was very well fulfilled. The nature of this one successful prediction compellingly suggested the hypothesis that K, the activity of the Go/No go decision-maker, is influenced only by the more preferred member of each pair of stimuli. Other predictions, modified by this empirically derived simple hypothesis, were successful in fitting the facts.

From the basic assumptions of the Threshold Model together with this empirical hypothesis, the black-headed gull data were used to derive actual values, in arbitrary units, for the time spent by

Variable X between the thresholds of the 6 colours; and the value of K associated with each of the colours was calculated. The two measures were found to be related negatively to each other, the relationship apparently being exponential.

These findings suggest that external stimuli play a dual role in controlling pecking. One of their effects is a discriminatory one, influencing percentage preferences. This effect is mediated by the biological analogue of the Threshold Model, the stimuli exerting their effects by determining threshold levels. The other effect is an indiscriminate one, affecting only the probability of a peck occurring, not its orientation. This influence works through the Go/No go decision-maker. In the black-headed gull the quantitative strengths of the two effects are inversely related. In the domestic chick the relationship is more complex, and has not yet been determined.

The model as described above is not the most general form capable of yielding the predictions tested, but it has the advantage over the more general form of being easier to represent physically or graphically. Other forms of the model include one called the Attention Threshold Model which embodies a suggested mechanism for the equal distribution of responses which is supposed to occur when more than one threshold is exceeded. This development of the model is more powerful than the original version in that it yields more predictions; it will be mentioned again below.

Deprivation of food and water reduces percentage preferences,

which suggests that it exerts a positive influence on the general level of Variable X. Training experiments performed jointly with Dr. M. Impekoven showed that changes in "hunger" and "thirst" can cause reversals of learned colour preference/domestic chicks, suggesting a direct influence of these variables on threshold levels.

The Attention Threshold Model mentioned above makes predictions about the effects of combining or opposing different stimulus dimensions or cues, which seem well fulfilled by results from mammals, for example the published results of Hara and Warren (1961). It also makes a prediction about an effect on preference of varying irrelevant cues, which is fulfilled by experiments on domestic chicks.

The Threshold Model is able to give a reasonable account of the experimental results considered here. It also makes further predictions not yet tested, for example predictions about percentage preferences which should be obtained when three, four, or more stimuli are presented together. I hope to test these soon. It would be most satisfactory if the model discussed here, and tested behaviourally, were to stimulate physiological research at a lower level of analysis.

In the first Appendix, Prediction 1 is tested on published data on human preferences. In most cases it gives a good fit, but there is a suggestion of consistent slight over-prediction.

The second Appendix is about the development of chicks' preferences for solid objects rather than flat. This preference, called the "Solidity preference", is shown by chicks reared in total

darkness. In unfed chicks reared in normal light, it increases in strength, probably because of selective waning in responsiveness to flat objects as a result of continued non-rewarded pecking at flat marks round the living cages.

Stereoscopy is not important for the solidity preference. Experiments with photographs of solid objects correctly oriented and inverted showed that surface-shading cues of solidity are important. A strong preference for the surface-shading properties of solid objects in overhead light, develops in animals with no experience of overhead light. This provides a good illustration for Lorenz's (1961) functional approach to the definition of the word "innate". However, the use of this word is not recommended here. The development of the Solidity preference can be used to illustrate a number of other general points about the ontogeny of behaviour.

Acknowledgements

I am very grateful to Dr. N. Tinbergen, F.R.S. for his enthusiastic encouragement and helpful advice. Space and facilities in the Department of Zoology, Oxford, were kindly made available by Professor J. W. S. Pringle, F.R.S. Financial support was received from the S.R.C. (formerly D.S.I.R.), and the Nature Conservancy.

For help of many kinds, I am extremely grateful to Dr. J. M. Cullen, Dr. J. D. Delius, and Dr. M. Impekoven. Dr. Impekoven and Drs. J. Kear, W. Muntz and C. Rees generously allowed me to use their unpublished data.

The original inspiration for beginning on the work described in the main part of the thesis, came from a lecture by Professor N. S. Sutherland, and subsequent discussions with Dr. J. M. Cullen and Dr. N. J. Mackintosh.

Mr. Jan Adam played the major part in the design and construction of the peck-counting apparatus. Messrs. Jennings of Garsington provided a practically unlimited supply of chicks. For help and instruction in computer programming, I am indebted to Dr. and Mrs. H. C. Dawkins.

I am also grateful to many other people who cannot all be mentioned individually.

CHAPTER 1 : A MODEL FOR CHOICE

INTRODUCTION

The behaviour of an animal, in the wild or in the laboratory, can be regarded as a succession of choices. There is choice between different alternative motor patterns, and choice between alternative external stimuli towards which a response might be directed, between models of different shapes colours or sizes, between alleys in a maze, between keys in a Skinner Box, between potential mates, nesting materials, habitats etc.

A number of different kinds of question can be asked about the causation of choice behaviour, some of which will be discussed in the next section with reference to the main subject of this study, selective pecking in the domestic chick. Here it is sufficient to say that, at least as far as choice between external stimuli is concerned, the questions most commonly asked are those about overall or average aspects such as tendency to respond to one colour more than to another. This study on the other hand is not concerned so much with the factors determining how the majority of an animal's responses will be directed, but rather with the determination of each individual response (Diamond, Balvin and Diamond 1963).

Therefore although the subject of this work is preferential responsiveness to external stimuli, it might be said to have more affinities with some studies of choice between alternative motor patterns, investigations into the mechanisms controlling short term switches in behaviour. Indeed the model to be proposed, called the Threshold Model, has similarities with models previously put forward in this

field (e.g. Bastock and Manning 1955).

The Threshold Model is, however, also relevant to another subject more traditionally associated with choice between external stimuli, that of the interactions between different stimulus dimensions in the determination of the effectiveness of stimulus objects (Seitz 1940, Tinbergen 1951, Weidmann 1959, Hara and Warren 1961, Baerends et al. 1964, Sutherland 1964). Indeed, as will be seen in Chapter 7 where these matters are discussed, the formula of the main prediction of the Threshold Model has been previously used in studies of Additivity of Cues.

Human psychologists have put forward a number of mathematical treatments of choice in man, from which predictions rivalling one of the Threshold Model's can be deduced (Thurstone 1927, Bradley and Terry 1952, Luce 1959, Audley 1960, Flament 1960). These will be discussed after the prediction concerned has been deduced from the Threshold Model.

Although it involves observations of the whole intact animal only, the ultimate aim of this study is a physiological one (Tinbergen 1963), to discover something about the mechanisms of decision-making. It is an example of a "high level" physiology, whose conceptual units are larger than those of neurophysiology. The Threshold Model is a "model" (Young 1964) in the sense that it could be built as an actual hardware machine, or as several analogous machines. (One machine, based on one version of the Threshold Model, has in fact

been built.) It embodies "hypothetical constructs" (MacCorquodale and Meehl 1948) of which, it is hoped, analogues, however distantly related, exist in the nervous system. Ideally this work might perhaps stimulate ideas in a neurophysiologist about how such biological analogues could work, and how they might be detected at a deeper level of analysis (Pringle 1963) than is possible by behavioural observations alone.

THE CONTROL OF PECKING IN CHICKS

In theory the model to be discussed might be applicable to any situation in which an animal responds to an external stimulus, or more particularly when it is given a choice between two external stimuli. However since it is easier to think in terms of a specific example, I will introduce the problem in terms of the one with which most of the work has been concerned.

If a chick is placed in front of two small coloured spots, say an orange one and a green one, the following facts may be noticed. Firstly, if given enough time it will probably peck at each of the spots, but it will give more pecks to the orange than to the green one, (Curtius 1954, Hess 1956). Secondly, it will spend much of its time not pecking, even if apparently looking at the spots. Thirdly its pecks, unless it is very young (Hess 1956 and many others), will be quite accurate, and if the spots are not placed too close together, it will nearly always be possible for an observer to tell at which, if either, of the two spots it is aiming. Observations of this kind raise a number of different questions about the mechanisms underlying pecking. I wish to discuss only one of these in any detail, but will mention the other obvious ones in order to clarify the nature of this main question. The four questions which I would pose are:

1. What is the mechanism which determines when pecks occur?

The importance of this question impresses one especially when one sees

a chick standing in front of a coloured spot say, looking at it but not making any obvious movement, and then quite suddenly giving a vigorous peck at the spot. The striking thing about this occurrence, which is quite common, is that the peck does not seem to be elicited by any change in the external environment, though it is of course impossible to be sure of this.

2. What is the mechanism of the stimulus preference shown by the response? Why for example does the chick peck more at the orange spot than at the green one? This is the phenomenon for which the metaphor of the "Filter" (Marler 1961), and the concept of the "I.R.M." (Schleidt 1962) have been used. It is with this question that one would be concerned for example if one asked whether colour preferences in young birds are determined by retinal oil droplets, (e.g. Hailman 1964).

3. What is the mechanism which determines at which of the two stimuli each individual peck is directed? This is the question with which this study is mainly concerned. It is important to demonstrate clearly how it differs from 1 and 2.

Question 2 is concerned with the fact that animals have a statistically greater tendency to respond to some external stimuli than to others. Question 3 arises because it is a fact that most animals, when offered a choice between several stimuli, although they give the majority of their responses to one of the stimuli - the "preferred" one - do nevertheless give some to the other stimuli. In the particular example we are considering, the chick will show a

statistical preference for the orange spot, but will give a fair number of pecks to the green one. Therefore a decision-making problem arises which is quite distinct from the stimulus evaluation problem of Question 2 (Diamond, Balvin and Diamond 1963, p.136). The question we are asking here (3), is not, "Why does the chick give the majority of its pecks to the orange spot?" - Question 2 - , but rather, "Given that the chick does have an overall statistical preference for the orange spot, but still gives some pecks to the green one, what is the mechanism which determines the target of each individual peck?"

The distinction of Question 3 from Question 1, that of the mechanism determining when pecks occur, is a difficult one to draw, because in principle both functions could be performed by the same mechanism. Thus the decision to peck might be identical with the decision to peck at a particular stimulus. However it may be helpful to emphasise at the outset the formal possibility of a distinct mechanism for the two functions, determining when a peck shall be given, and determining the stimulus at which it is to be directed, since this distinction is to play a key role in the work to be described.

4. Finally, when the decision to peck has been taken, and the object at which it is to be directed has been determined, there are still questions to be asked about the executive machinery which actually carries out these decisions, the "Pecker" itself. For example we might ask how the bill is guided accurately towards the chosen target.

Provisionally then we can postulate four different kinds of mechanism involved in selective pecking, and the classification could be generalized to many other situations in which animals respond to external stimuli.

1. The "Go/No go" decision-making mechanism.
2. The Stimulus Evaluating mechanism.
3. The Directing, or "Left/Right", decision-making mechanism.
4. The Executive mechanism or "Pecker".

The course of events determining a peck then can be visualised as follows: The "Go/No go" decision-maker determines that a peck may be given at a certain instant in time. No doubt many things, hunger etc., will influence this decision. The Directing decision-maker will decide at which of the available stimuli the peck is to be given. In making its decision it will be influenced or biased by the Stimulus Evaluator, and perhaps by other factors as well. Finally the decisions taken will be carried out by the Executive mechanism, and if it is successful the bill will hit the chosen target.

Obviously this classification of "mechanisms" is a functional one with no pretentions to structural or spatial validity: it would be naively underestimating biological complexity to think for example of a single, well defined brain locus acting as a "Go/No go" decision-maker for pecking. Equally obviously it is not the only possible functional classification. It is one which I happen to find satisfying, and it also serves as a good introduction to the Threshold Model, and

the role which some kind of neural analogue of the Threshold Model might play. The classification will be used again in Chapter 6 in which evidence from the intervening chapters about the workings and interrelations of some of the proposed functional units will be brought together.

The Threshold Model now to be described then is put forward primarily as an analogue of a possible mechanism performing the Directing decision-making function. Though it was thought of mainly in terms of pecking in the domestic chick, other types of selective responses in this animal are looked at; and also by courtesy of other workers, it has proved possible to apply the model to other species.

THE MODEL : INTRODUCTION

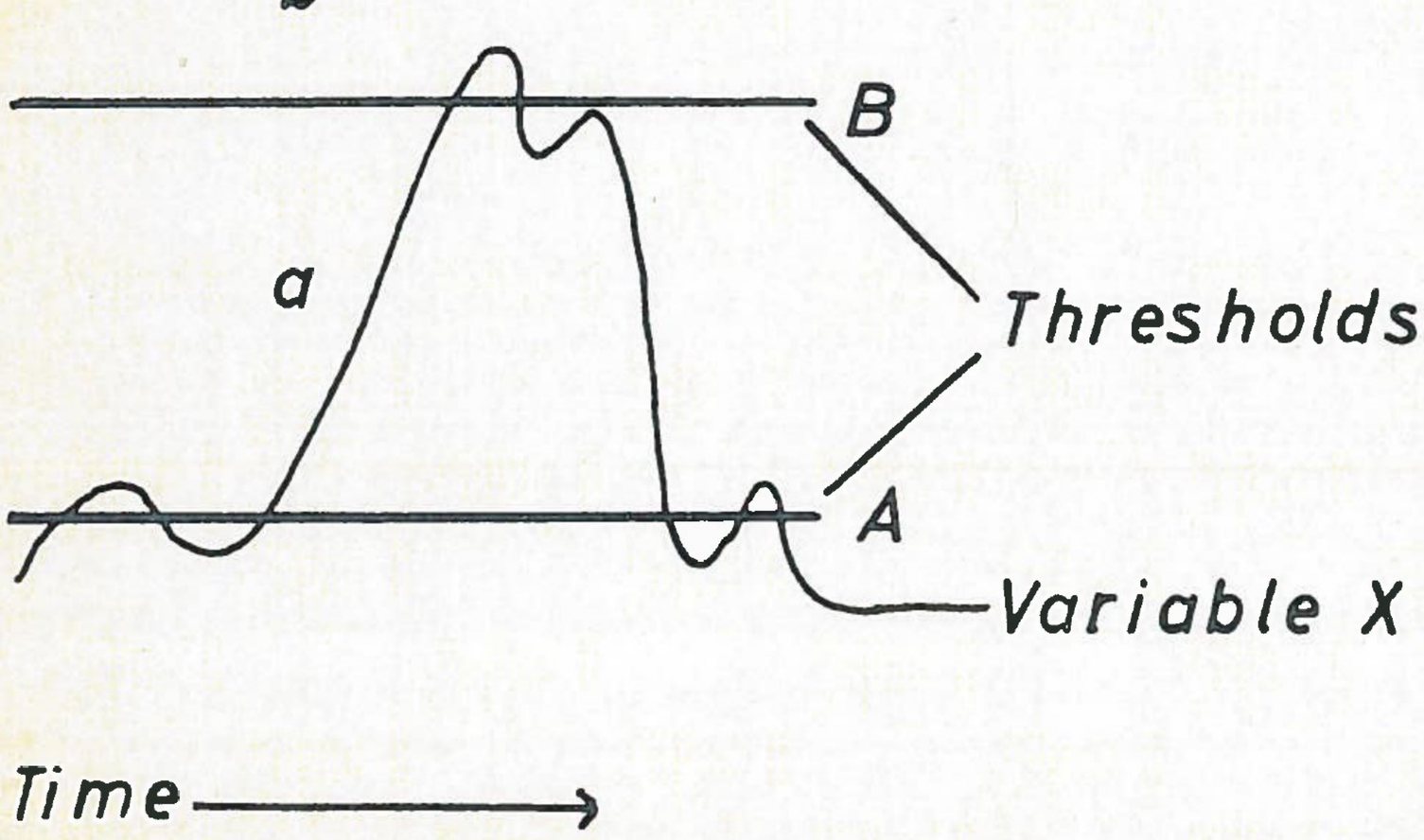
A number of workers have proposed what may be called Threshold Models to explain short term switches in behaviour (e.g. Bastock and Manning 1955, van Iersel and Bol 1958, Andrew 1961, Tugendhadt Gardner 1964). The models of these workers have in common the postulation of a fluctuating internal variable usually given a name like "Drive" or "Excitation". The different items of behaviour are thought to be activated by the same "Drive" (or "Excitation" etc.) but at different threshold levels. von Holst and von Saint Paul came to a similar idea as a result of brain-stimulation of chickens (1963). In the case of all the studies mentioned the different items of behaviour concerned have involved different motor patterns, which have usually been fuctionally related. Models of this kind seem quite plausible and satisfactory, although it is difficult to obtain good supporting evidence for them. One major difficulty is that the behavioural predictions by which they could be tested might also be expected by other simpler types of theory (Cane 1961). This is a problem with all models which can only be tested by behavioural predictions. However it can be said that the more complex or quantitatively precise a prediction is, the more likely it is to be deducible from one model rather than many.

I wish to propose a threshold model of the same general type as those mentioned above. In this case the different items of behaviour between which the animal is observed to choose do not differ in motor pattern, but in the stimuli to which they are directed.

The basic principles of one version of the model will first be described, and then the deduction of the most important prediction, called Prediction 1, will be given.

Figure 1

Simple Threshold Diagram
for two stimuli, A & B.



THE THRESHOLD MODEL : BASIC ASSUMPTIONS

The principles of the model are illustrated in Figure 1. They can be expressed in the form of three basic assumptions.

1. There is a fluctuating variable inside the animal, (fluctuatingin <u>time</u> not space), called <u>Variable X</u>, corresponding as far as the threshold models are concerned, with the "Excitation" of Bastock and Manning, and the "Drive" of van Iersel and Bol.

2. In order that a peck shall occur, Variable X must exceed a <u>threshold</u> level determined by an available external stimulus. Preferred stimuli have lower thresholds than less preferred ones.

3. When the threshold levels of more than one external stimulus are exceeded, each of those stimuli has an exactly <u>equal</u> chance of being pecked.

For example if in a simultaneous choice test a chick gives 80% of its pecks to an Orange spot, and 20% to a Green one, the interpretation according to the model would be that during 60% of the time that Variable X was above any threshold, it was above the threshold for Orange, but below that for Green and the Orange spot received all the pecks; during the remaining 40% of the time that Variable X was above any threshold, it was above the threshold for Green, and therefore also above that for Orange, and the two stimuli each received exactly 50% of the pecks. Thus the total percentage of pecks to Orange is $60 + \frac{40}{2} = 80$, while the total percentage to Green is $\frac{40}{2} = 20$.

If three stimuli are presented and all three thresholds are exceeded, each stimulus will receive one third of all the pecks. If the thresholds of four stimuli are exceeded, each will receive 25% and so on.

SYMBOLS USED IN THE THRESHOLD MODEL

Obviously if the assumptions of the model as given above are to be of any practical interest they must be treatable in a quantitative way. The detailed uses of the algebra will be seen as each prediction is deduced. However it will clarify matters later if the terms are introduced now.

Symbols

Four basic types of symbol are used. They will be briefly discussed one by one.

1. P The capital letter P is used to denote percentage preference, defined as the number of pecks (or other responses) at the normally preferred stimulus (multiplied by 100) divided by the total number of pecks at both stimuli. In practice it is often convenient to omit the 100 and work with preference proportions. It is rather tedious continually to make the distinction between these two, and I use the terms Percentage Preference, and P to cover both.

P may be followed by a subscript which is simply a label to denote the stimulus referred to.

2. Other capital letters (except K, P and X): These refer to stimuli, for example coloured spots in pecking experiments, A and B in Figure 1. Sometimes they may be initial letters standing for colours e.g. Y for Yellow. Another convention which I sometimes use is to denote order of preference by alphabetical order. This is particularly used when, as is very often the case, the stimuli are considered

in groups of 3, in which case A denotes the normally preferred stimulus, B the intermediate one, and C the least preferred one. These symbols are labels only. They may be used as sub-scripts, labelling other symbols which have quantitative significance such as P and K.

The following convention is used to represent the number of pecks received by each member of a pair of stimuli. The capital letter referring to the stimulus at which the counted pecks are directed, is written outside brackets. Inside brackets and immediately following, is the letter referring to the stimulus with which it is paired. Thus for example A(B) = the number of pecks given to stimulus A when presented with stimulus B. B(A) is the number given to B in the same pair choice test.

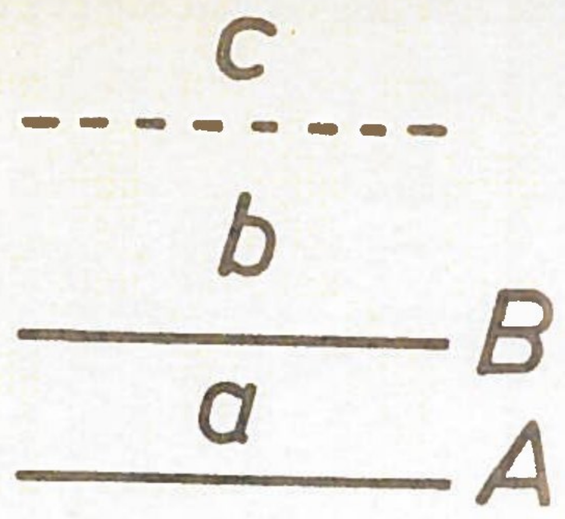
3. Small letters. These are used for "Threshold Values", measures of the time spent by Variable X between (or above) the different threshold lines. The "Interthreshold Value" between two stimuli is the time spent by Variable X between the Thresholds of those two stimuli. Thus in Figure 1, the Interthreshold Value between stimulus A and stimulus B is a. The Total Threshold Value of a given stimulus is the total time spent by Variable X above the threshold of that stimulus. In Figure 1 the Total Threshold Value of A is a+b, and the Total Threshold Value of B is b.

The positioning of the Threshold Value symbols between the threshold lines concerned, in Figure 1, and in similar diagrams to follow, is a convenience in some respects, but it might be misleading

if not clarified at this stage. It is not intended to imply physical distance: the Threshold Values are measures of time. Thus if the values of a and b are to be given graphical representation, it would most precisely be done along the horizontal axis of Figure 1. Nevertheless spacing out of the lines in proportion to the intervening Interthreshold Values is a useful pictorial device (see for example Chapter 5) but it is important to remember that this has purely pictorial significance.

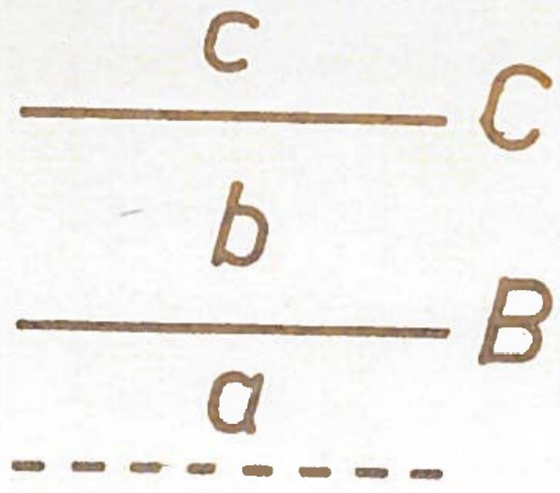
The choice of how many small letter symbols are used to represent Threshold Values in any given case is somewhat arbitrary, and depends on the total number of stimuli which need to be considered. For example if in the situation depicted in Figure 1 we wanted to consider a third stimulus C, not necessarily at the same time, but in the same whole experiment, it would be necessary to denote the appropriate Threshold Value c, as in Figure 2.

4. K The capital letter K is used as a measure of the activity of the "Go/No go" decision-making mechanism. (See below for explanation.) The number of pecks which a stimulus should receive according to the simple Threshold Model by itself, must be multiplied by K in order to obtain the number of pecks which it actually receives. Like P, K may be labelled with subscripts.



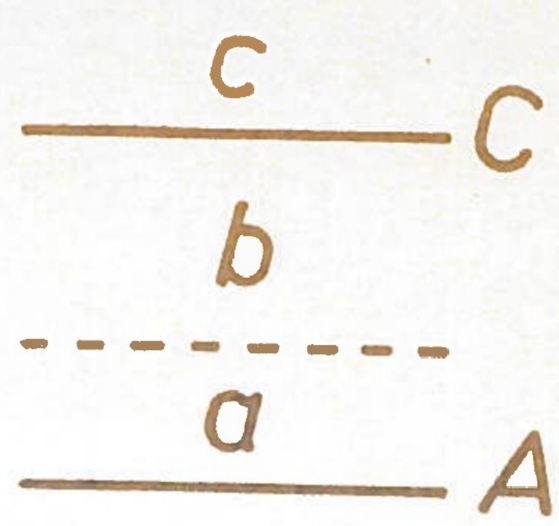
$A : a + \frac{b+c}{2}$

$B : \frac{b+c}{2}$



$B : b + \frac{c}{2}$

$C : \frac{c}{2}$



$A : a + b + \frac{c}{2}$

$C : \frac{c}{2}$

$$P_1 : \frac{2a+b+c}{2(a+b+c)} \qquad P_2 : \frac{2b+c}{2(b+c)} \qquad P_3 : \frac{2(a+b)+c}{2(a+b+c)}$$

$$P_3 = 2(P_1 + P_2 - P_1 P_2) - 1$$

Figure 2

THE DEDUCTION OF PREDICTION 1

This will serve as a good example of the way in which the assumptions of the model may be treated quantitatively using elementary algebra. Basically the method is to assign unknown values to the time spent by Variable X between the various threshold lines, and then apply the assumptions of the model in a particular practical situation. It is usually not necessary to know the actual values, since they can be eliminated at a later stage in the calculations.

The practical situation for Prediction 1 is as follows: The animals are presented at different times with any three stimuli in all three possible pair combinations. If the three stimuli are called A, B, and C, this means that we present separately A with B, B with C, and A with C. We then measure the percentage preference in each case where percentage preference is defined as

$$\frac{\text{No. responses to preferred stimulus}}{\text{Total no. responses}} \times 100$$

Figure 2 shows threshold diagrams for each of the three situations. The Ks, (see below), are omitted for simplicity. A is represented as being the preferred stimulus, then B then C. The thresholds for the two stimuli actually presented in each case are drawn as solid lines, while that for the third stimulus not presented is drawn as a dotted line. The time spent by Variable X above A's threshold but below B's is represented as a. The time spent between B's threshold and C's is b, and the total time spent above C's threshold

is c. (Strictly speaking we should consider many other possible stimuli D, E etc., which might be deliberately presented by the experimenter, or which might be little pieces of dirt lying around. c in this example then should perhaps be written c --- or c etc., to show that c really stands for c+d+e+ etc. It makes no difference whatever to the deduction of Prediction 1. It also makes no difference if D, E etc. are preferred to any of the test stimuli. The only thing that matters is that these extra stimuli should be constant factors in the environment, and not present during some tests more than others.)

Consider the case when A is presented with B, C being absent. The number of pecks at A will be proportional to $a+\frac{b+c}{2}$, since during time a only A will be pecked, while during time b or time c both thresholds will be exceeded, and both stimuli will therefore receive exactly half of the pecks. The number of pecks at B will be proportional to $\frac{b+c}{2}$ since it will only be pecked when its own threshold is exceeded, i.e. during times b and c, but during these times it has to share the pecks with A, and each will receive half. The constant of proportionality for this case may be called K_1 (and those of the other two pair combinations K_2 and K_3). Thus the number of pecks at A = $K_1(a+\frac{b+c}{2})$ and the number of pecks at B = $K_1(\frac{b+c}{2})$. The percentage preference for A over B is therefore

$$\frac{K_1(a+\frac{b+c}{2})}{K_1(a+\frac{b+c}{2}) + K_1(\frac{b+c}{2})} \times 100 .$$

K_1 cancels out and the expression for the percentage preference A over B reduces to $\frac{2a+b+c}{2(a+b+c)}$. (The 100 is omitted for convenience as explained before. Strictly speaking the expression represents the proportion of pecks to A.) This expression can be called P_1.

Now consider the case when B is presented with C, A being absent. In this case there will be no pecks at all during time a; B will receive all the pecks during time b, and each stimulus will receive half the pecks during time c. The number of pecks at B will therefore equal $K_2\ (^{b+\frac{c}{2}})$ and the number of pecks at C will equal $K_2\ (\frac{c}{2})$. The percentage preference for B over C then is $\frac{K_2(^{b+\frac{c}{2}})}{K_2{}^{(b+\frac{c}{2})} + K_2{}^{(\frac{c}{2})}}$ which equals $\frac{2b+c}{2(b+c)}$. Let this be called P_2. Finally in the case when A is presented with C, B being omitted from the experiment, during times a and b only A will be pecked. During time c the two stimuli will share the pecks. Thus No. of pecks at A = $K_3(^{a+b+\frac{c}{2}})$ and No. of pecks at C = $K_3(\frac{c}{2})$. The percentage preference for A over C therefore equals $\frac{K_3(^{a+b+\frac{c}{2}})}{K_3(^{a+b+\frac{c}{2}}) + K_3(\frac{c}{2})} = \frac{2(a+b)+c}{2(a+b+c)}$. Let this be called P_3.

We have then three expressions P_1, P_2, and P_3 expressed in terms of unknowns, a, b, and c. a, b, and c can be eliminated between the three equations which then conveniently reduce to

$$P_3 = 2(P_1+P_2-P_1P_2)-1$$

This is of course a testable prediction. It is the one which I call Prediction 1.

Before going on to describe tests of Prediction 1, I will just point out that while it is an "improbable" prediction in one sense since it is quantitatively precise, it is fully in accordance with common sense. Thus P_3 must always be larger than either P_1 or P_2 except in two special cases. One of these is when either P_1 or P_2 is 50% in which case P_3 will be identical with the other one. The second special case is when P_1 or P_2 is 100% in which case P_3 will also be 100%. Thus Prediction 1 so far does not violate common sense. Further, provided the values of P_1 and P_2 fed into the formula are possible, i.e. not above 100%, the value of P_3 given by the formula also will not exceed 100%.

To take definite hypothetical examples, if P_1, the percentage preference for A over B is 70% and P_2 that for B over C is 80%, we should expect on common sense grounds that P_3 the percentage preference for A over C should be higher than either of the other two. Prediction 1 also expects this, but it is more precise. P_3 should be 88%. If both P_1 and P_2 are 99%, common sense again tells us that P_3 should be higher, but that it should not be greater than 100%. Prediction 1 says it should be 99.98%. If P_1 is 70% and P_2 is 50% common sense tells us that P_3 should also be 70% since there is absolutely no preference between two of the stimuli (B and C say) and therefore the percentage preference for A over C should be exactly the same as that for A over B. Prediction 1 agrees. (It makes no difference of course which percentage preference we decide to call P_1 and which P_2. Only P_3 is specified. This is also in accordance with common sense.)

A SIMPLER EQUIVALENT TO THE FORMULA OF PREDICTION 1

Another formula, exactly equivalent to that given above for Prediction 1, but simpler, can be obtained, if instead of considering the percentage numbers of pecks at the preferred stimuli - the "correct" responses - we take the percentage numbers at the less preferred stimuli - the "mistakes". Thus if q is defined as 1-P, Prediction 1 may be rewritten $q_3 = 2q_1q_2$

One should not therefore pay too much attention to the apparent complexity of Prediction 1 as given above, for it is equivalent to something much simpler. But however it is expressed, it is quantitatively precise.

I use the more complex form partly because I have always thought in terms of it, and partly because it is customary and convenient to work with "percentage preferences" (P), rather than with "percentage avoidances" (1-P or q). However this is largely a matter of personal taste. It makes no material difference. I think it is a good thing for me to mention that there are these two alternative ways of expressing it, because the chance of somebody else thinking of an alternative model expecting Prediction 1 might thereby be increased.

ALTERNATIVE MODEL : PREDICTION 1A

The principal test of the Threshold Model, Prediction 1, is a quantitatively precise prediction (Coombs 1950). That is to say it is not merely an expectationthat one quantity will be larger than another, or smaller than another, but that one quantity, P_3 will have a definite specified value, and will be on average neither too high nor too low. Now statistical tests of significance are normally concerned with demonstrating differences, not similarities as would be required in this case. It is therefore particularly important that the successes of the Threshold Model in predicting the facts be compared with those of other models. I have tried out some alternative models, some of them variants of the Threshold Model itself. The one which came closest to fitting the facts was not one of these. I call it the Set Releasing Value model. It is based upon what are probably the simplest possible assumptions for the situation.

The Set Releasing Value model assumes that every stimulus object possesses a characteristic, unvarying stimulating value for the animal, and the number of responses which it elicits is always proportional to this value. Thus if we take two stimuli A and B, whose "releasing values" are respectively a and b, P, the "percentage" preference for A over B will be $\frac{a}{a+b}$. In the experimental situation appropriate for Prediction 1, P_1 will be $\frac{a}{a+b}$, P_2 will be $\frac{b}{b+c}$, and P_3 will be $\frac{a}{a+c}$. The equivalent of Prediction 1 is then P_3 =

$\frac{P_1P_2}{P_1P_2+(1-P_1)(1-P_2)}$. This I will call Prediction 1A. It will be compared with the observed data along with Prediction 1 itself.

Other alternative models will not be considered in detail. As will be seen below, those found in the literature which yield predictions for this situation, give either Prediction 1A, or its practical equivalent, and no others that I have been able to think of even approach the success of Prediction 1 and Prediction 1A in fitting the facts.

Prediction 1A then is the best alternative to Prediction 1 that I have been able to find, and as will be seen in Chapter 2 they are both very good. Since they both give very much the same results, Prediction 1A always predicting a slightly higher P_3 than Prediction 1, (except of course when any of the Ps is 50% or 100%), it is inevitable that if one of them fits the facts perfectly, the other one must seem to be almost perfect as well. However if enough data are obtained it is possible to show that one of them differs significantly from the facts, and to fail to show that the other one does. This will be taken up again when the results are discussed in Chapter 2.

PREVIOUS WORK

Predictions applying to the same situation as that for Prediction 1 have been considered before by human psychologists, under the names Stochastic Transitivity (Marschak 1960) and Monotonicity (Coombs 1958), and even by economists (Papandreou 1957). These authors have usually been concerned with qualitative aspects, for example in terms of the symbols A, B, and C used above, with whether if A is preferred to B, and B is preferred to C, A will be preferred to C; (Weak Stochastic Transitivity); and whether the preference for A over C will be stronger than both the other two preferences (Strong Stochastic Transitivity); or than only one of the two other preferences (Mild or Moderate Stochastic Transitivity). (I use the word "prefer" here for ease of comparison with my chick situation. In practice authors on "Transitivity" have as often been concerned with psychophysical problems of discrimination etc.) Where it has been looked at in man, (Papandreou 1957, Coombs 1958, Davidson and Marschak 1959, McLaughlin and Luce 1965, this thesis Appendix 1.) evidence for Strong Stochastic Transitivity has usually been found, but there are exceptions, (Coombs 1958, Smedslund 1960). Coombs's finding of a departure from Strong Stochastic Transitivity will be mentioned below, because it provides an interesting parallel with one of my chick results.

Prediction 1 and Prediction 1A are of course both predictions of Strong Stochastic Transitivity, but they are precise quantitative ones (Coombs 1950). Most writers have not concerned themselves with

quantitative aspects of Transitivity, other than with whether it is "Strong", "Moderate" or "Weak".

However Luce's Axiom (1959) leads to consequences which are basically similar in this situation to the "Set Releasing Value" Model discussed above, and Luce's prediction for the Transitivity situation is in fact identical to Prediction 1A. Luce also discussed the expectation of Thurstone's "Law of Comparative Judgement (Case V)" (1927), and finds the prediction (of P_3 in the terminology used here), to be always slightly higher than the prediction of his own model, Prediction 1A in the present terminology. As we have seen above, Prediction 1A is always higher than the Threshold Model's Prediction 1. It therefore follows that if Prediction 1 is found to be closer to the facts in the experiments to be described than Prediction 1A, there will be no need to test Thurstone's prediction since it is bound to be further from Prediction 1 than Prediction 1A is.

Audley (1960) proposes another model for choice in man. He does not explicitly derive a prediction for the Transitivity situation, but it is possible to work out using sample figures what his model with K = 2 would predict. It proves to be extremely close to but consistently slightly higher than, Prediction 1A, so that the same argument as was used for the case of the Thurstone prediction applies.

Flament's (1960) model is for the experiment situation discussed here, equivalent to Luce's, and it gives the same prediction, Prediction 1A.

CHAPTER 2 : METHODS AND PREDICTION 1 RESULTS

INTRODUCTION

In Chapter 1, the model was discussed with reference to pecking in chicks. This was for convenience only. It might of course apply equally well to any choice test in any animal. The bulk of my work on the Threshold Model has in fact been done on chick pecking, but I have also done a few experiments on different kinds of choice situation, again using chicks. The methods used in all these cases will be described in this chapter, along with the results.

A number of other workers on animal preferences have for reasons of their own used an experimental design which incidentally makes it possible to test Prediction 1. I have been very fortunate in that four such workers have very kindly given me access to their original unpublished data so that I could calculate observed and predicted P_3s, and thereby obtain a far more substantial test of my prediction than I was able to achieve with my own results alone. I will not in this chapter mention any more about their experimental methods than is necessary for the present purpose of testing Prediction 1. For further details reference should be made to their own papers, either published or soon to be published. I shall however say something about the way in which the raw data were treated in order to test Prediction 1.

RECAPITULATION : PREDICTION 1 and PREDICTION 1A

The experimental situation is one in which any three stimuli, A, B, and C, are presented in all three possible pair combinations. If they are preferred in that order, let P_1 be the percentage preference for A over B, P_2 that for B over C, and P_3 that for A over C.

Prediction 1, which follows directly from the basic assumptions of the Threshold Model, states that P_3 should equal $2(P_1+P_2-P_1P_2)-1$.

Prediction 1A, which follows from the simpler Set Releasing Value model, and also from a number of other models, states that P_3 should equal $\frac{P_1P_2}{P_1P_2+(1-P_1)\ (1-P_2)}$.

REJECTION OF NON-SIGNIFICANT PREFERENCES

The deduction of Prediction1depends on the assumption that there is no variation in the rank order of preference of the different stimuli, either between different animals or within any one animal at different times. That is to say, in the terms of the Threshold Model, in order for Prediction 1 to follow, it is necessary that there be no variation in the rank order of the different threshold lines. There can be variation in the relative time spent by Variable X between the thresholds, but this variation must never extend to the lines actually "crossing" each other. i.e. there can be "quantitative" but not "qualitative" variations (Coombs, 1950).

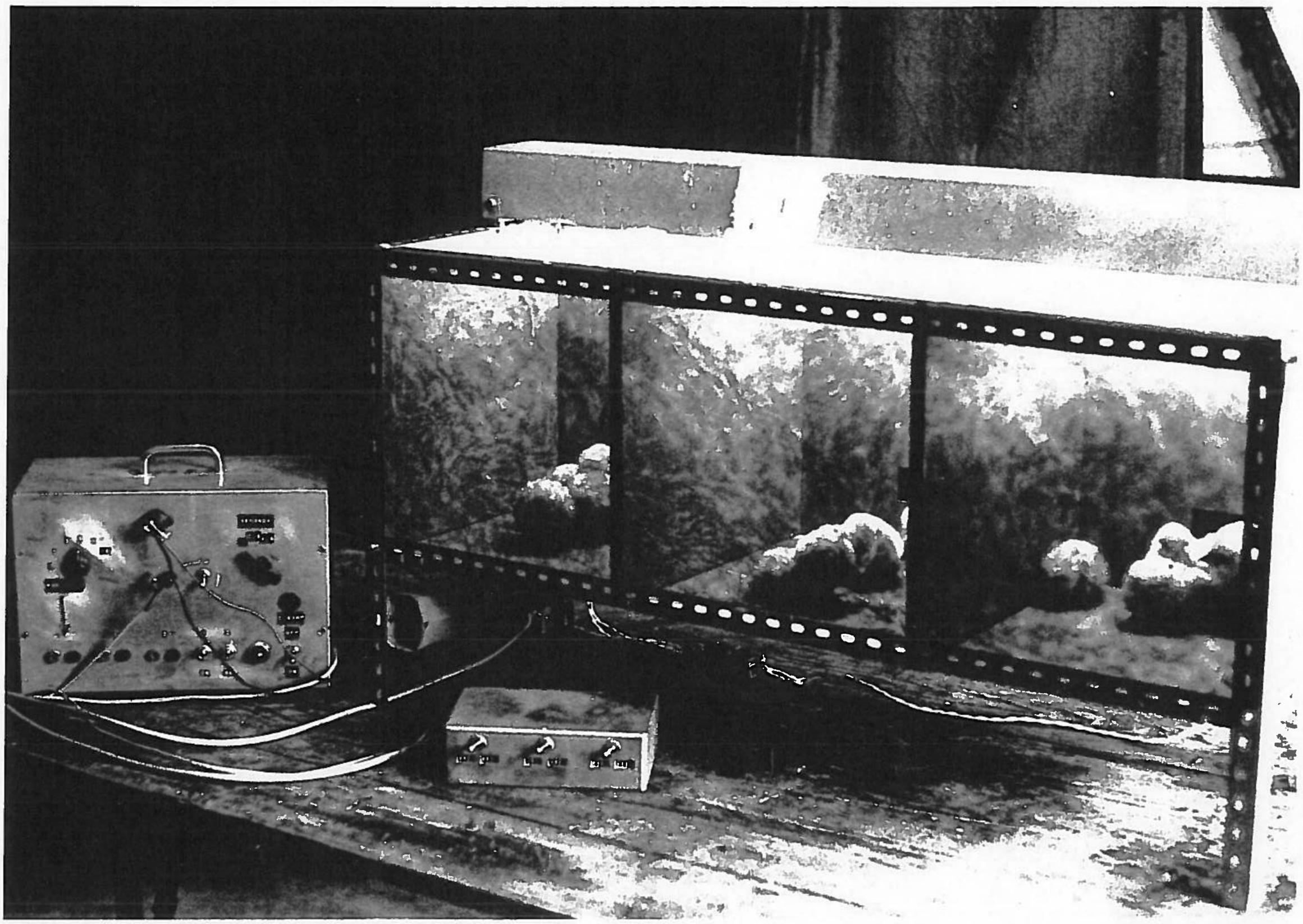
Note that the Threshold Model does not necessarily predict that this assumption is true: it may very well be false. But if it is false, Prediction 1 cannot be deduced.

In testing Prediction 1 therefore, it is necessary to reject any cases where this assumption is not true. One has to have an objective criterion for such rejection, and the most reasonable seemed, (before the experiments were done, but see the conclusion to this chapter), to be based on statistical significance. Accordingly any experiments in which all three preferences did not reach the significance level of 0.05 (1 tailed), were rejected. For example if in an experiment chicks were presented with three stimuli A, B, and C, in all possible pair combinations, and it proved impossible to reject the null hypothesis that say A and B were equally likely to

be pecked, the whole experiment would be discarded.

Fortunately not many of my experiments had to be rejected because of this: my chicks seemed remarkably uniform in their preference rank orders, though they varied considerably in strength of preference. The few experiments which have been rejected were all rather small pilot experiments which might well have been rejected on other grounds in any case.

In treating the data of other workers I have adopted the same criterion for rejection. In some cases this has meant the loss of somewhat larger numbers of data.



Peck counting apparatus. Chicks are visible through the "one way screen".

1. CHICK PECKING PREFERENCE TESTS

Subjects Messrs. Jennings of Garsington, near Oxford, allowed me every week to collect as many "day-old" male chicks as I wanted - usually several hundred for each experiment. The chicks were of a Light Sussex/White Leghorn cross-bred strain. They were hatched in large incubators, sexed, and put into boxes each containing 25, in which they were transported to the laboratory. There they were kept in the light in large living areas 180 x 45 cms, at a temperature of around 30°C, until tested. They received no food or water before testing. Their ages at the time of testing ranged roughly between 12 and 60 hrs. This was partly because of the spread in hatching times, and partly because my tests took place over three days. After testing they were killed, unless required for other experiments in which case they were fed.

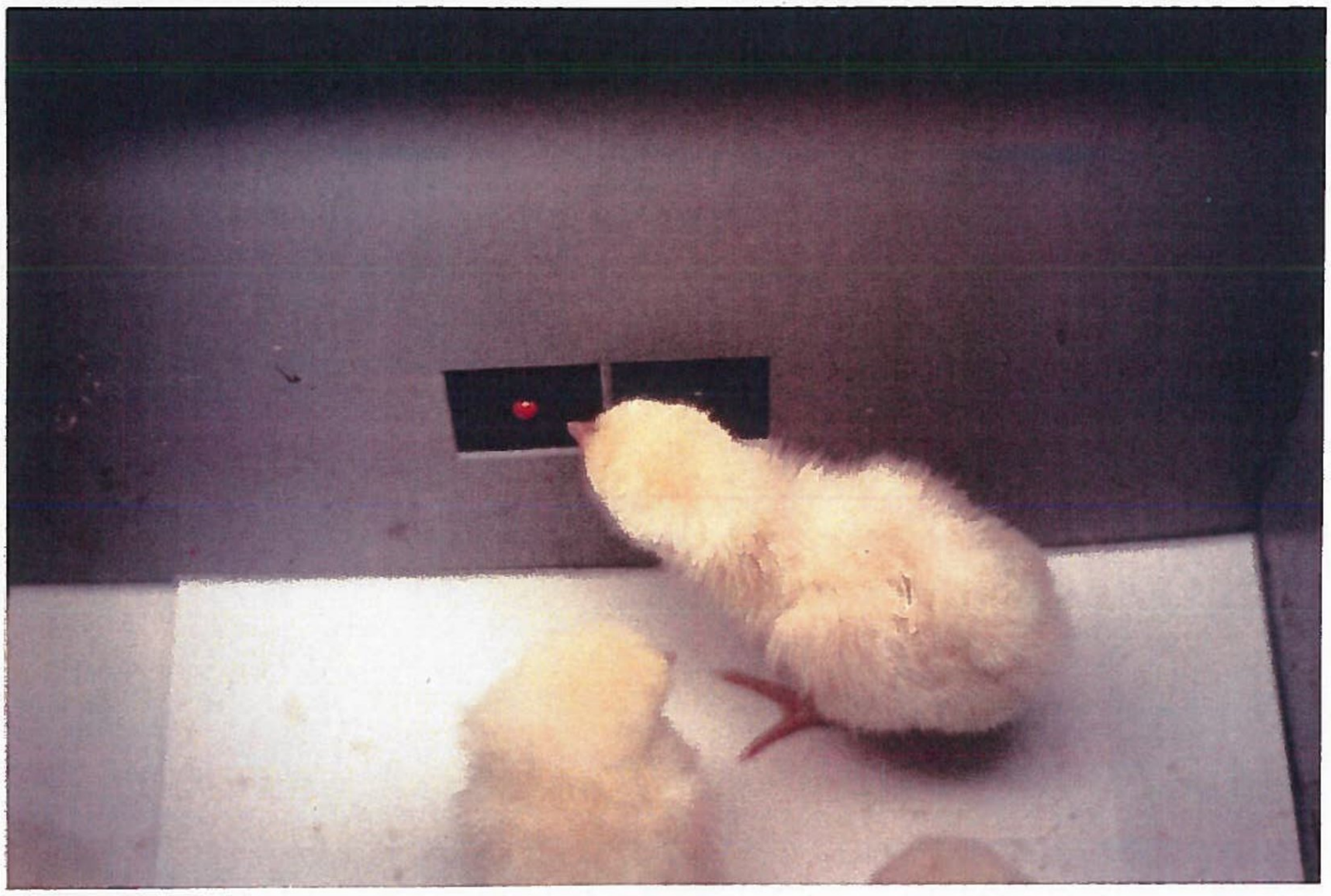
Apparatus Pecks were counted automatically by means of microswitches. The apparatus used for most of the experiments consisted of three cubical compartments, in one wall of each of which were windows through which the stimuli were presented. In earlier experiments of the series, another piece of apparatus was used, identical except in that there was only one compartment instead of three, and in that it was illuminated by an ordinary Tungsten bulb instead of a fluorescent tube. Both were largely built by Mr. Jan Adam. I am very grateful to him.

Each of the cubical testing compartments had a side length of 30 cms; three of the walls were painted neutral grey and the fourth

served as a crude one-way viewing screen made of 6 layers of black netting. A 30 w. fluorescent tube lay along the top of all three cubicles, shaded so that most of its light ("daylight") fell into the cubicles. Enough of the top of the apparatus was left uncovered to allow the chicks to be put in and removed. In the wall opposite the netting screen, two 33 mm square windows were cut, 3 mm apart, with their tops 8.5 cms above the floor. The stimulus objects appeared in the middle of these windows, mounted on rectangular plates of thin tinplate, painted black. (In earlier experiments stiff black cardboard was used instead of tinplate. Tinplate proved easier to clean.) These plates were held in delicate little frames, hinged at the top so that when they were pecked they swung backwards. Behind the lower rim of these hinged frames, Bulgin Microswitches* (Type M, S 530) were attached. They were connected up to counters and a 48 volt supply.

---

* It is difficult to find a good Microswitch for this purpose. Most microswitches manufactured require a higher activating force than chicks normally give when they peck. On the other hand one extremely sensitive switch which I tried, although its lever was easily depressed by the chicks, passed such a brief pulse of current that almost none of the pecks was registered by the counters, even though the latter were relatively sensitive. The best solution which I could discover was to use the Bulgin switch mentioned above but with the springs inside weakened by bending so that the chicks are able to work them. This is a difficult operation however, since if the springs are bent too far, there is a danger of the switches sticking. Inevitably there was some variation in the force necessary to activate the different switches. This could have no systematic influence on the preferences measured since the experiments were always designed to exclude this possibility - i.e. the stimulus objects were rotated systematically through the different holders. This remains however a slightly unsatisfactory feature of the apparatus, and one which I would like to rectify in future work if I can find a way.



Peck counting apparatus: inside one compartment during a test.

A large majority, though not all, of the pecks, were registered by the counters.

Experimental procedure This differed in minor details in the different experiments, but was basically as follows:

Each chick was tested only once. They were tested in groups of six for five minutes. Each group of six was put in the middle of one of the three compartments of the apparatus, in nearly complete darkness. The light and the peck-counting circuit were then simultaneously switched on, and a stop-clock started. After exactly five minutes the peck-counting apparatus was switched off, and the chicks discarded. The numbers of pecks registered by each of the counters was noted down, and the next lot of chicks was tested.

Since a test of Prediction 1 requires that 3 separate percentage preferences be known, it was convenient to present each of the three choice tests simultaneously in different compartments. A typical experiment thus might consist of say 20 successive 5-minute test periods, in each of which all three choices were given.

The positions of the individual stimulus objects in the apparatus were rotated in such a way that:

a. Any individual choice test did not appear systematically more often in one compartment than in the others.

b. In successive trials the left-right positioning of the stimuli in each choice pair was alternated.

c. A similar alternation occurred when each choice pair was presented in any one compartment, i.e. every third trial.

These conditions were achieved by a simple rotation schedule in which only one member of each pair of stimuli was moved after each trial.

Treatment of data For every 5-minute choice test a percentage preference was calculated as

$$\frac{\text{No. of pecks at normally preferred stimulus}}{\text{Total number of pecks}} \times 100$$

Then at the end of the experiment, for each of the three choice tests (AB, BC, and AC) the mean of all the percentage preferences was calculated. The three Mean Percentage Preferences so obtained were the figures used in testing Prediction 1.

This method was used rather than that of adding up all the individual pecks throughout the whole experiment, because the variation between the different groups of chicks was very large with respect to the total number of pecks given, but was comparatively small with respect to percentage preference. The decision to use this method was taken before the experiments were done.

Also predetermined, was another rule of procedure: any single trials in which a total of less than 10 pecks was recorded, were rejected. When deciding to use the method of working out the percentage preference for each individual trial, I realised that at times this would lead to rather absurd results: thus a single peck would have to contribute to the mean percentage preference, either as 100% or as 0%. Two pecks in a trial could contribute only as 100%

0% or 50%. It seemed reasonable therefore to reject all trials in which very few pecks were given. The choice of a criterion of 10 was arbitrary. It did not greatly affect the results; (there seems to be no correlation between total number of pecks in a trial, and percentage preference).

Details of individual experiments and Results Eight experiments satisfied the significance criterion. The results of each experiment will be given separately together with details of the stimuli used, and any special remarks.

Experiment 1

Stimuli: All 3 were painted aluminium hemispheres, 6 mm in diameter, stuck on a black background. They were painted respectively Blue, Red, and Green. (Priosin Co. colour names: Light Blue, Orange, and Light Green. I use the name "Red" for Priosin "Orange" to distinguish it from a yellower orange that I mixed later. Priosin "Orange" is in fact rather a reddish orange.)

Special remarks: From previous experience I was doubtful whether the preference for "Red" over Green would be very strong, so I took steps to increase it by leaving the chicks overnight with green spots painted round the walls of their living cages. From previous experiments I though this would have the desired effect. It should of course in no way affect the validity or invalidity of Predictions 1 and 1A. Nothing like this was done in any other pecking experiment of this series.

Results: Experiment 1

TABLE 1

Colour			Percentage preference		
Better	Worse		Found	Prediction 1	Prediction 1A
Blue	Red	P1	54.6		
Red	Green	P2	74.0		
Blue	Green	P3	77.5	76.4	77.3

Experiment 2

Stimuli: The stimuli were hemispheres as above, but painted "Orange", Blue and Green. The blue and green are the same Priosin colours as in Experiment 1, but the orange is a mixture of Priosin Orange and Yellow.

Special remarks: Note the mildly surprising fact that although Blue is preferred to "Red", and also to Yellow as was shown in another experiment not of the present series, "Orange", a mixture of the same "Red" and Yellow, is preferred to Blue.

Results: Experiment 2

TABLE 2

Colour			Percentage preference		
Better	Worse		Found	Prediction 1	Prediction 1A
Orange	Blue	P_1	76.0		
Blue	Green	P_2	65.0		
Orange	Green	P_3	83.5	83.2	85.3

Experiment 3

Stimuli: The same kind of hemispheres were used, but

painted "Orange" (as for Experiment 2), "Red" (as for Experiment 1), and Green (as for both other experiments).

Results: Experiment 3

TABLE 3

Stimuli			Percentage preference		
Better	Worse		Found	Prediction 1	Prediction 1A
Orange	Red	P_1	61.1		
Red	Green	P_2	80.2		
Orange	Green	P_3	84.7	84.6	86.4

Experiment 4

Stimuli: These were a Blue hemisphere and a "Red" hemisphere the same as for Experiment 1, and a flat "Red" disc of the same diameter.

Special remarks: This experiment and the 3 which follow it can have a special interpretation different from that of Prediction 1. This will be discussed in Chapter 7.

Results: Experiment 4

TABLE 4

Stimuli			Percentage preference		
Better	Worse		Found	Prediction 1	Prediction 1A
Blue solid	Red solid	P_1	69.9		
Red solid	Red flat	P_2	85.9		
Blue solid	Red flat	P_3	91.0	91.6	93.5

Experiment 5

Stimuli: As for Experiment 4.

Special remarks: As for experiment 4. This experiment and Experiment 6 differ from Experiment 4 only in that they were performed on different batches of chicks, and were done at different times.

Results: Experiment 5

TABLE 5

Stimuli			Percentage preference		
Better	Worse		Found	Prediction 1	Prediction 1A
Blue solid	Red solid	P_1	75.4		
Red solid	Red flat	P_2	82.3		
Blue solid	Red flat	P_3	88.6	91.2	93.4

Experiment 6

Stimuli and special remarks: As for Experiments 4 and 5.

Results: Experiment 6

TABLE 6

Stimuli			Percentage preference		
Better	Worse		Found	Prediction 1	Prediction 1A
Blue solid	Red solid	P_1	78.7		
Red solid	Red flat	P_2	83.8		
Blue solid	Red flat	P_3	90.3	93.1	95.0

Experiment 7

Stimuli: A hemisphereof the usual type painted light grey; a photograph of a hemisphere of the same size, taken in directed light, oriented with the lighter side uppermost; and a photograph of a flat disc. (See Appendix 2.)

Special remarks: As for Experiment 4

Results: Experiment 7

TABLE 7

Stimuli			Percentage preferences		
Better	Worse		Found	Prediction 1	Prediction 1A
Grey solid	Photo solid	P_1	70.8		
Photo solid	Photo flat	P_2	70.5		
Grey solid	Photo flat	P_3	86.0	82.8	85.3

Experiment 8

Stimuli: All were hemispheres of the same type as in other experiments. They were painted 3 different shades of blue, Pricsin "Prussian Blue" (very dark), "Light Blue" (a bright sky blue), and "Pottery Blue" (a very pale blue). These will be called respectively, Dark, Medium and Light.

Special remarks: In this and another experiment using these stimuli, which had to be rejected since it did not meet the significance criterion, there were very strong indications of a real "non-conformity" in the preference order of different chicks for these 3 stimuli. To some extent the same thing was shown in this experiment (Experiment 8) but it just reached the necessary significance criterion, and therefore could not be rejected.

Results: Experiment 8

TABLE 8

Stimuli			Percentage preferences		
Better	Worse		Found	Prediction 1	Prediction 1A
Medium	Light	P_1	81.5		
Light	Dark	P_2	67.9		
Medium	Dark	P_3	68.7	88.0	90.3

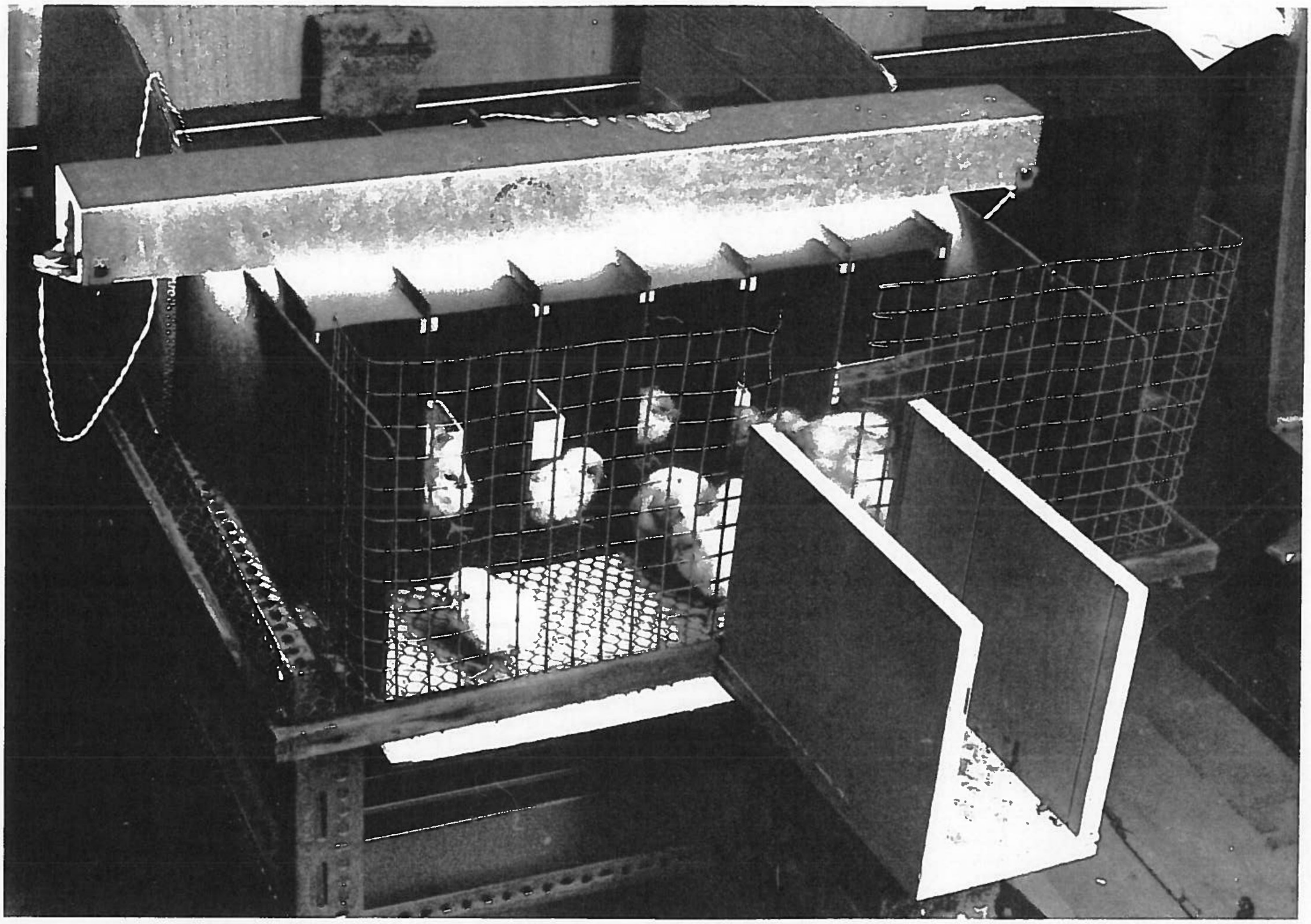
2. EXPERIMENTS WITH DOMESTIC CHICKS, USING LEARNED PREFERENCES IN AN APPROACH RESPONSE

Subjects The same source of chicks was used as for the pecking experiments.

Apparatus and Experimental procedures Two types of apparatus were used. Earlier experiments were done with a crude Y-maze, before this was superseded by the much more efficient coloured-light apparatus.

The Y-maze This was made by placing cardboard boxes on a flat table in such a way that they enclosed a Y-shaped area. The stem of the "Y" consisted of a wooden box with a sliding door - the "start box". At the end of each arm of the "Y" was a small round plastic dish, 6 cms. in diameter and 2 cms. deep. Dishes of different colours were used, one red, one green, and one yellow.

Only one chick was used. The experiment consisted of two phases, the training phase and the testing phase. The object of the preliminary training phase was not to measure anything, but simply to establish in the animal a preference for the red dish over the yellow one, and the yellow one over the green one. The animal was given a large number of trials in quick succession. For each trial it was placed hungry in the start box, and then the sliding door was raised thereby allowing it to walk out into one of the arms of the maze, and eat if it chose the right one, since one of the dishes always contained food and the other one was empty. Only 2 combinations of colours were used in the training phase: Red with Yellow, Red containing food,



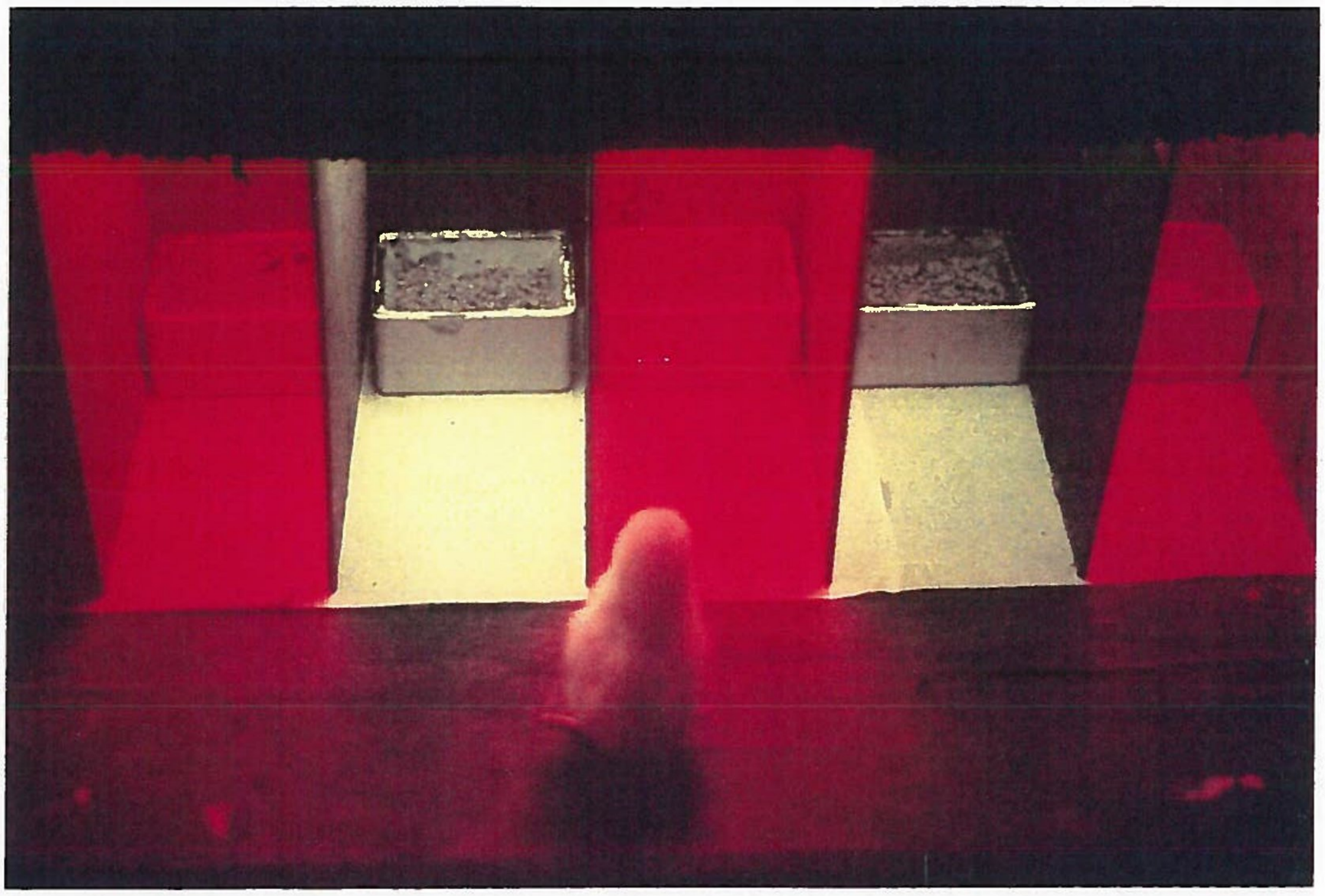
Coloured light apparatus: training situation.
In this picture the chicks have access to only one half of the apparatus.

and Yellow with Green, Yellow containing food. Thus it was hoped that this training procedure would build into the chick the preference order Red; Yellow; Green. The training phase ended and the testing phase began when the animal seemed to have learned both preferences reasonably well, but was still making some mistakes.

In the testing phase, all three possible colour pairs, Red-Yellow, Yellow-Green, and Red-Green, were presented (left/right positions being randomly varied, as they were in the training phase). Reward was administered as before, but in addition the choice of Red was rewarded when it was presented with Green. A total of 90 testing trials was given, 30 with each colour combination.

The coloured-light apparatus The chicks, many at a time, had free access to 12 cubicles, 6 on each side of a central partition, each 9.5 cms wide by 20 cms long by 24.5 cms high. At the end of each cubicle was a rectangular glass dish, painted white, 9 cms by 7 cms by 4.5 cms deep. Half the dishes contained food, and the other half, alternating with the full ones, were empty. Light was provided by a single 30 w fluorescent tube lying along the length of the row of cubicles. Before entering the cubicles the light had to pass through coloured filters, made by painting clear perspex rectangles, 19.5 cms by 9.5 cms. The filters were supported above the cubicles in such a way that they were easily detachable and interchangeable.

The training method was simply to leave the chicks for a few days in these conditions, deliberately placing food under certain



Coloured light apparatus: testing situation.

coloured filters, (the positions of which were changed round at intervals), thereby "rewarding" choice of certain colours. Water was available elsewhere in the area.

Many of the chicks fed very successfully in this apparatus, though regrettably there was a high mortality. At the end of the training period, the colour preferences of the chicks as shown in the approach response in the apparatus were tested as follows.

A wooden start box with two vertically sliding doors, one opaque and the other of transparent perspex was placed against a gap in the wall of the training apparatus, so that the sliding doors faced the middle of the row of cubicles on one side of the apparatus. Between 12 and 24 hours before the start of testing the chicks were removed from the apparatus and kept without food or water in another cage. They were tested individually. Each chick in its turn was placed in the start box, the opaque door was lifted and it was allowed 5 seconds to look through the perspex door before that too was raised and it was released into the apparatus proper. All six of the cubicles facing the chick had coloured filters over them and all contained dishes.

When the perspex door was lifted the chick was free to enter any of the cubicles. This it usually did within a few seconds. In the experiments in which reward was used during the test each chick was allowed to eat for about two seconds if it chose a rewarding cubicle. If it made a wrong decision it was not allowed to correct

its mistake, i.e. it was removed before it could leave the cubicle and enter another one. A "decision" was considered to have been made when the chick put any part of one foot on the slightly raised floor of a cubicle. The latency of such decisions was measured. If a decision was not made within 2 minutes the trial was abandoned. Normally each chick was tested only a few times, and large numbers of chicks were tested in any one experiment.

Surprisingly the method proved extremely effective, and it is strongly recommended as a quick and trouble-free way of training chicks when the detailed course of learning is not in itself of interest to the experimenter. The most surprising and fortunate fact is that chicks showed no tendency to develop position preferences - colour seemed to be a much more important "cue" than position. As a matter of form the positions in the row of cubicles where food was to be found were changed around at frequent intervals during training, and of course during testing when it mi_ht have been really important colour-position was systematically varied, in a strict way. However, I am inclined to think that in fact this precaution was unnecessary.

Another fact which emerged from other experiments using this apparatus not reported here, (joint work with Dr. Monica Impekoven) is that colour seems also to be a more important cue than brightness. To the human eye, the red filters used here let through much more light than the blue ones, and this was confirmed with a light meter . If chicks trained on these filters were tested under the opposite conditions,

with red dimmer than blue (both to the human eye and to the light meter), they showed the same preferences as usual, apparently just as strongly. Conversely when tested with white filters letting through different amounts of light all chicks, however trained, showed a slight preference for the brighter light (Pletnjev, 1937).

Two batches of chicks were trained and tested in this apparatus. In both cases the preference order established in the chicks and used in the test of Prediction 1 was Blue over Green over Red. The paints with which filters were coloured were not the same as those used for painting the pecking stimuli. They were Robbialac Emulsion Paints, and the trade names of the colours were respectively Gentian, Evergreen, and Fiesta Red. The methods of training and testing in the two experiments were slightly different from each other, and will therefore be considered separately.

The testing of Prediction 1 was not the only object of these experiments. The secondary purposes are not relevant here and will not be discussed, but their existence is mentioned in order to explain the slight differences in design between the experiments, which might otherwise be rather puzzling.

1st Experiment: Training The chicks after having been used for pecking experiments on days 2 and 3 of their lives, were placed in the apparatus on day 5, and kept there till day 9 or 10 when they were tested. During the training period they could obtain food only by going into cubicles, 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 rewarded. The positions of the colours and food were changed throughout the training period, usually twice a day, so that the chicks had plenty of experience on both sides of the apparatus of all three colour combinations, which were as follows:

Blue with Green, Blue rewarded.

Green with Red, Green rewarded.

Blue with Red, Blue rewarded.

There was no need to give exactly controlled amounts of experience with all the colour combinations since the object of the training was simply to build into the chicks colour preferences, and a tendency to approach the cubicles when hungry.

Testing Fifty chicks were tested, 20 on day 9 and 30 on day 10, respectively 4 and 5 days after the beginning of training. Each chick received all three colour combinations twice, once with each left-right positional arrangement, and they were rewarded for choosing correctly in each case. Five (or on the 2nd day 10) chicks in succession were each given one trial with one colour combination in one position. Then they were each given, in the same order, another colour combination, also in one positional arrangement, and then the third colour combination. They then received the second colour pair again, this time in reversed position, then the third and then the first, also in reversed position. That was the end of the testing of that particular group of 5 (or 10) chicks. Another such group of 5 (or 10) were then treated

in the same way except that the order in which they received the three colour pairs was different. On the first day 4 groups of 5 were tested in this way, and on the second day 3 groups of 10. For each of the three colour combinations therefore 100 separate choices were recorded, since in all of the 300 trials a definite choice was made within the two minute time limit. The number of correct choices out of this 100 in each case then is the P value to be substituted in the formula of Prediction 1.

2nd Experiment: Training In the second experiment using this apparatus to test Prediction 1, the chicks had experienced during most of the training period, only one of the three colour combinations to be used in the final test, namely Blue with Red, Blue being rewarded. It was hoped that generalisation, (transposition along the spectrum) would provide the other two preferences, Blue over Green, and Green over Red. The training period was 2 weeks from day 2, during which time the chicks were used in other tests not directly relevant here. One of the things which emerged from these earlier tests was that the chicks would indeed generalise in the expected way - along the spectrum (Honig, 1962). It also appeared that the learning was so thorough that the chicks made hardly any mistakes especially in the two choice tests involving blue. For Prediction 1 to be tested in a worthwhile way, the preferences must be less than 100%. It was therefore necessary to try to increase the number of "mistakes" by, in the terms of the Threshold Model, reducing the distance between the threshold lines.

Accordingly, on the evening of Day 16, 2 days before testing, the dishes in all the cubicles were filled with food, and all three colours were distributed evenly over both rows of cubicles.

Thus the chicks would now be rewarded for entering cubicles other than blue ones. I hoped that this procedure would reduce the strength of the preferences while keeping the preference rank order the same, namely Blue over Green over Red./ As an incidental observation, I noticed next morning that considerably more of the food had been eaten from the blue cubicles than from either the green ones or the red ones.

This did indeed happen.

Testing The 36 chicks/were tested on Day 18. Each chick received 6 trials in quick succession, with the same colour combination, in the same left-right positional arrangement. It was then not tested again. Twelve (one third) of the chicks received each of the three choice tests, each left-right arrangement being seen by 6 chicks. There were therefore 216 trials in all. There was no reward. Contrary to expectation - investigating this was the other purpose of the experiment - there was no reduction in responsiveness over the 6 trials, as measured by latency. Indeed the only significant latency effect that was shown, indicating a "warm-up" effect, was that the latency of the first trial was significantly greater than those of all the others. There was no tendency for latency to increase over the successive ("extinction") trials.

Out of the 72 trials with each colour combination, (in

some cases slightly fewer than 72, as not all the chicks responded within the 2 minute time limit), the proportion of choices of the "correct" colour is the P value used for testing Prediction 1.

Results: The training experiments

Experiment 9: The "Y-maze" experiment

Table 9a gives the actual numbers of choices of the rewarded colour out of the 30 test trials with each colour combination. It also gives the numbers of choices for Red when presented with Green predicted by the two models. Table 9b gives the same information but in percentage form to be more directly comparable with other experiments.

TABLE 9a

Stimuli		Nos. of "correct" choices		
Better	Worse	Found	Prediction 1	Prediction 1A
Red	Yellow	26		
Yellow	Green	24		
Red	Green	29	28.4	28.9

TABLE 9b

Stimuli			Percentage preferences		
Better	Worse		Found	Prediction 1	Prediction 1A
Red	Yellow	P_1	86.7		
Yellow	Green	P_2	86.0		
Red	Green	P_3	96.7	94.4	96.3

Experiment 10: (The first coloured-light experiment)

Table 10 shows the percentage preferences, found and

predicted, in the same way as in earlier experiments. In this case, since there were exactly 100 choices per colour pair, the same figures can be read as the absolute numbers of choices.

TABLE 10

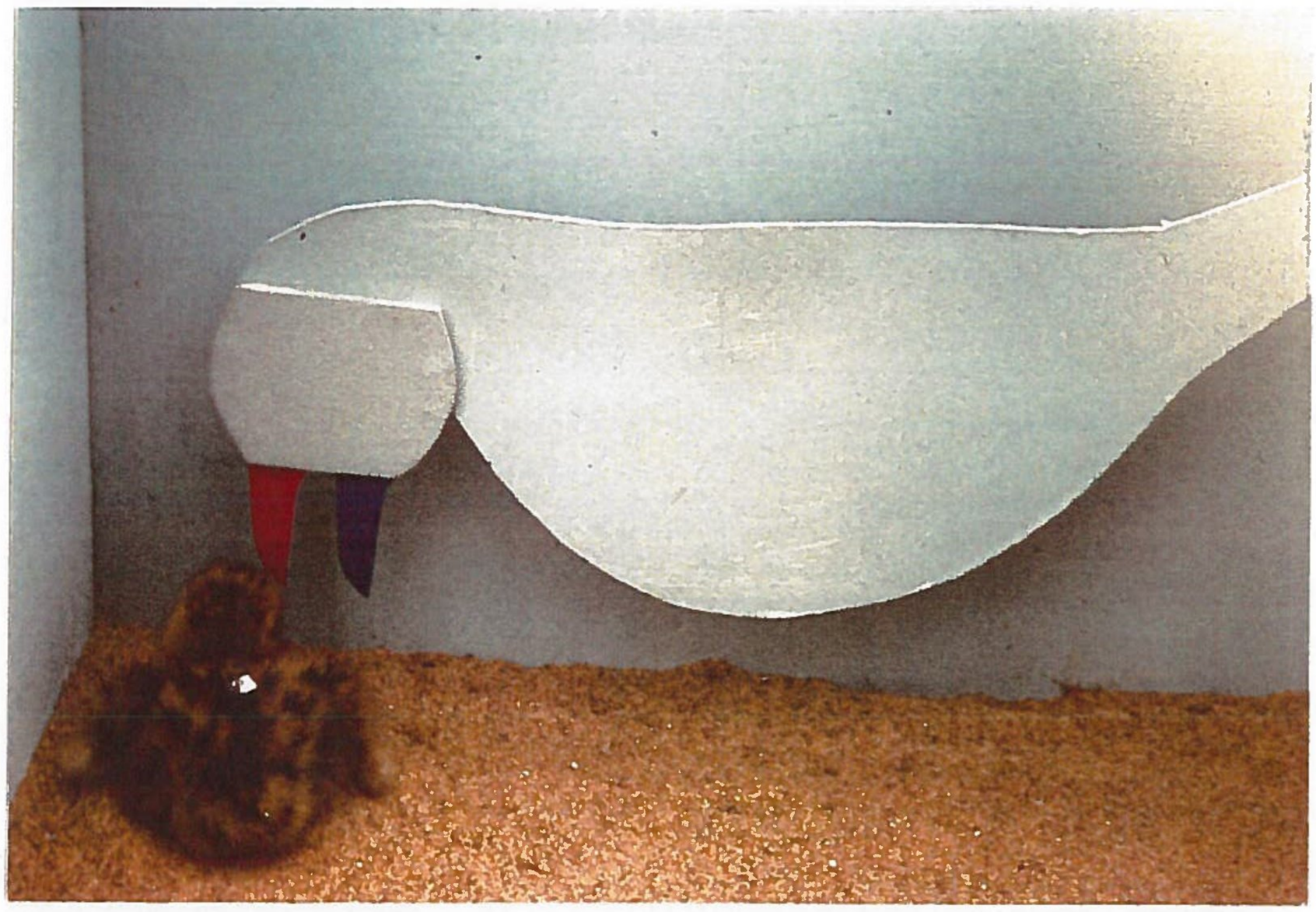
Stimuli			Percentage preferences (Or nos. of "correct" choices)		
Better	Worse		Found	Prediction 1	Prediction 1A
Blue	Green	P_1	81		
Green	Red	P_2	75		
Blue	Red	P_3	88	90.6	92.7

Experiment 11: (The second coloured-light experiment)

Since a few chicks did not respond within the 2 minute time limit, it is not convenient to present the absolute numbers of correct choices - there is no common denominator. Table 11 gives the results in percentages in the usual way.

TABLE 11

Stimuli			Percentage preferences		
Better	Worse		Found	Prediction 1	Prediction 1A
Blue	Green	P_1	84.2		
Green	Red	P_2	61.2		
Blue	Red	P_3	89.3	87.0	89.4



Black-headed gull chick pecking situation
(M.Impekoven).

DR. M. IMPEKOVEN'S EXPERIMENTS ON PECKING AND APPROACH COLOUR PREFERENCES IN THE BLACK-HEADED GULL CHICK: (Larus ridibundus)

This work is not yet published, and the following account is based on a manuscript by Dr. Impekoven. I have made extensive use of her data on pecking preferences, since for some of my purposes it is more useful than my own.

Methods

1. Pecking tests

An approximately life-size, moving, flat, grey model of an adult gull was presented to the chicks individually against a grey background. It had two "bills" attached to its "head", one posterior to the other of different colours (see photograph). Each chick was placed singly in front of the "head" and the number of pecks at each of the "bills" in a half minute test period counted. (This arrangement with a whole model gull, which is not important for the present purpose, was for the purpose of more direct comparison between these pecking tests, and the approach tests to be described.)

Six different Ostwald "colours" (including Black and White), were presented in all possible pair combinations, controls against position biases of course being made. Many chicks were tested with each colour pair, and most of the chicks gave many pecks in the half minute period, suggesting that they may be better subjects for this kind of work than domestic chicks though they are of course less readily available.

2. Approach tests

The experimental situation was a Y-shaped choice apparatus in which the individual chicks were required to approach one of two model gulls, similar to the one described above but differing in colour. These models were coloured in a uniform way, and they had only one "bill" each. They were moved uniformly back and forth. Each chick was placed 45 cms away from the models, and was given a maximum of 10 minutes in which to make its choice, which consisted of approaching one of the models close enough to touch it.

Chicks given two different treatments were tested (this was the main object of the experiment). These do not concern us here, but they must be considered separately since they had different colour preferences. This is a very interesting finding in itself, (see Impekoven in prep.), but since the precise nature of the treatments is not relevant to the present discussion I shall refer to them simply as Treatment 1 and Treatment 2. The method of testing was the same in both cases.

Treatment of data and results

Pecking

Of the 15 pair preferences measured, one did not meet the significance criterion, and had to be rejected. (This made little difference to the overall result.)

The 14 percentage preferences were combined into the 16 possible triplets, and the predictions of the two models calculated

for each in the same way as for the domestic chick. The results are summarised in Table 12. The Table is arranged in a different way from those above. In the left had column the 3 colours entering into each triplet are represented by initial letters with the most preferred one on the left, and the least preferred one on the right. The symbols used are: (The 'colours" are preferred in this order.)

B Blue

R Red

Y Yellow

G Green

D Black (stands for Dark)

W White

Approach

As explained above, it is necessary to divide these results up into two groups, according to the different treatments of the chicks.

The same 6 "colours" were used as for the pecking tests, and they were combined in all possible ways. However of the 15 preferences so obtained with each treatment a number did not reach the significance criterion, and had to be rejected. This left 7 triplets with one treatment, and only two with the other. The number of choices entering into each percentage preference is not large, and therefore the results from the individual triplets will not be given. Table 13 gives the mean observed ahd predicted P_3s for both treatments.

TABLE 12

Triplet	P_1	P_2	P_3	Prediction 1	Prediction 1A
BRG	60.2	80.8	82.9	84.8	86.5
BRD	60.2	84.5	88.1	87.6	89.1
BRW	60.2	97.5	97.4	98.0	98.3
BYG	73.3	69.6	82.9	83.8	86.3
BYD	73.3	76.3	88.1	87.4	89.9
BYW	73.3	94.9	97.4	97.2	98.0
BGD	82.9	62.5	88.1	87.2	89.0
BGW	82.9	94.3	97.4	98.0	98.7
BDW	88.1	94.6	97.4	98.8	99.3
RGD	80.8	62.5	84.5	85.4	87.5
RGW	80.8	94.3	97.5	97.8	98.6
RDW	84.5	94.6	97.5	98.4	99.0
YGD	69.6	62.5	76.3	77.2	79.2
YGW	69.6	94.3	94.9	96.6	97.5
YDW	76.3	94.6	94.9	97.4	98.2
GDW	62.5	94.6	94.3	96.0	96.7
Mean			91.3	92.0	93.2

TABLE 13

		P_3	
Treatment	Found	Prediction 1	Prediction 1A
1	95.0	97.5	98.2
2	100.0	95.3	97.7

DR. J. KEAR'S EXPERIMENTS ON PECKING PREFERENCES IN YOUNG BIRDS

Details of the method and results are given in Kear (1964). Young birds of many different species were tested. The birds were placed, in pairs, in choice boxes in which they were presented with 3 pairs of coloured spots at different levels on a vertical surface. In any one test only 2 colours were presented: all the spots on the left were of one colour, and all the spots on the right were of the other colour. Thus the arrangement was essentially similar to my own for the domestic chick, except that each pair of stimuli was replicated 3 times. Only the first peck in each test was counted.

Each pair of birds received each of the 15 possible pair combinations of the 6 colours used, 4 times, making a total of 60 presentations for each pair of birds. Of the many species tested, the following met the criterion for acceptance, of at least 10 responses per percentage perference:

mallard, Anas platyrhynchos; carolina duck, Aix sponsa; emperor goose, Anser canagicus; herring gull, Larus argentatus; lesser black-backed gull, Larus fuscus; moorhen, Gallinula chloropus; and coot, Fulica atra.

The number of figures entering into each percentage preference is not large, and therefore I will not present long lists of individual triplets, but instead will simply give the mean observed and predicted P_3s for each species.

TABLE 14

Species	Found	P_3 Prediction 1	Prediction 1A
mallard	96.5	94.7	96.1
carolina duck	94.7	100.0	100.0
emperor goose	96.3	95.7	97.0
herring gull	88.6	89.3	91.3
lesser black backed gull	97.2	90.3	92.2
moorhen	94.8	94.1	95.6
coot	93.7	93.7	95.4

DR. W. R. A. MUNTZ'S EXPERIMENTS ON FROG COLOUR PREFERENCES

Details of method are given in Muntz 1962 and Muntz 1964.

Adult Rana temporaria were placed singly in a choice box from which they jumped through one of two windows illuminated with light of different colours. Seven "colours" including "darkness" were presented in all 21 possible pair combinations. Each of the 8 frogs received each of the 21 combinations twice, once in each left/right arrangement. Thus a total of 16 choices was recorded for each of the 21 pairs of colours. Table 15 gives the mean results, from the triplets which met the significance criterion.

TABLE 15

		P_3	
	Found	Prediction 1	Prediction 1A
Mean	97.5	93.7	95.4

DR. C. J. C. REES'S EXPERIMENTS ON HUMIDITY PREFERENCES IN THE BEETLE PHYLLOBIUS

This account is based on an unpublished manuscript of Dr. Rees.

The subjects were beetles of the nettle-eating species Phyllobius urticae. The apparatus was a form of Y "maze" - a bifurcated tube, made of glass covered with light-proof material. Air streams of different carefully controlled humidities were drawn through the arms of the "maze" into the stem, so that at the choice point the two arms of the "maze" differed according to the humidity of the air stream coming from them.

If left in complete darkness in the apparatus the insects tended to remain where they were placed, in the stem of the "maze", and lights of equal intensity were therefore shone at the far ehds of both arms of the maze to attract them.

Each beetle was placed individually in the stem of the "maze" and left there for 10 minutes, after which the experimenter recorded in which of the arms it was. Some individuals still remained in the stem. This was recorded as "no choice".

There were 7 different humidities, and they were combined in all possible pair combinations. There was a maximum of 24 choices for each of the 21 pair combinations, but in practice a few insects usually made no choice. (I did not consider those cases where each humidity was paired with itself.) For each pair combination

a percentage preference is worked out as the number of choices of the preferred humidity divided by the total number of choices (x 100). Those percentages which meet the significance criterion are combined in triplets in the usual way, and means of Observed P_3 compared with the means of the two predictions are given in Table 16.

TABLE 16

P_3		
Found	Prediction 1	Prediction 1A
88.6	88.4	90.7

DISCUSSION OF TESTS OF PREDICTION 1

1. Domestic chick

Eleven experiments were done, eight on pecking preferences, and three on learned preferences in an approach situation. Table 17 summarises the results: the left hand column shows the mean observed P_3 for each experiment, and the other two columns the predictions of the two models calculated from the observed P_1s and P_2s.

TABLE 17

P_3s from all chick tests, Found and Predicted

Experiment	Found	Prediction 1	Prediction 1A
1	77.5	76.4	77.3
2	83.5	83.2	85.3
3	84.7	84.6	86.4
4	91.0	91.6	93.5
5	88.6	91.2	93.4
6	90.3	93.1	95.0
7	86.0	82.8	85.3
8	68.7	88.0	90.3
9	96.7	94.4	96.3
10	88.0	90.6	92.7
11	89.3	87.0	89.4

In ten out of the eleven experiments the two predictions come rather close to the observed P_3s. Whether it is possible to say that one of the predictions is better than the other will be considered

later. First the one anomolous result must be discussed:

An exceptional result

In Experiment 8 both Prediction 1 and Prediction 1A strongly overestimate: P_3 is not noticeably larger than P_1 and P_2 and is indeed smaller than one of them. This result not only is surprising from the point of view of the Threshold Model and the Set Releasing Value Model. It seems, at least on a naive level, to go against "common sense", in that it violates the principle of "Strong Stochastic Transitivity". Another experiment using exactly the same stimuli failed by a long way to reach the significance criterion and is not included in the table results. It showed a precisely similar departure from "Strong Stochastic Transitivity". These two experiments differed from others on pecking preferences only in the stimuli presented, which suggests that the exceptional results may be connected with the stimuli, or with how they differ from each other.

Experiment 8 was designed as a crude test of brightness preferences. No elaborate precautions were taken to eliminate the possibility of the chicks using other cues such as colour, but the three stimuli were chosen so that to the human eye the most prominent difference between them was one of brightness. It is possible that violation of Strong Transitivity is a peculiar property of brightness discriminations, which would fit with Coombs's (1958, 1964) finding of a similar departure from Strong Transitivity in human subjects under some circumstances when given choices between different shades of grey.

Coombs offers an explanation for this "inconsistency" which is impressive in that it makes correct predictions about circumstances when Strong Transitivity should and should not be found. The circumstances of Experiment 8 might indeed be of the latter kind, and it is possible that Coombs's explanation could be used to account for the Experiment 8 result. If so it would represent a special case of violation of the assumption of Constancy of Preference Rank Order, necessary for the deduction of Prediction 1 from the Threshold Model.

It may well be then that Experiment 8 ought to have been eliminated from consideration on grounds of non-constancy of preference rank order. However, it technically cannot be rejected since the objective criterion/significance is achieved, and it must be considered along with all the other experiments in the general discussion of the success of Prediction 1.

Conclusion : Domestic chick

Taking the results as a whole then, both Prediction 1 and Prediction 1A come fairly close to the observed P_3s. The departure of Prediction 1 from observed is somewhat smaller that that of Prediction 1A, but the difference is not significant. What is significant however is the fact that Prediction 1A is consistently higher than the observed P_3. (0.05, 2 tailed Wilcoxon test.) Prediction 1 shows no tendency to be consistently larger or smaller than the observed P_3.

Thus despite the fact that Prediction 1A is bound to give closely similar results to Prediction 1, the experimental tests have

proved sufficiently sensitive to show that one differs significantly, though admittedly only just, from the observed facts, while the other does not. As far as the domestic chick is concerned, we may tentatively reject Prediction 1A, and conclude that Prediction 1 cannot be rejected, and indeed seems to fit the facts as well as could possibly be hoped.

2. Other species

In all the other species considered, the individual stimulus triplets are not independent of each other: any given percentage preference result enters into several different triplets. It is therefore not possible to perform statistical tests in the same way as was done for the domestic chick. We cannot then with these species decide very clearly in favour of one of the two models in preference to the other, but we can obtain some idea of whether the two models come at all close to predicting the observed facts.

Of these other experiments, those on pecking in the black-headed gull chick (Impekoven) provide the most data for any one species. Those on the approach response of this species contain rather few results owing to the data rejection procedure, and are perhaps better not taken too seriously. Neither of them provide any grounds for rejecting either of the two predictions. In the case of the pecking experiments, although technically we cannot use a statistical test to reject Prediction 1A, it is a fact that this prediction overestimates in all fifteen triplets. Prediction 1 overestimates in eleven of them, but nevertheless it does seem to come remarkably cose to the observed P_3 in most of them.

Dr. Kear's experiments give no cause to reject either of the two predictions. Once again Prediction 1 seems to give a slightly better fit than Prediction 1A.

Prediction 1A on the other hand is closer to the observed P_3 than Prediction 1 in the case of Dr. Muntz's Frog experiment. This possibly might indicate that this animal is different from birds in this respect, but before this intriguing possibility can be taken seriously of course, much more evidence will be needed.

In the beetle case (Rees), Prediction 1 gives a very close fit to the observed P_3, but here again of course it is not possible to draw any firm conclusions with regard to the relative merits of the two predictions.

Figure 3

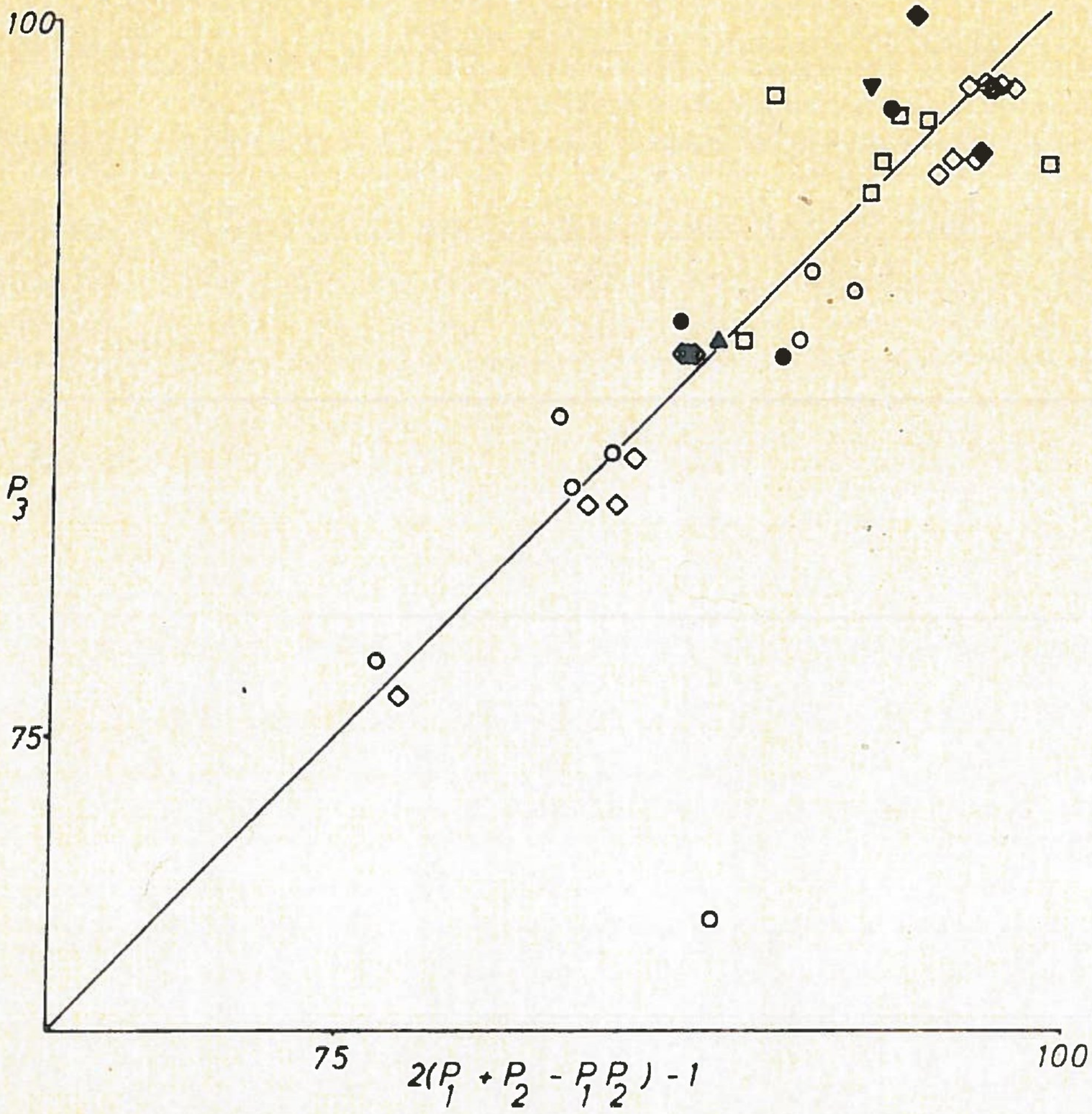
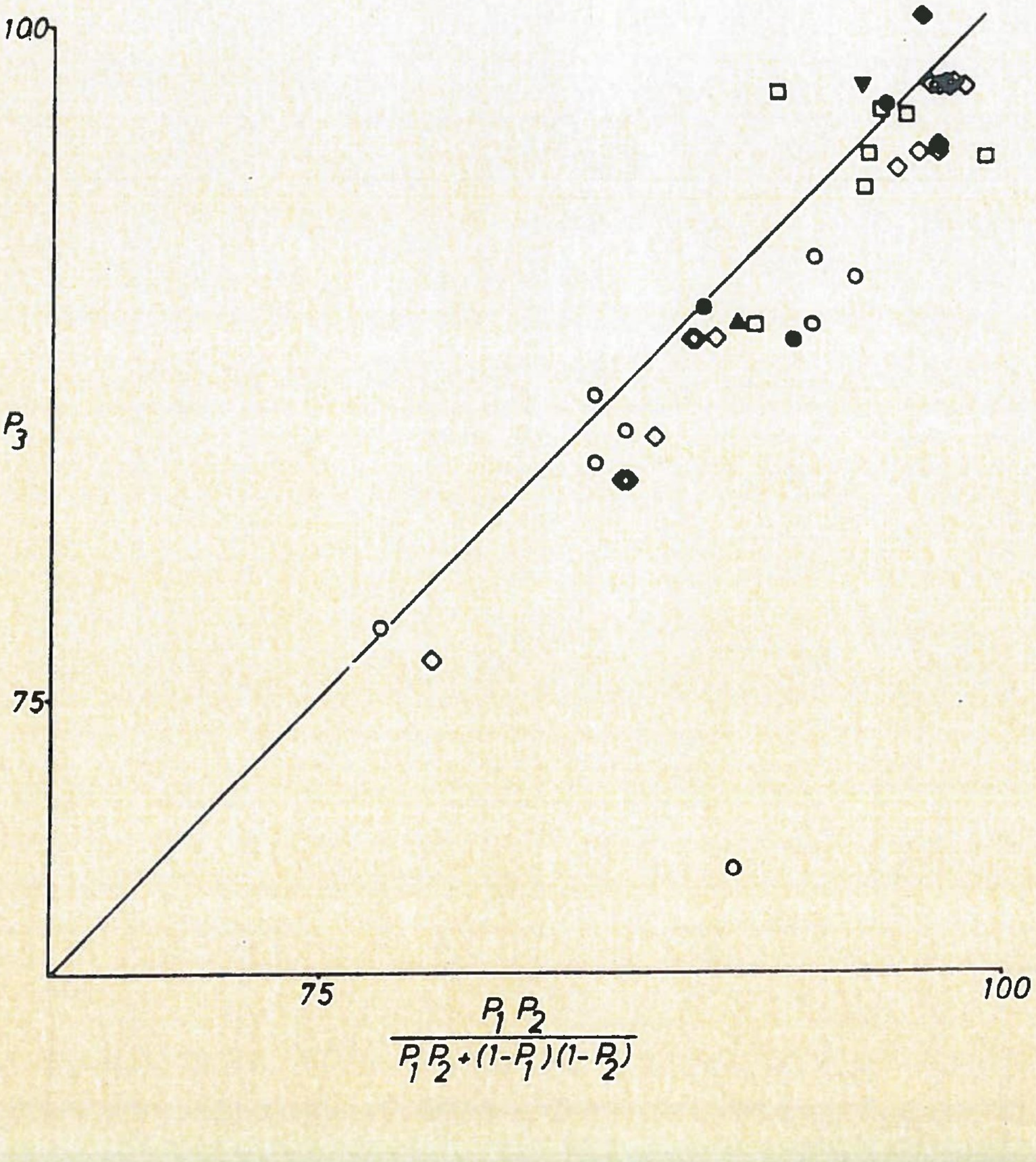


Figure 4



Key to Figures 3 and 4

○ Domestic chick pecking

● " " approach

◇ Black-headed gull chick pecking (Impekoven)

◆ " " " " approach "

□ Various young birds pecking (Kear)

▼ Frog (Muntz)

▲ Phyllobius Beetle (Rees)

CONCLUSION:

Results from 11 species have been discussed. Figures 3 & 4 show scatter diagrams of observed against predicted P_3s for the two models. The data used are those from Tables 12 to 17. If the predictions were perfectly fulfilled, all the points should lie along the 45 degree lines drawn on the respective graphs.

In nearly all the species, both predictions were reasonably successful. In three of the species, mallard, lesser black-backed gull and frog, Prediction 1A was better. In seven of the species, Prediction 1 was more successful. (In the carolina duck case they were equal at 100%.) In the only two species where a substantial number of data could be used, the domestic chick and the black-headed gull it is possible to say with some confidence that Prediction 1 is more successful. In the only species where tests of significance are possible, the domestic chick, Prediction 1A is actually significantly disproved, while Prediction 1 shows no consistent tendency to err on either side of the observed figure.

Though for the latter two species the case in favour of Prediction 1 rather than Prediction 1A seems quite strong, it is by no means certain for the other nine species. Further-more, it should be remembered that the conditions of testing may have been biased in favour of the Threshold Model. The rule about rejecting non-significant preferences was necessary for the Threshold Model, but not for the Set Releasing Value Model, but in the present account the same selected

data were used for testing both predictions. In this particular case it makes hardly any difference to the relative success of the two models: if non-significant preferences are used, there is a marginal shift in favour of Prediction 1A in two of the species, coot and herring gull. However if one were to attempt a full scale comparison between the Threshold Model and one of the other published models, say that of Luce, one should in fairness look carefully into the effects of the rule about rejecting non-significant preferences, and also see whether the other models required some similar selection of data. For example, Luce's model strictly requires to be tested on data from single individuals rather than the pooled data from several individuals.

One thing which the experimental results seem to show is that in practice the anticipated effect of the inclusion of non-significant preferences was overestimated. Prediction 1 seems to be well fulfilled whether or not they are rejected. This might mean that statistical significance is a bad criterion for identifying "non-conformity" of threshold rank order (see for example the discussion of Experiment 8), and indeed it is obvious that it must be a bad one in those cases where Threshold Lines are very close together. For this reason, and for the sake of fair comparison between the Threshold Model and other models, it might be better if future tests of Prediction 1/were to abandon the rejection of non-significant preferences, unless there is clear evidence of definite variation in preference rank order.

Of these experiments only those on pecking preferences in domestic and black-headed gull chicks are to be discussed in the remainder of this thesis. Thus the success of Prediction 1 with the other nine species is not vital to the arguments to follow. We can however take encouragement from the results using these nine species, for they indicate that the theory with which we are dealing may have very wide applicability.

CHAPTER 3 : THE "GO/NO GO" DECISION-MAKING MECHANISM

DEDUCTION OF PREDICTIONS 2, 3, 4, 5, and 6

INTRODUCTION

In Chapter 1 the possibility was mentioned that the process by which a chick "decides" to peck might be quite distinct from the process by which it decides which of the alternative stimuli to peck at. A separate "Go/No go" decision-making mechanism was suggested, determining the precise moments of time when the decisions of the "Directing decision-maker", perhaps an analogue of the Threshold Model, are put into effect. In Chapter 1, no reasons were given for supposing that such a separation of mechanisms did exist, but the formal possibility was raised. In the next three chapters, support for the separation, and evidence on the functional connections between the two proposed mechanisms will be given.

Before the experimental evidence is discussed, there are three preliminary reasons why it is convenient to postulate a separate "Go/No go" decision-making mechanism:

a. Pecks are discrete units of activity, while Variable X is regarded as a continuously fluctuating variable. The deduction of Prediction 1 assumes that the number of pecks given to a stimulus is some function of the time spent by Variable X above its threshold. Somehow "time spent" must be translated into "number of discrete pecks". Some kind of "pulse generator" must therefore be postulated.*(see next page)

b. If the decision about when to peck were entirely under the

control of the Threshold Model Analogue, one would suppose that the first peck of any new bout would have to be directed at the preferred stimulus, since Variable X would have to cross the lower threshold before it could reach the higher one. This is certainly not the case. It would of course be possible to explain this by making other kinds of assumption, for example about the "slope" of the Variable X graph. However the postulation of a separate "Go/No go" decision-maker is an adequate and economical solution.

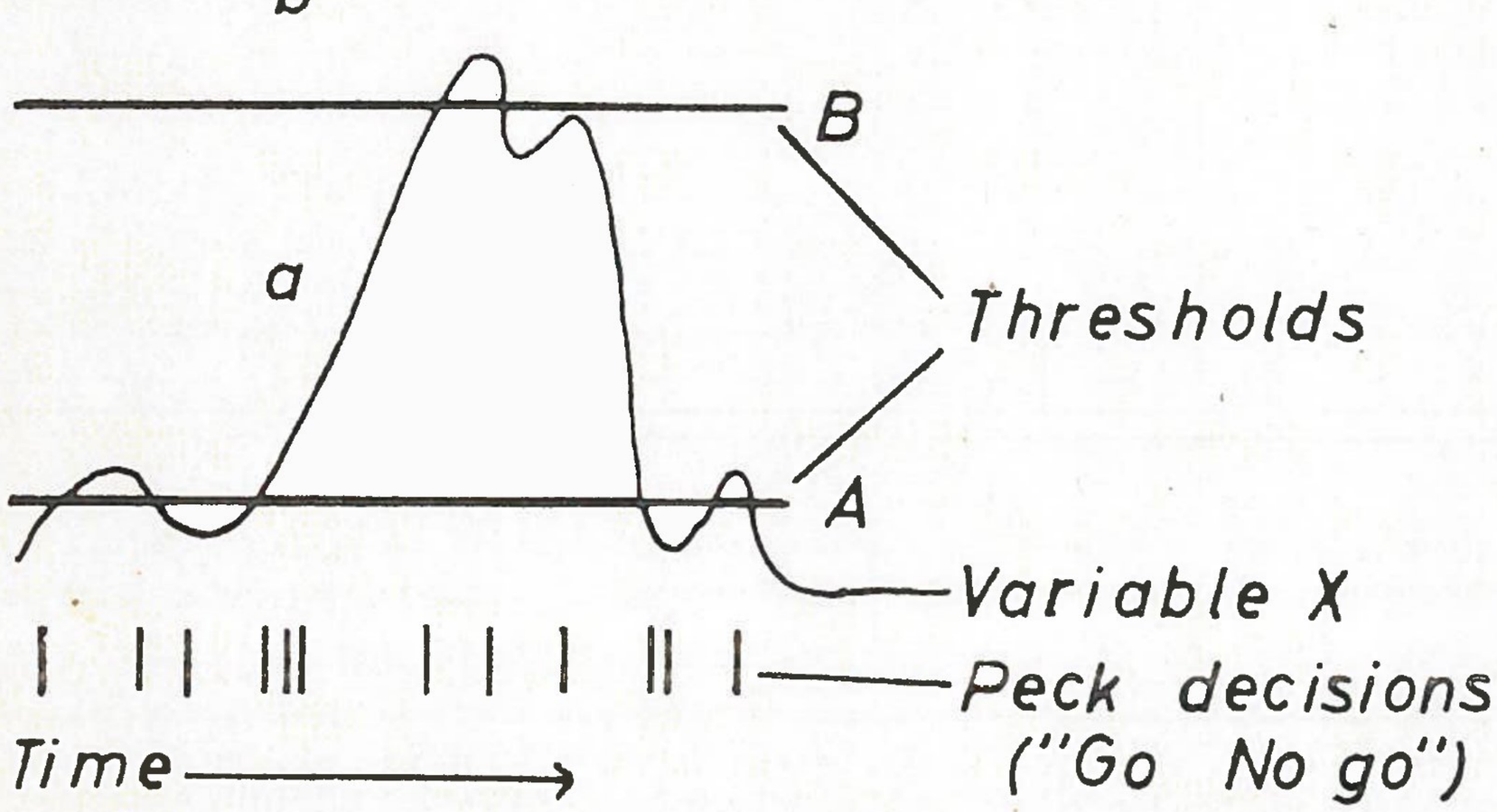
c. If the Threshold Model Analogue is the main determinant of the absolute number of pecks given, as well as of percentage preferences, there should be a negative correlation between the number of pecks in a trial, and the percentage preference shown in the trial: when Variable X has a tendency to be high, more pecks should be given, and it will spend more time above the thresholds of inferior stimuli. In fact, however, there is no such correlation, either in domestic or black-headed gull chicks. If the Threshold Model is to explain this rather disappointing result, it must work in collaboration with

---

* I was first impressed with the importance of this when making a mechanical/electrical analogue of the Threshold Model, out of a vertical tube containing a mercury electrode whose level fluctuated ("Variable X"), making contact with wires lowered into the tube to different levels ("thresholds"), connected up to impulse counters. This toy showed the properties of the Threshold Model and obeyed Prediction 1 only when the current was supplied in brief pulses. A pulse generator ("Go/No go" decision-maker) was needed. Incidentally the pulse generator I used, lent by Dr. J. D. Delius, was equipped with a variable frequency control, which provided a striking demonstration of the unimportance, for Prediction 1, of the rate of activity (K) of the "Go/No go" decision-maker.

Figure 5

Simple Threshold Diagram
for two stimuli, A & B.



an independent agency which plays the greater part in determining variations in numbers of pecks.

The decisions to peck of the supposed "Go/No go" decision-maker are represented by the vertical strokes at the base of Figure 5. These vertical strokes may be regarded as instants of time in which the position of Vafiable X relative to the thresholds is sampled, and a peck directed accordingly.

If, at one of these sampling instants, Variable X does not lie above the threshold of any available stimulus, there will of course be no peck. Thus the Threshold Model Analogue must have some influence on the absolute number of pecks.

The frequency with which these sampling instants occur is measured by K. Questions about the effects of variables on the "Go/No go" decision-maker are equivalent to questions about their effects on K, and this briefer terminology will often be used in the following discussions.

In the deduction of Prediction 1, it will be remembered, K was introduced, but was of no practical consequence as it cancelled out in the computation of percentage preferences. It was therefore not necessary to make any assumptions about K being constant through different choice tests. Thus when A was presented with B, K was called K_1, when B was presented with C, it was called K_2 etc. However it is very important for Prediction 1 that K has the same value when the animal is pecking at either of the stimuli in any one choice test.

For example, as was assumed in Chapter 1, the same K_1 must apply when the chick is pecking A as when it is pecking B. Thus K and Variable X must be entirely independent of each other. This law, which may be called Additional Assumption 1, is absolutely necessary for the deduction of Prediction 1, and indeed all the other predictions to be discussed.

For Prediction 1, as we have just seen, there is no need to assume that K is constant in different choice tests: K_1, K_2, and K_3 may have different values. However if it is assumed that the value of K is constant, or rather that it does not vary systematically in different choice tests, several further predictions can be deduced. Tests of these predictions therefore constitute tests of the validity of this assumption, which may be called Additional* Assumption 2.

Another way to look at these further predictions is not only as tests of Additional Assumption 2, but as devices for measuring the relative values of K in different situations. For example, Prediction 2 provides a method of estimating the ratio K_3 over K_1. In this terminology Additional Assumption 2 could be expressed as

---

* These assumptions are called "Additional" to distinguish them from the three basic assumptions of the Threshold Model discussed in Chapter 1. The Additional Assumptions only arise as a result of the postulation of a separate "Go/No go" decision-maker, which is not an essential part of the basic theory.

$K_3/K_1 = 1$. (In the black-headed gull chick as we shall see the mean ratio comes to 0.990.)

I shall however treat Predictions 2 and 6 in the way first mentioned, as tests of Additional Assumption 2. The use of the word "assumption" should not give the impression that this assumption is an essential part of the Threshold Model. If it does give such an impression, the word "condition" would be preferable. Thus for example, $K_1 = K_2 = K_3$ is a necessary condition for Prediction 5 to follow from the Threshold Model.

Predictions 2 to 6 may all be tested in the same experimental situation as Prediction 1, and I have used the same data, from the experiments on pecking in domestic and black-headed gull chicks. The other experiments discussed in Chapter 2 are not suitable because "Go/No go" decisions are not counted.

Most of the predictions apply to absolute numbers of pecks given to the stimuli, in each of the three choice tests presented for a test/Prediction 1. The numbers of pecks per unit time predicted by the Threshold Model, as calculated in Chapter 1 are reproduced in Table 18. Each expression in the body of the table represents the expected number of pecks at the stimulus indicated at the head of the column, in the choice pair indicated on the left.

In this chapter and the next two, much use will be made of the convention introduced in Chapter 1 for representing the numbers of pecks in a pair choice test. Thus A(B) = the number of pecks per

unit time given to A when it is paired with B. Brackets around small letters have their normal algebraic significance. The unit of time for counting pecks is of course arbitrary. It will be taken as one minute. Thus the figures used in testing the predictions and in calculating values for K and Threshold Values, will be mean numbers of pecks per minute.

TABLE 18

Theoretical numbers of pecks at stimuli A, B, and C, in different simultaneous choice tests.

Choice test	A	B	C
A with B	$K_1(\frac{a+b+c}{2})$	$K_1(\frac{b+c}{2})$	
B with C		$K_2(\frac{b+c}{2})$	$K_2(\frac{c}{2})$
A with C	$K_3(\frac{a+b+c}{2})$		$K_3(\frac{c}{2})$

THE SET RELEASING VALUE MODEL AND THE "GO/NO GO" DECISION-MAKER

Many of the things said about the Threshold Model and the "Go/No go" decision-maker apply also to the Set Releasing Value Model. For the deduction of Prediction 1A it is not necessary to assume that the actual number of pecks per minute which a stimulus receives is the same in any choice situation, but only that it is <u>proportional to</u> the set releasing value of that stimulus. Again therefore K can vary in different choice tests, and again if we assume (Additional Assumption 2) that K does not vary, further predictions can be deduced, equivalent to Predictions 2 to 6. They will be identified as in the case of Prediction 1A, by the number of the corresponding Threshold Model prediction followed by the letter A. They are of course extremely simple, and can easily be seen to amount to the one prediction that the number of pecks per minute received by any stimulus is independent of what it is paired with.

PREDICTIONS 2 TO 6 AND 2A TO 6A

<u>Prediction 2</u>

This is concerned with only two of the three choice tests of Table 18, those when A is presented with B, and A is presented with C.

From Table 18 the total number of pecks given when A is presented with B, that is, A(B)+B(A), is

$$K_1\left(\frac{a+b+c}{2}\right) + K_1\left(\frac{b+c}{2}\right) = K_1(a+b+c)$$

In the same way $A(C) + C(A) = K_3\left(\frac{a+b+c}{2}\right) + K_3\left(\frac{c}{2}\right) = K_3(a+b+c)$.

Therefore if $K_1 = K_3$, it follows from the Threshold Model

that A(B) + B(A) should equal A(C) + C(A), or more generally in words, that in all choice tests in which the preferred stimulus is the same (say A), the total number of pecks given to both stimuli should be the same, regardless of what the less preferred stimulus is.

Prediction 2A

From the assumption that a given stimulus receives the same number of pecks regardless of what it is paired with, the Set Releasing Value Model obviously predicts that A(B) + B(A) should be larger than A(C) + C(A).

Prediction 3

Prediction 3 concerns the choice tests A with B and B with C.

From Table 18, $B(C) + C(B) = K_2(b+c)$. If $K_1 = K_2$, this is exactly double the value $K_1(\frac{b+c}{2})$ of B(A). Prediction 3 then is that the number of pecks which any stimulus B receives when paired with a superior one should be exactly half the total number of pecks given to both stimuli when that stimulus B is paired with an inferior one.

Prediction 3A

The Set Releasing Value Model, also assuming $K_1 = K_2$, predicts that B(A) should be more than half B(C) + C(B), since B(A) should equal B(C), and C(B) should be smaller than B(A).

Prediction 4

Prediction 4 is concerned with the remaining one of the three choice tests, B with C.

From Table 18, $C(B) = K_2\left(\frac{c}{2}\right)$, and $C(A) = K_3\left(\frac{c}{2}\right)$. Therefore if $K_2 = K_3$, C(B) should equal C(A), or in words, the number of pecks which a stimulus receives when it is the inferior member of a pair should be the same regardless of what it is paired with.

Prediction 4A

Prediction 4A is exactly the same as Prediction 4, and it depends on the same additional assumption, that $K_2 = K_3$.

Prediction 5

Predictions 2, 3, and 4 have all needed to make only weak versions of Additional Assumption 3. They have made assumptions involving only two of the three Ks. Now in Prediction 5 we come to a prediction which needs to make Additional Assumption 3 in its strong form, $K_1 = K_2 = K_3$. The unsubscripted letter will stand for the common K.

From Table 18 $A(C) - A(B) = K\left(\frac{a+b+c}{2}\right) - K\left(\frac{a+b+c}{2}\right) = K\left(\frac{b}{2}\right)$

$$B(C) - B(A) = K\left(\frac{b+c}{2}\right) - K\left(\frac{b+c}{2}\right) = K\left(\frac{b}{2}\right)$$

Therefore if $K_1 = K_2 = K_3$, A(C) - A(B) should equal B(C) - B(A).

Prediction 5A

According to the Set Releasing Value Model with Additional Assumption 3, $A(C) = A(B) \neq B(A)$ and $B(C)$. Therefore Prediction 5A does not contradict Prediction 5, but could be regarded as a special case of it: $A(C) - A(B) = B(C) - B(A) = 0$.

Prediction 6

Predictions 1 to 5 are all specifically concerned with one particular experimental situation - that when 3 stimuli are presented

in pair choice tests in all possible pair combinations, (or 2 of the 3 pair combinations). We now come to a prediction which has wider applicability. It concerns the relative sensitivity of simultaneous and successive presentation methods in measuring preferences, using percentage preference as a measure of "sensitivity".

Consider two stimuli A and B, A being preferred to B. Let the time spent by Variable X between their 2 threshold lines be a, and the time spent above B's threshold be b, as in Figure 1.

When A and B are compared in a simultaneous choice test, the value of K is irrelevant to the determination of the percentage preference. Thus the number of pecks at A will be proportional to $a + \frac{b}{2}$, and the number of pecks at B will be proportional to $\frac{b}{2}$: therefore the percentage preference for A over B will be $\frac{2a + b}{2(a + b)}$. K, whatever its value will cancel out, and can therefore be ignored.

When A and B are compared successively on the other hand, K will not necessarily cancel out. It will only do so if Additional Assumption 2 is true. Thus if K_A applies when A is presented by itself, and K_B, when B is presented by itself, the number of pecks at A will be $K_A(a+b)$, and the number of pecks at B will be $K_B(b)$. If we make Additional Assumption 3, $K_A = K_B$, the percentage preference for A over B will then be $\frac{a + b}{a + 2b}$.

Making Additional Assumption 2 then we have arrived at two different theoretical values of the percentage preference for A over B, one for the simultaneous choice test situation, and the other

for the successive presentation situation. It is possible to test these predictions. In the first place we can easily show that the Simultaneous presentation percentage preference must be higher than that for the Successive situation, except in those cases when a or b or both are zero in which case the two are equal. These exceptions are in accordance with common sense, since they represent respectively those cases when there is no preference at all, when there is 100% preference for A, and when there is no pecking at all.

However we can go further than this by producing an actual quantitative relationship between the two percentage preferences. If $P_{sim} = \frac{2a + b}{2(a + b)}$ and $P_{suc} = \frac{a + b}{a + 2b}$, it necessarily follows that

$$P_{suc} = \frac{1}{3 - 2P_{sim}} .$$

Prediction 6 then states that for any given pair of stimuli, the percentage preference which will be obtained if the two are presented successively can be predicted from the percentage preference obtained in a simultaneous choice test by means of this formula.

Prediction 6A

Prediction 6A is very simple. Since according to the Set Releasing Value Model with Additional Assumption 2, the number of pecks at a given stimulus should be the same whatever it is paired with, there should be no difference between percentage preferences obtained from simultaneous and from successive presentation tests.

CONCLUSION

Predictions 2 to 6, and 2A to 6A, follow from the Threshold and Set Releasing Value Models respectively on condition that K is not systematically different in the different choice tests involved, or in other words if Additional Assumption 2 is made.

Owing to the fact that there is an important difference in the way K is determined in the two species tested, it is convenient to depart from the practice used for Prediction 1, and discuss them in separate chapters. Chapter 4 will be about the domestic chick, and Chapter 5 about the black-headed gull.

CHAPTER 4 : THE "GO/NO GO" DECISION-MAKER IN THE DOMESTIC CHICK

TESTS OF PREDICTIONS 2 to 6

In testing all these predictions I have used the same data as were used for testing Prediction 1. In all cases the information needed for testing them consists of the numbers of pecks per unit time given to each of the stimuli in each of the different choice tests. This information is given in Table 19. The rows of the table correspond to the 8 experiments. Each column shows the mean number of pecks per minute given to the stimulus indicated at its head by means of the convention used in the last chapter

TABLE 19

Experiment	Mean no. pecks per minute					
	A(B)	A(C)	B(A)	B(C)	C(A)	C(B)
1	14.3	12.2	12.3	15.6	2.8	3.8
2	19.8	22.3	6.6	6.6	3.3	2.4
3	37.6	46.2	24.2	41.7	7.5	8.4
4	26.5	24.0	10.0	20.0	2.0	1.8
5	20.3	23.5	5.8	15.5	2.1	2.3
6	37.89	34.9	9.2	23.5	3.3	4.2
7	35.4	33.7	13.6	21.8	4.9	10.1
8	22.6	16.1	5.4	22.4	5.2	11.0

Prediction 2 Prediction 2 is that in each experiment A(B) + B(A) = A(C) + C(A); Prediction 2A is that A(B) + B(A) will be greater than

A(C) + C(A). Table 20 compares these sums for the different experiments.

TABLE 20

Experiment	A(B) + B(A)	A(C) + C(A)
1	26.6	15.0
2	26.4	25.6
3	61.8	53.7
4	36.5	26.0
5	26.1	25.6
6	47.1	38.2
7	49.0	38.6
8	28.0	21.3

Using a Wilcoxon matched pairs test, the figures in the left hand column are significantly larger than those in the right hand column. ($P < 0.01$ 2 tailed.) Prediction 2 is therefore significantly disproved, ahd Prediction 2A significantly fulfilled.

Prediction 3 Prediction 3 is that B(C) + C(B) should equal 2B(A).

Prediction 3A is that B(C) + C(B) should be smaller than 2B(A). Table 21 makes the comparison for the different experiments.

TABLE 21

Experiment	B(C) + C(B)	2B(A)
1	19.4	24.6
2	9.0	13.2
3	50.1	48.4
4	21.8	20.0

(cont.)

TABLE 21 cont.

Experiment	B(C) + C(B)	2B(A)
5	17.8	11.6
6	27.7	18.4
7	31.9	27.2
8	33.4	10.8

The difference is not significant but there seems to be a tendency for B(C) + C(B) to be larger than 2B(A), that is in the opposite direction from that predicted by the Set Releasing Value model (Prediction 3A). Thus Prediction 3 may be wrong, but if it is, Prediction 3A is even more so.

Prediction 4 Both Predictions 4 and 4A are that C(A) should equal C(B).

They may be tested directly by reference to Table 19, the two columns on the right.

Again it is not significant, but there seems to be a tendency for the predictions to be disproved. C(B) seems to be somewhat larger than C(A). We cannot then reject these predictions, but they are not convincingly fulfilled.

Prediction 5 Prediction 5 is that A(C) - A(B) should equal B(C) - B(A).

Prediction 5A is that A(C) - A(B) and B(C) - B(A) should both equal zero.

Table 22 makes the necessary comparison.

TABLE 22

Experiment	A(C) - A(B)	B(C) - B(A)
1	- 2.1	3.3
2	2.5	0.0
3	8.6	17.5
4	- 2.5	10.0
5	3.2	9.7
6	- 3.0	14.3
7	- 1.7	8.2
8	- 6.5	17.0

Prediction 5 is significantly disproved. (Wilcoxon matched pairs test, $p < 0.02$ 2-tailed.) Prediction 5A is significantly disproved as far as the B figures are concerned - there is a significant tendency for B(C) to be larger than B(A). (Wilcoxon matched pairs, $p < 0.02$ 2-tailed.) However it is not significantly disproved as far as the A figures are concerned.

Prediction 6 Prediction 6 is that simultaneous choice tests should give higher percentage preferences than successive ones. More precisely the relationship between these two should be $P_{suc} = \frac{1}{3-2P_{sim}}$.

Prediction 6A is that simultaneous and successive presentation tests should give the same percentage preference.

I have not done any experiments specifically to test this prediction. However the experiments originally done to test Prediction 1

can be used in the following way:

Consider three stimuli A, B, and C, presented in all pair combinations. If we take the preference for A over B first, the simultaneous presentation percentage preference is of course obtained when A is paired with B. A form of successive presentation percentage preference can be obtained from the numbers of pecks which go to A when it is paired with C, compared with the number which go to B when it is paired with C. The third stimulus C then can be regarded as part of the background just as little pieces of dirt etc. must always be regarded as part of the background in any pecking test. This makes no difference to the deduction of Predictions 6 and 6A. Similarly, though perhaps slightly more surprisingly, Predictions 6 and 6A remain exactly the same if we consider the most preferred stimulus A as part of the background, and compare the number of pecks at B when paired with A with the number at C when paired with A. Prediction 6 cannot however be tested on the preference for A over C, because in one of the "successive" tests the "background" B is the preferred stimulus, and in the other case it is the less preferred.

If the use of the term "successive presentation preference" in this way is objected to, it does not really matter. Whatever one calls it, they are testable predictions that if $P_{sim} = \frac{A(B)}{A(B) + B(A)}$ and $P_{suc} = \frac{A(C)}{A(C) + B(C)}$, $P_{suc} = \frac{1}{3 - 2P_{sim}}$, and that if $P_{sim} = \frac{B(C)}{B(C) + C(B)}$, and $P_{suc} = \frac{B(A)}{B(A) + C(A)}$, P_{suc} also should equal

$\frac{1}{3 - 2P_{sim}}$, and finally that the same formula relating P_{suc} and P_{sim} should also hold if these two are simultaneous and successive percentage preferences in the ordinary sense of the words.

The "simultaneous" percentages are taken from Tables 1 to 8 in Chapter 2. The comparison between "simultaneous" and "successive" percentage preferences is made in Table 23, which also gives the predicted "successive" figures calculated from the "simultaneous" ones by means of the formula Predicted $P_{suc} = \frac{1}{3 - 2P_{sim}}$. Figure 6 gives the same information in graphical form. It is a scatter diagram of successive against predicted successive percentage preferences.

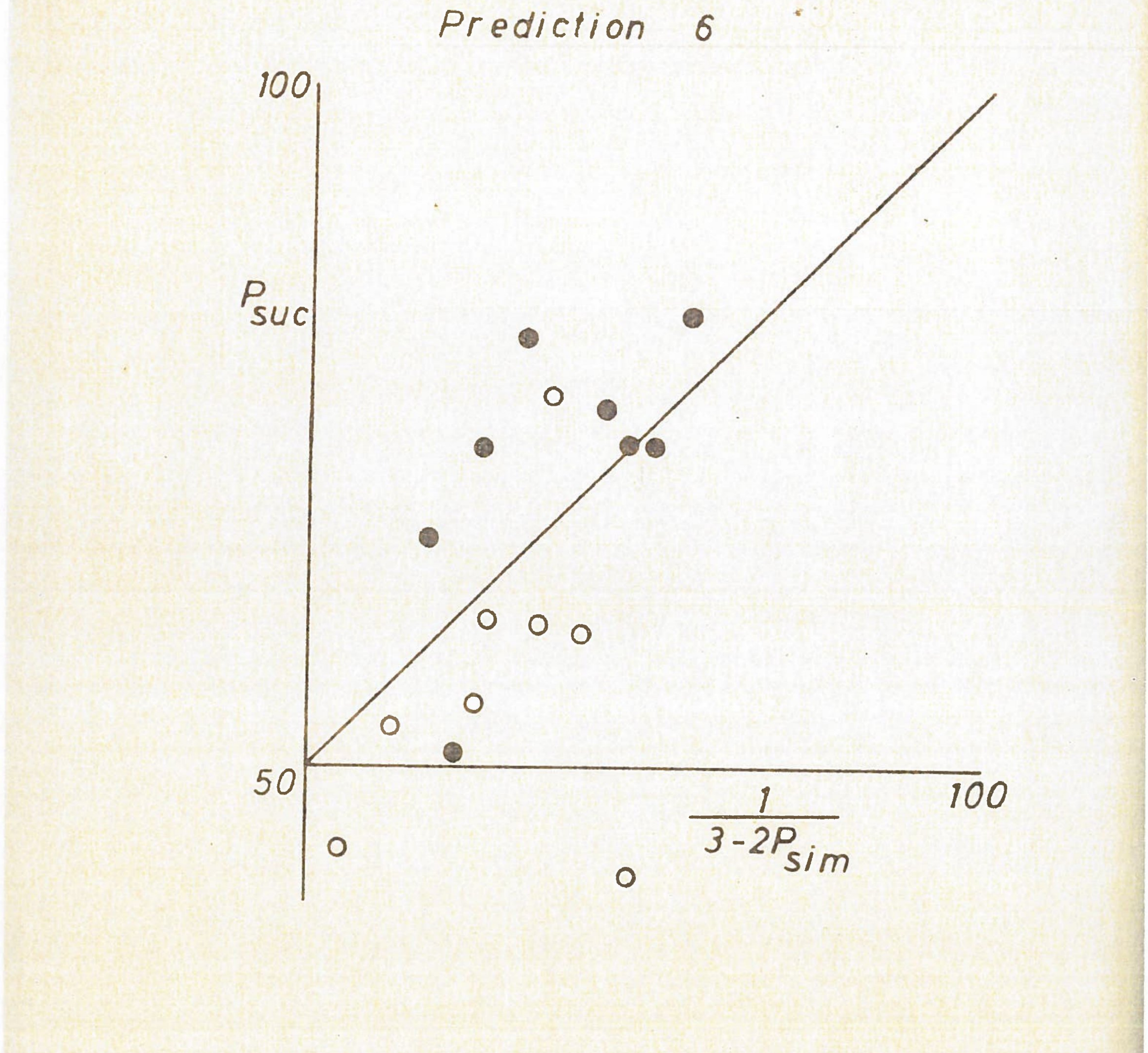
Both in Table 23 and Figure 6 a separation is made between those figures representing percentage preferences for A over B (i.e. when the "background" stimulus in the "successive" situation is inferior), and those figures representing percentage preferences for B over C (when the "background" stimulus is superior). This is important as will be seen in the discussion. In Figure 6 open circles are used for percentage preferences for A over B, and solid circles for percentage preferences for B over C.

The results show that the Set Releasing Value model's Prediction 6A is definitely wrong. "Simultaneous" percentage preferences are significantly higher than the corresponding "successive"

TABLE 23

Stimuli	Experiment	P_{sim}	$\frac{1}{3 - 2P_{sim}}$	P_{suc}
A B	1	54.6	52.4	43.9
	2	76.0	67.6	77.2
	3	61.1	56.2	52.6
	4	69.9	62.4	54.5
	5	75.4	67.0	60.3
	6	78.7	70.1	59.8
	7	70.8	63.1	60.7
	8	81.5	73.0	41.8
B C	1	74.0	65.8	81.5
	2	65.0	58.8	66.7
	3	80.2	71.6	76.3
	4	85.9	78.0	83.3
	5	82.3	73.9	73.4
	6	83.8	75.5	73.6
	7	70.5	62.9	73.5
	8	67.9	60.9	50.9
Mean		73.6	66.2	64.4

Figure 6


Prediction 6
100
P_{suc}
50
$\frac{1}{3-2P_{sim}}$
100
● B versus C, A in background
○ A " B C " "

ones.($P < 0.01$, Wilcoxon matched pairs test, 2 tailed.) Superficially there seems to be rather a good fit to the Threshold Model's Prediction 6. Thus there is no consistent overall tendency for the figurds in the two right hand columns of Table 23 to differ from each other. However a closer inspection of the results - it is especially clear from Figure 6 - will reveal a marked difference between the "AB results" and the "BC results". When the percentage preferences concerned are those for A over B, Prediction 6 tends to overestimate, ($P < 0.08$ 2 tailed); when the percentage preferences concerned are those for B over C, Prediction 6 underestimates. (Not significant.)

Prediction 6 (and Prediction 6A) depends on the assumption that K is the same in both the presentations which enter into each "successive" percentage preference. In those cases where the number of pecks at A is being compared with the number at B, with C a constant factor in the background, the Ks concerned are respectively K_3 and K_2. Now according to the Threshold Model's explanation of the near disproof of Prediction 4, K_3 should be smaller than K_2. This would have the effect of making the percentage preference for A over B lower than expected by Prediction 6, which is of course the result obtained.

On the other hand, when the "successive" presentation preference is that for B over C with A a constant factor in the background the two Ks concerned are K_1 and K_3. The direction of departure of the observed figures from Prediction 2 suggests that K_1 is larger

than K_3. This would lead to the percentage preference for B over C being higher than expected by Prediction 6. Again this seems to be the case.

At first sight then there seems to be no great deviation of Prediction 6 from the facts. A closer examination reveals that this is only a superficial impression. The figures fall into two groups, one group giving an overprediction, and the other an underprediction. The directions of these errors of Prediction 6 are clearly consistent with the errors already found of the other predictions about total peck numbers.

DISCUSSION OF TESTS OF PREDICTIONS USING ABSOLUTE PECK NUMBERS

With the exception of Prediction 2A of the Set Releasing Value model, none of these additional predictions of either model has been successful. In some cases the predictions have been definitely disproved, and in other cases they have been very far from convincingly fulfilled. In the last chapter it was pointed out that these predictions do not necessarily have to follow from the basic models themselves, but depend upon some version of Additional Assumption 2 as well. Thus the failure of these predictions does not imply any inadequacy of the Threshold Model and the Set Releasing Value Model themselves. In both cases we have only to assume that K changes systematically in the different choice tests.

At first sight it might seem obvious that making such a liberal assumption as this would make it easy for both models to be compatible with the results. There is evidence however that although this may be the case for the Threshold Model, the Set Releasing Value Model is unable to explain the results, no matter how freely K is adjusted.

Prediction 2 assumed that $K_1 = K_3$, Prediction 3 assumed that $K_1 = K_2$, Prediction 4 assumed that $K_2 = K_3$. The corresponding assumptions were made for the Set Releasing Value Model. The results of each of the experiments should therefore give us values for the ratios between the Ks in each case.

Thus for the Threshold Model,

$$\frac{K_3}{K_1} = \frac{A(C) + C(A)}{A(B) + B(A)} \quad \text{(From Prediction 2)}$$

$$\frac{K_1}{K_2} = \frac{2B(A)}{B(C) + C(B)} \quad \text{(From Prediction 3)}$$

$$\frac{K_3}{K_2} = \frac{C(A)}{C(B)} \quad \text{(From Prediction 4)}$$

Therefore, since $\frac{K_3}{K_2} = \frac{K_1}{K_2} \times \frac{K_3}{K_1}$, it follows that

$\frac{C(A)}{C(B)}$ should equal $\frac{2B(A)}{B(C) + C(B)} \times \frac{A(C) + C(A)}{A(B) + B(A)}$

This compound derivative of Predictions 2, 3, and 4 is then a prediction of the Threshold Model which should be fulfilled regardless of the value of K, just like Prediction 1. It cannot however be treated as a separate prediction since it is logically derivable from Prediction 1, and Prediction 1 from it. Therefore the fact that Prediction 1 has been found to give a good fit to the results already, suggests that the Threshold Model could indeed, if K were suitably varied, be compatible with the absolute peck number results.

Doing the same for the Set Releasing Value Model, we find:

$$\frac{K_3}{K_1} = \frac{A(C)}{A(B)} \quad \text{(From Prediction 2A)}$$

$$\frac{K_1}{K_2} = \frac{B(A)}{B(C)} \quad \text{(From Prediction 3A)}$$

$$\frac{K_3}{K_2} = \frac{C(A)}{C(B)} \quad \text{(From Prediction 4A)}$$

Therefore since $\frac{K_3}{K_2} = \frac{K_1}{K_2} \times \frac{K_3}{K_1}$, it follows that $\frac{C(A)}{C(B)}$ should equal $\frac{B(A)}{B(C)} \times \frac{A(C)}{A(B)}$.

Table 24 gives $\frac{C(A)}{C(B)}$ for each of the experiments together with the ratios predicted by the two models. The Set Releasing Value Model's predictions are, as expected wrong: they differ from the observed ratios significantly (Wilcoxon Matched Pairs Test, $P < 0.01$ 2-tailed). The Threshold Model's predictions do not differ significantly from the observed ratios, but the fit is not so good as that of Prediction 1 when mean percentage preferences were used.

TABLE 24

Experiment	$\frac{C(A)}{C(B)}$	$\frac{2B(A)}{B(C) + C(B)} \times \frac{A(C) + C(A)}{A(B) + B(A)}$	$\frac{A(C)}{A(B)} \times \frac{B(A)}{B(C)}$
1	0.74	0.71	0.67
2	1.38	1.42	1.13
3	0.89	0.84	0.71
4	1.11	0.65	0.46
5	0.91	0.64	0.44
6	0.79	0.54	0.36
7	0.49	0.68	0.41
8	0.47	0.36	0.17
Mean	0.85	0.73	0.54

This might mean that some of the close fits of Prediction 1 described in Chapter 2 were fortuitous. However since the mean percentage preference method used there was chosen especially to eliminate the effect of the enormous inter-trial variation in total peck numbers, it seems more probable that the less good fit obtained when peck numbers are used is due to this extra error.

In conclusion, both models have failed almost completely in predictions based on the assumption that K is constant. If this assumption is waived, the Threshold Model is potentially able to explain the facts; the Set Releasing Value Model is not. For these animals in these situations then, the Set Releasing Value Model can probably be rejected. The Threshold Model cannot be rejected.

These results confirm that the Threshold Model Analogue cannot be considered as the main determinant of peck frequency in the domestic chick. As suspected, there must be an independent "Go/No go" decision-maker, which, since K_1, K_2, and K_3 systematically differ from each other, must be influenced by the stimulus situation.

CHAPTER 5 : THE "GO/NO GO" DECISION-MAKER IN THE BLACK-HEADED GULL CHICK (All data from Dr. M. Impekoven.)

The same data are used here as were used in percentage form for testing Predictions 1 and 1A. (With the exception that the one non-significant preference is included. This is for the sake of symmetry and completeness in the calculations of K and "Threshold Values" later in this chapter. As mentioned at the end of Chapter 2, the importance of the rejection of non-significant preferences for testing Prediction 1 seems to have been exaggerated.)

Table 25 gives the mean numbers of pecks per minute to each of the colours in each of the different pair situations. The symbols at the heads of the columns have the same meaning as in Table 19. The colour triplets are named on the left using the same notation as in Table 12.

In assessing the success of the predictions no use can be made of tests of statistical significance. This is because, as already pointed out, the data entering into the different triplets are not independent. From my point of view this is the only disadvantage of this multi-stimulus pair choice test design.

As for the domestic chick, the predictions will be dealt with one by one. At the beginning of each section, the predictions of the two models will be briefly restated in symbols.

TABLE 25

Mean numbers of pecks per minute

Triplet	A(B)	A(C)	B(A)	B(C)	C(A)	C(B)
B R Y	21.15	26.21	13.95	19.93	8.72	14.81
B R G	21.15	28.05	13.95	29.00	5.17	6.93
B R D	21.15	29.16	13.95	28.84	4.64	5.16
B R W	21.15	34.10	13.95	31.68	0.86	0.84
B Y G	26.21	28.05	8.72	21.44	5.17	8.47
B Y D	26.21	29.16	8.72	24.00	4.64	7.74
B Y W	26.21	34.10	8.72	32.30	0.86	1.60
B G D	28.05	29.16	5.17	14.74	4.64	9.26
B G W	28.05	34.10	5.17	18.42	0.86	2.08
B D W	29.16	34.10	4.64	21.60	0.86	1.68
R Y G	19.93	29.00	14.81	21.44	6.93	8.47
R Y D	19.93	28.84	14.81	24.00	5.16	7.74
R Y W	19.93	31.68	14.81	32.30	0.84	1.60
R G D	29.00	28.84	6.93	14.74	5.16	9.26
R G W	29.00	31.68	6.93	18.42	0.84	2.08
R D W	28.84	31.68	5.16	21.60	0.84	1.68
Y G D	21.44	24.00	8.47	14.74	7.74	9.26
Y G W	21.44	32.30	8.47	18.42	1.60	2.08
Y D W	24.00	32.30	7.74	21.60	1.60	1.68
G D W	14.74	18.42	9.26	21.60	2.08	1.68
Mean (For Prediction 4)					3.46	5.21

PREDICTION 2

Prediction 2 states that A(B) + B(A) should equal A(C) + C(A).

Prediction 2A states that A(B) + B(A) should be greater than A(C) + C(A).

Table 26 makes the comparison.

Prediction 2 seems remarkably well fulfilled, and Prediction 2A not so. Thus the mean of all the A(B) + B(A)s is 33.56, while the corresponding mean for all the A(C) + C(A)s is 33.21.

PREDICTION 3

Prediction 3 states that 2B(A) should equal B(C) + C(B).

Prediction 3A states that 2B(A) should be larger than B(C) + C(B).

Table 27 makes the comparison.

Despite the fact that we cannot use a significance test, there can be almost no doubt that B(C) + C(B) is very much larger than 2B(A). Indeed this is the case for all 20 of the triplets. Thus Prediction 3 is disproved, and Prediction 3A is more decisively so.

PREDICTION 4

Prediction 4 states that C(A) should equal C(B)

Prediction 4A is exactly the same as Prediction 4.

The comparison may be made directly from Table 25, the two right hand columns.

Predictions 4 and 4A are disproved. In all 20 of the triplets, C(B) is larger than C(A).

TABLE 26

Mean numbers of pecks per minute

Triplet	A(B) + B(A)	A(C) + C(A)	
B R Y	35.10	34.93	1.005
B R G	35.10	33.22	1.057
B R D	35.10	33.80	1.038
B R W	35.10	34.96	1.004
B Y G	34.93	33.22	1.051
B Y D	34.93	33.80	1.033
B Y W	34.93	34.96	0.999
B G D	33.22	33.80	0.983
B G W	33.22	34.96	0.950
B D W	33.80	34.96	0.967
R Y G	34.74	35.93	0.967
R Y D	34.74	34.00	1.022
R Y W	34.74	32.52	1.068
R G D	35.93	34.00	1.057
R G W	35.93	32.52	1.105
R D W	34.00	32.52	1.045
Y G D	29.91	31.74	0.942
Y G W	29.91	33.90	0.882
Y D W	31.74	33.90	0.936
G D W	24.00	20.50	1.171
Mean	33.56	33.21	1.014

TABLE 27

Triplet	2B(A)	B(C) + C(B)		
B R Y	27.90	34.74		
B R G	27.90	35.93		
B R D	27.90	34.00		
B R W	27.90	32.52		
B Y G	17.44	29.91		
B Y D	17.44	31.74		
B Y W	17.44	33.90		
B G D	10.34	24.00		
B G W	10.34	20.50		
B D W	9.28	23.28		
R Y G	29.62	29.91		
R Y D	29.62	31.74		
R Y W	29.62	33.90		
R G D	13.86	24.00		
R G W	13.86	20.50		
R D W	10.32	23.28		
Y G D	16.94	24.00		
Y G W	16.94	20.50		
Y D W	15.48	23.28		
G D W	18.52	23.28		
Mean	19.43	27.73		

PREDICTION 5

Prediction 5 is that A(C) - A(B) should equal B(C) - B(A).

Prediction 5A is that A(C) - A(B) and B(C) - B(A) should both equal zero.

Table 28 gives the differences.

In 18 out of the 20 triplets, B(C) - B(A) is larger than A(C) - A(B), and the mean of the former is more than double that of the latter. Both are obviously larger than 0. Both Prediction 5 and Prediction 5A then are disproved.

TABLE 28

Triplet	A(C) - A(B)	B(C) - B(A)
B R Y	5.06	5.98
B R G	6.90	15.05
B R D	8.01	14.89
B R W	12.95	17.73
B Y G	1.84	12.72
B Y D	2.95	15.28
B Y W	7.89	23.58
B G D	1.11	9.57
B G W	6.05	13.25
B D W	4.94	16.96
R Y G	9.07	6.63
R Y D	8.91	9.19
R Y W	11.75	17.49
R G D	-0.16	7.81
R G W	2.68	11.49
R D W	2.84	16.44
Y G D	2.56	6.27
Y G W	10.86	9.95
Y D W	8.30	13.86
G D W	3.68	12.34
Mean	5.91	12.83

DISCUSSION OF TESTS OF PREDICTIONS 2 TO 5

As for the domestic chick, it is clear that in general the predictions of neither of the two models about absolute peck numbersare true. Once again we shall have to reject Additional Assumption 3 if not the basic models themselves.

However in this case, one interesting fact from the point of view of the Threshold Model is the success of Prediction 2. According to the Threshold Model, what this means is that $K_1 = K_3$. From the direction of the error of Prediction 3 the model would say that K_2 is larger than K_1. Since we are postulating that $K_1 = K_3$ we should therefore expect K_2 to be larger than K_3, and this is confirmed by the direction of the error of Prediction 4. Thus all these findings, confirmed by the direction of error of Prediction 5 seem likely to be interpretable by the Threshold Model on the assumption that K_1 equals K_3, both being smaller than K_2.

In words what this means is that the Go/No go decision-maker is equally active when the preferred stimulus is paired with the least preferred, and when it is paired with the intermediate stimulus, but it increases its activity when the two least preferred stimuli are presented together. This suggests that the activity of the Go/No go decision-maker is determined by the best stimulus available, and is entirely independent of what it is paired with. The general significance of this hypothesis will be discussed later, but first we must deal with its consequences for Prediction 6.

PREDICTION 6

The facts discussed in the previous section strongly suggested the hypothesis that in the black-headed gull chick, K is determined solely by the most preferred stimulus available. Thus K is the same when A is paired with B as when A is paired with C, but different when B is paired with C. In Prediction 6 we have an excellent test of this hypothesis, as well as of the Threshold Model itself of course.

It will be remembered that according to Prediction 6, the percentage preference obtained in a "successive" presentation test should be related to that given by a "simultaneous" choice test by the formula $P_{suc} = \frac{1}{3 - 2P_{sim}}$. This prediction of course is based on the assumption that K is constant in the successive tests.

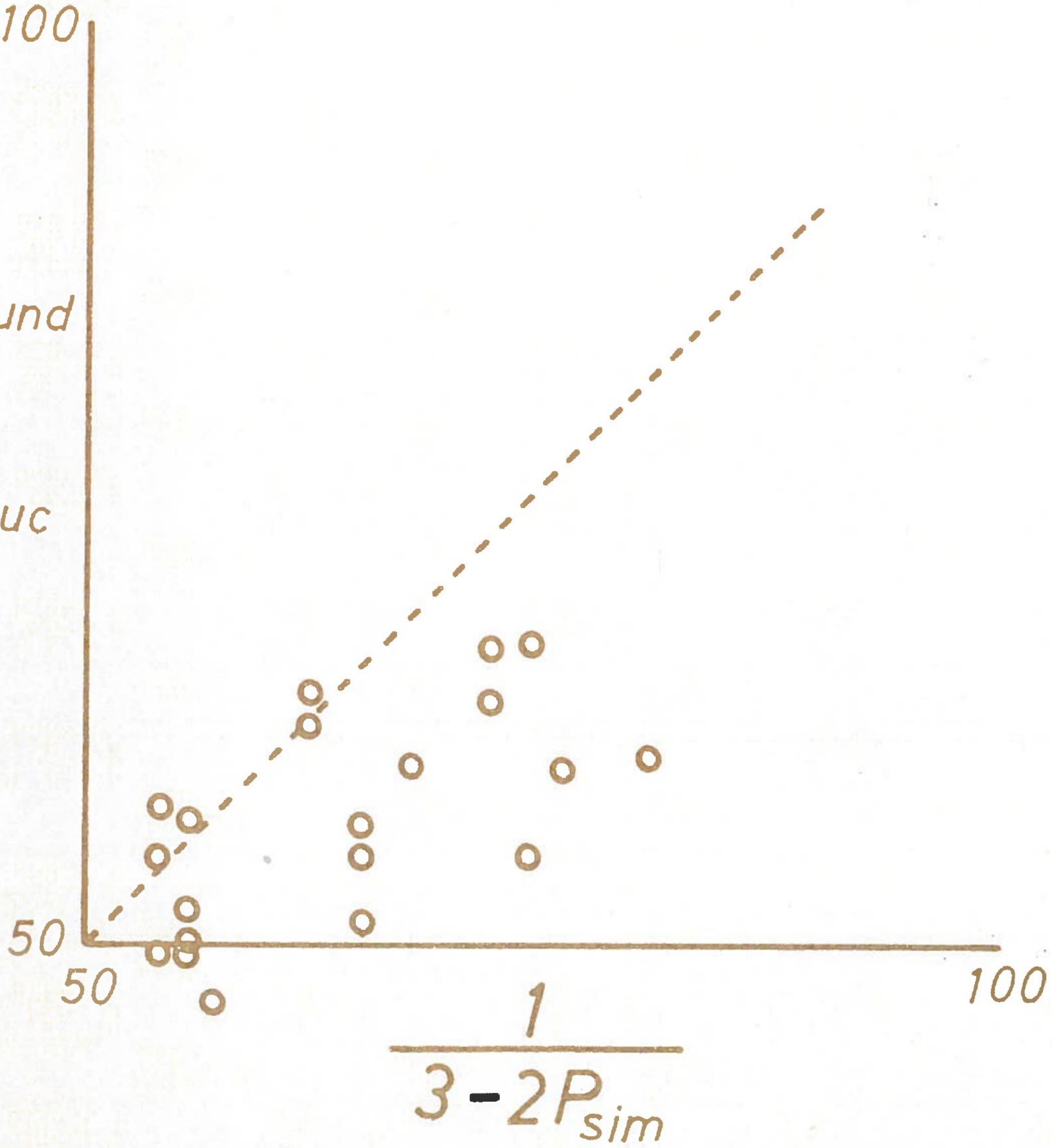
Now our hypothesis arising out of the previous section would expect that K would indeed by constant if, throughout the "successive" tests, there were present in the "background" a constant stimulus, preferred to both the test stimuli. Thus if we count the number of pecks at B when A is also present, and then count the number of pecks at C when A is also present, K will be determined by A and therefore constant in both cases. Under such circumstances we should expect Prediction 6 to be fulfilled. On the other hand if we do a "successive" test of the preference for A over B with C a constant factor in the background we shall expect no such good fit to Prediction 6. When A

is present with C, K will be determined by A, and when B is present with C, K will be determined by B. From the finding of the previous section that K_2 seems to be larger than K_1 or K_3, we should expect that K will be larger in the successive test when B is present with C than when A is present with C. Therefore we should expect that in the "successive" test B should receive more pecks than the basic assumptions of the Threshold Model alone would give it, and therefore that Prediction 6 should overestimate.

The results, worked out in the same way as for the domestic chick, are given in Tables 29 and 30, and Figures 7 and 8. Prediction 6A seems to be disproved in both situations. In Table 29 and Figure 7 the "successive" presentation percentage preferences were all obtained with an inferior stimulus in the "background". As expected, Prediction 6 overestimates. In Table 30 and Figure 8 on the other hand, a preferred stimulus was constantly in the "background", and as expected, Prediction 6 is in this case well fulfilled.

The success of this restricted form of Prediction 6 is very encouraging, because like Prediction 1 it is a quantitatively precise prediction which is not obviously expected by common sense. The case for the Threshold Model is strengthened more by this result than by many replicated tests of Prediction 1. There may be models, quite distinct from the Threshold Model, from which one of these two predictions could be deduced, but it is less likely that there are other models which could yield both.

Figure 7



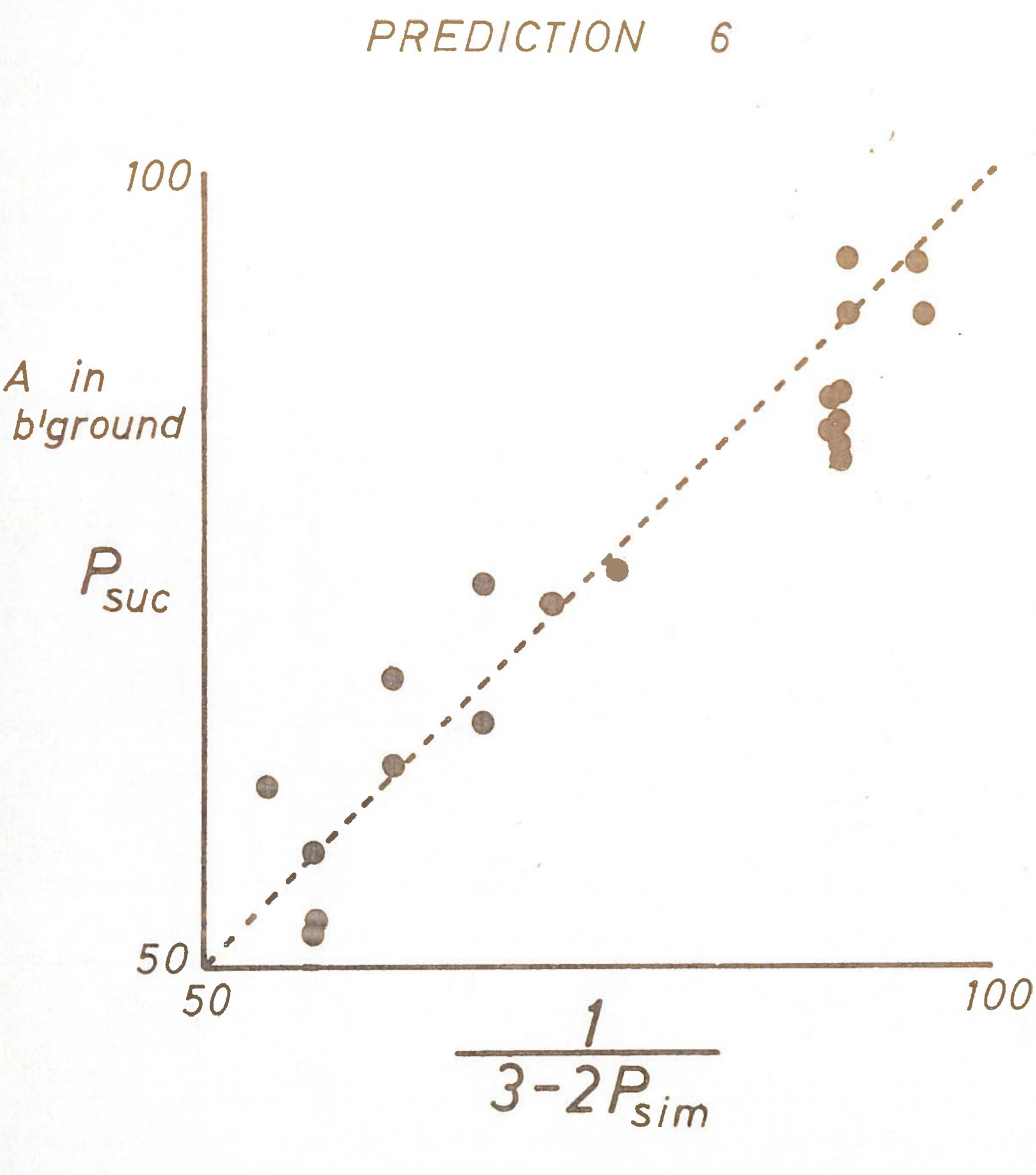
Black-headed gull chicks

(M. Impekoven)

TABLE 29

"Background stimulus" C	Test stimuli	P_{sim}	P_{suc}	$\frac{1}{3 - 2P_{sim}}$
Y	B R	60.2	56.8	55.7
G	B R	60.2	49.2	55.7
G	B Y	73.3	56.7	65.2
G	R Y	57.5	57.5	54.1
D	B R	60.2	50.3	55.7
D	B Y	73.3	54.9	65.2
D	B G	82.9	66.4	74.5
D	R Y	57.5	54.6	54.1
D	R G	82.9	66.4	74.5
D	Y G	69.6	61.9	62.2
W	B R	60.2	51.8	55.7
W	B Y	73.3	51.4	65.2
W	B G	82.9	64.9	74.5
W	B D	88.1	61.2	80.8
W	R Y	57.5	49.5	54.1
W	R G	80.8	63.2	72.3
W	R D	84.5	59.5	76.3
W	Y G	69.6	63.7	62.2
W	Y D	76.3	59.9	67.8
W	G D	62.5	46.0	57.1
Mean		70.6	57.3	64.1

Figure 8



Black-headed gull chicks
(M. Impekoven)

Table 30

"Background stimulus" A	Test stimuli	P_{sim}	P_{suc}	$\frac{1}{3 - 2P_{sim}}$
B	R Y	57.5	61.5	54.1
B	R G	80.8	73.0	72.3
B	R D	84.5	75.0	76.3
B	R W	97.5	94.2	95.2
B	Y G	69.6	62.8	62.2
B	Y D	76.3	65.3	67.8
B	Y W	94.9	91.0	90.7
B	G D	62.5	52.7	57.1
B	G W	94.3	85.8	89.8
B	D W	94.6	84.4	90.3
R	Y G	69.6	68.1	62.2
R	Y D	76.3	74.2	67.8
R	Y W	94.9	94.6	90.7
R	G D	62.5	57.3	57.1
R	G W	94.3	83.7	89.8
R	D W	94.6	86.0	90.3
Y	G D	62.5	52.2	57.1
Y	G W	94.3	84.1	89.8
Y	D W	94.6	82.9	90.3
G	D W	94.6	81.6	90.3
Mean		82.5	75.5	77.1

DISCUSSION OF TESTS OF PREDICTIONS USING ABSOLUTE PECK NUMBERS

The consequences of the verification of Prediction 2 will be developed later. Meanwhile we must do the same for the gull chick as for the domestic chick with respect to the capacities of the two models to account for the data if K is allowed to vary.

It will be remembered from the last chapter that a composite prediction derived from Predictions 2, 3, and 4, and independent of K, could be worked out for the Threshold Model, and a corresponding calculation done for the Set Releasing Value Model. These two predictions are formally identical to Prediction 1 and 1A respectively, and therefore cannot be treated as independent evidence. The fact that Prediction 1 gave a good fit to the mean percentage data from the gulls, while Prediction 1A did not, is a good indication that the Threshold Model could account for the absolute peck number data if K were allowed to vary, while the Set Releasing Value Model could not.

The two composite predictions are:

For the Threshold Model: $$\frac{C(A)}{C(B)} = \frac{2B(A)}{B(C) + C(B)} \times \frac{A(C) + C(A)}{A(B) + B(A)}$$

For the Set Releasing Value Model: $$\frac{C(A)}{C(B)} = \frac{B(A)}{B(C)} \times \frac{A(C)}{A(B)}$$

Table 31 gives $\frac{C(A)}{C(B)}$ for each colour triplet, together with the predictions of the two models.

TABLE 31

Triplet	$\frac{C(A)}{C(B)}$	$\frac{2B(A)}{B(C) + C(B)} \times \frac{A(C) + C(A)}{A(B) + B(A)}$	$\frac{B(C)}{A(B)} \times \frac{B(A)}{B(C)}$
B R Y	0.59	0.80	0.87
B R G	0.75	0.74	0.64
B R D	0.90	0.79	0.67
B R W	1.02	0.86	0.71
B Y G	0.61	0.55	0.44
B Y D	0.60	0.56	0.40
B Y W	0.54	0.52	0.35
B G D	0.50	0.44	0.37
B G W	0.41	0.53	0.34
B D W	0.51	0.41	0.25
R Y G	0.82	1.02	1.01
R Y D	0.67	0.86	0.89
R Y W	0.53	0.82	0.73
R G D	0.56	0.55	0.47
R G W	0.40	0.61	0.41
R D W	0.50	0.42	0.26
Y G D	0.84	0.75	0.64
Y G W	0.77	0.94	0.75
Y D W	0.95	0.71	0.48
G D W	1.24	0.68	0.54
Mean	0.69	0.68	0.56

As would be expected from the percentage data of Chapter 2, the Threshold Model's predictions are quite close to the observed results. Those of the Set Releasing Value Model are less so.

The evidence suggests then, that if K is allowed to vary, the Threshold Model is well able to account for the absolute peck number results. The Set Releasing Value model is less likely to be able to do so.

With the domestic chick this was as far as we were able to go. In the gull chick however, as already pointed out, it appears that working within the framework of the Threshold Model, $K_1 = K_3$. It is interesting therefore to repeat the calculation of the "composite prediction" making this restraining assumption, to see whether the Threshold Model is still able to account for the absolute peck number results.

If $K_1 = K_3$, $\frac{A(C) + C(A)}{A(B) + B(A)}$ ought to equal 1. In fact the mean ratio comes to 0.990.

If $\frac{K_1}{K_2} = \frac{K_2}{K_2}$, $\frac{2B(A)}{B(C) + C(B)}$ ought to equal $\frac{C(A)}{C(B)}$. The mean ratios are respectively 0.685 and 0.685. (All to 3 places of decimals.)

Like the partial success of Prediction 6, this gives some grounds for confidence, both in the ThreshddModel itself, and in the empirically derived hypothesis that $K_1 = K_3$, or in other words that the activity of the Go/No go decision-maker is controlled entirely by the most preferred stimulus of each pair.

CALCULATION OF THRESHOLD VALUES, AND K VALUES

If $K_1 = K_3$, as argued in the last section the most obvious hypothesis is that the Go/No go decision-maker's activity in so far as it is controlled by external stimuli at all, is determined entirely by the most preferred of the available stimuli. For example K will be the same when Blue is paired with Red or with Yellow or with any other of the test colours. This K may be called K_B. A different K (K_R) will operate however when Red is paired with any other colour "inferior" to it. When Green is paired with Black or with White, K_G will apply, but when Green is paired with Yellow K_Y will apply, and when Green is paired with Red K_R will.

According to this hypothesis then, each colour affects the animal in two ways:

1. By determining a Threshold Value, preferred colours having lower thresholds than less preferred ones. If percentage preferences in simultaneous choice tests are measured, only this effect of external stimuli can be demonstrated.

2. By determining K, the activity of the Go/No go decision-maker.

The essential difference between the two ways is that Effect 2 works on the number of pecks at both stimuli indiscriminately: therefore percentage preferences are unaffected. Effect 1 is a discriminative effect, and is the determinant of percentage preferences.

What of the quantitative relationship between these two effects? Do "preferred stimuli" as measured by percentage preference

(i.e. according to Effect 1), also exert the greatest effect (2) on the Go/No go decision-maker? Or is there an inverse relationship between these two effects? Or is there no relationship at all? If there is a relationship, is it a lawful one?

We can answer these questions by using the data to calculate actual Threshold Values and Ks of the different colours. These values will be relative ones in arbitrary units, all based on a single definition, namely that the Total Threshold Value of White is 1. (See the explanation of symbols in Chapter 1.) What this means in practice is that if K were 1, the number of pecks per minute, received by White when presented by itself should be 1. Figure 9 is a threshold diagram showing the symbols whose quantitative values are to be discovered.

FIGURE 9

w = 1	K_W (undiscoverable from present data but see below)
d = ?	K_D = ?
g = ?	K_G = ?
y = ?	K_Y = ?
r = ?	K_R = ?
b = ?	K_B = ?

The information used to calculate the Threshold Values is the percentage preference in each case, and the Threshold Values already calculated, (or in the case of w, previously defined).

Thus d, the Threshold Value of Black, is obtained from the

percentage preference for Black over White by solving the equation $P_{DW} = \frac{2d + w}{2(d + w)}$, which is of course derived from the basic assumptions of the Threshold Model as put forward in Chapter 1.

g, the Threshold Value of Green can then be calculated either from the percentage preference for Green over Black, or that for Green over White. In both cases the already calculated d must be used, as well as the defined w. The two equations are $P_{GD} = \frac{2g + d + w}{2(g + d + w}$ and $P_{GW} = \frac{2(g + d) + w}{2(g + d + w)}$. The value of g finally accepted is the arithmetic mean of these two.

This mean g is then used to calculate y from the three percentage preferences P_{YG}, P_{YD}, and P_{YW}. The mean y so obtained is then used to calculate four values of r, and the mean r to calculate five values of b. This is therefore a cumulative calculation in which many of the values depend upon others and it may be that the effects of errors are exaggerated by accumulation.

When the mean Threshold Values have been calculated from the percentage preferences, they can be used to calculate K for each colour.

K is the number by which it is necessary to multiply the theoretical number of pecks at a stimulus, in order to obtain the actual number of pecks. Therefore for example the number of pecks D(W) given to Black when it is paired with White equals $K(d + \frac{w}{2})$. K can be calculated from this since we already know the values of d and w, and D(W). On the hypothesis that K is determined solely by

Figure 10

Threshold Scale Diagram
(threshold values proportional to distance)

C ——— z
B ——— y
A ——— x

P = 1 ——— White

a = 8·26

d = 1·30 ——— Black $K_D = 2·92$
Green $K_G = 2·62$

c = 5·01

——— Yellow $K_Y = 2·14$

b = 8·35

——— Red $K_R = 1·46$

a = 5·72

——— Blue $K = 1·18$

Black-headed gull chicks
(M. Impekoven)

the preferred stimulus, the K so calculated is K_D. Another value of K_D can be obtained from W(D). Thus $W(D) = K_D(\frac{W}{2})$.

Similarly 4 different values of K_G can be calculated, two from the Green/Black choice test, and two from the Green/White test. Six values may be obtained of K_Y, eight of K_R and ten of K_B. The final K accepted in each case is the arithmetic mean of all the individual Ks for each colour, which incidentally turn out to be rather similar to each other. (See Table 32.)

Figure 10 is a threshold diagram corresponding to Figure 9 but with the unknowns filled in, and with the lines spaced in proportion to the Threshold Values. It is important that this spacing out should not be misunderstood: it is a pictorial convenience only. Thus the values b, r, etc. are not measures of distance in space but measures of time, a point which has already been made in Chapter 1. If the threshold lines for Green and Black are drawn close together, it means that Variable X spends relatively little time between them. Diagrams of this type enable one to see at a glance how Variable X distributes its time between the threshold lines, and they could be regarded as the Threshold Model's equivalent of the preference scale diagrams constructed by psychologists (Guilford 1954, Woodworth and Schlosberg 1954, other references in Appendix 1). However the relationship between scale value and preference actually shown is in the case of the Threshold Model a complex one.

We are now in a position to answer the questions posed

TABLE 32

	K_B	K_R	K_Y	K_G	K_D
Paired with					
R	1.20				
R	1.16				
Y	1.20	1.24			
Y	1.12	1.90			
G	1.16	1.56	2.08		
G	0.98	1.32	1.60		
D	1.16	1.50	2.20	2.48	
D	1.00	1.12	1.68	2.00	
W	1.18	1.36	2.14	1.84	2.46
W	1.72	1.68	3.20	4.16	3.36
Mean	1.18	1.46	2.14	2.62	2.92

above about the quantitative relationship between the K and the Threshold Value of any colour. A glance at Figure 10 shows that the relationship is a negative one. Blue, which has the lowest threshold, (and which is therefore preferred in simultaneous choice tests) has the lowest K, that is stimulates the Go/No go decision-making mechanism least. The negative rank correlation is complete, as far as the five preferred colours are concerned. (White's K cannot of course be calculated because it is never the preferred member of a pair.) In practice the result of this negative correlation will be that in successive presentation tests in which the stimui are presented singly, or together with a less preferred "background stimulus", the two effects of a stimulus will tend to cancel each other out, with the result that it will be very difficult to demonstrate strong preferences. This is of course the result already obtained and described in Figure 7. (See also Franck in prep.).

Having found a negative relationship by rank order, the next question to ask is whether the relationship is a parametric lawful one.

TABLE 33

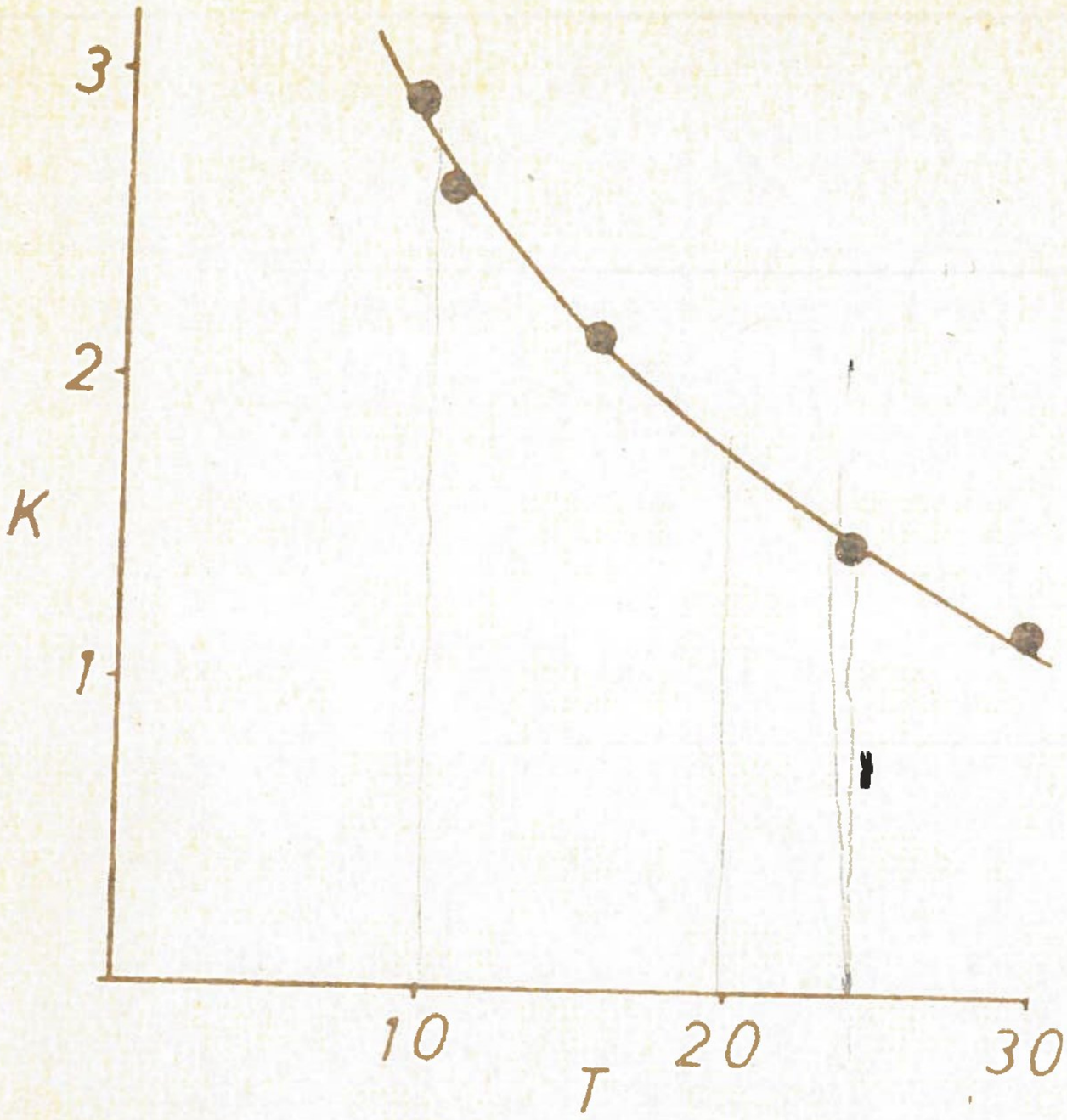
Mean K and T for each colour

Colour	T	K
Blue	29.64	1.18
Red	23.92	1.46
Yellow	15.57	2.14
Green	10.56	2.62
Black	9.26	2.92
White	1.00	Unknown

Figure 11

Black-headed gull chicks

(M Impekoven)



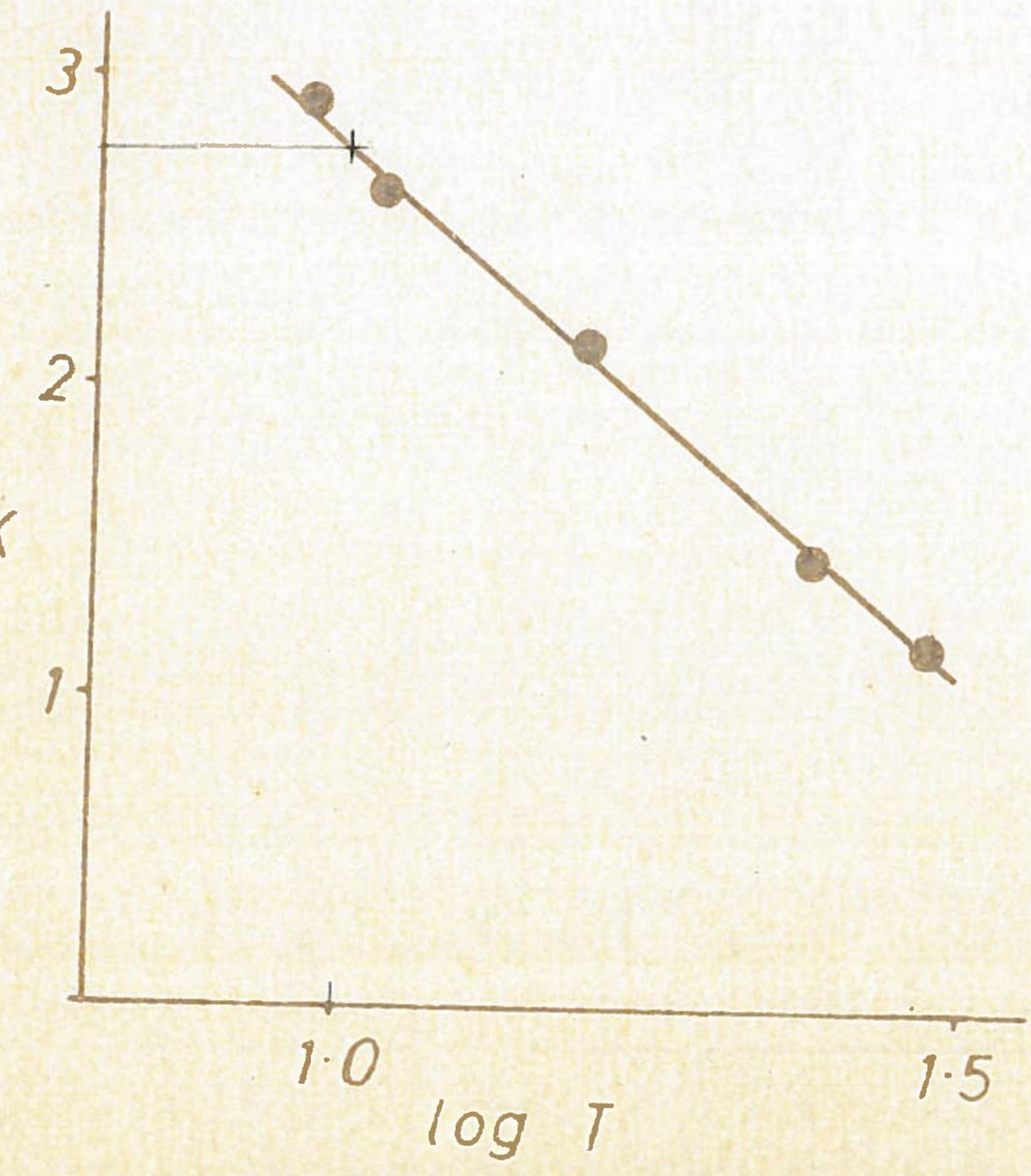


Table 33 gives the mean Total Threshold Value (T), and mean K for each colour. (Total Threshold Value it will be remembered is a measure of the total time spent by Variable X above the threshold concerned. Thus that of B is b+r+y+g+d+w = 29.64; that of R is r+y+g+d+w = 23.92 and so on.) Figure 11 shows the same information in graphical form.

Two different graphs are plotted in Figure 11. The first is a simple graph of T against K. It will be seen that the points seem to fall on a curved line suggesting that the relationship is a lawful one. The second graph is a plot of K against $\log_{10}T$. The points apparently fit a straight line indicating that the relationship is exponential. The calculated regression line for these points is drawn in on the log graph, and its equivalent in the natural graph. It is the line of $K = 6.15 - 3.39 \log T$.

If this regression is indeed a good expression of the law relating K to T, K_W which we have hitherto been unable to calculate should be around 6.15. Therefore, since w is defined as 1, we should expect that W presented by itself should receive about 6 pecks per minute.

It is of course true that both K and T have been calculated ultimately from the same data. The suspicion must arise therefore that a lawful relationship of this kind is an artifact of the methods of calculation, and does not reflect a real biological fact. However this is not the case: testing with artificially concocted figures

shows that any relationship between K and T, lawful or chaotic, positive or negative, is in principle possible. The smooth negative relationship shown by Figure 8 seems to be a property of the chicks.

CHAPTER 6 : FACTORS AFFECTING THE FUNCTIONAL UNITS POSTULATED; RELATIONSHIPS BETWEEN THEM; RELATED MODELS

INTRODUCTION

In this chapter a number of miscellaneous topics will be brought together. The classification given in Chapter 1 of possible functional units involved in pecking will be used as the basis for a discussion of what has been learnt from the experiments. As stated there, I recognize that this classification may not be a realistic one. However it is useful for my purpose, and I intend to take it as far as possible, and to use it as a framework for discussion. Therefore terms such as "Stimulus Evaluator" will be used without apology, though it is realised that unitary concepts like this are helpful only in a limited way. The different functional units will be dealt with separately. In the section on the Left/Right decision-maker, alternative ways in which the Threshold Model can be expressed will be mentioned. One of these alternatives, called the Attention Threshold Model is more powerful than the original one in that it can make more predictions. It will be developed in Chapter 7.

The four functional units postulated were:

1. The Go/No go decision-maker.
2. The Stimulus Evaluator.
3. The Left/Right decision-maker.
4. The Executive mechanism or "Pecker".

THE GO/NO GO DECISION-MAKER

This was mentioned as a possibility in Chapter 1. At the beginning of Chapter 3, preliminary reasons for believing in the existence of a separate mechanism determining when pecks occur were mentioned.In Chapters 4 and 5 further evidence from domestic and black-headed gull chicks respectively was given.

The Go/No go mechanism is influenced by the Stimulus Evaluator in the two species studied. In the domestic chick the precise relationship remains obscure. In the black-headed gull chick the relationship between the two effects of the Stimulus Evaluator, that on the Left/Right and that on the Go/No go decision-maker is a negative exponential one. It is possible that this difference between the results obtained from the two species is due to a difference in experimental method rather than to a real species difference.

The deduction of Prediction 1 depends on the assumption that there is no correlation between the activity of the Go/no go decision-maker, and that of Variable X.

For the purpose of this work so far it has been sufficient to treat the Go/No go decision-maker as a single functional unit, without enquiring about its own internal workings. I have at present no evidence on this. Ideas might be provided by information about the temporal patterning of pecks. I intend to build an apparatus for continuously recording pecks on paper tape. At present I can only give some general impressions gained over long periods of watching

domestic chicks pecking.

Pecks are not independent of each other. They tend to occur in runs during which the frequency of pecking is typically about 3 per second. My impression is that within such bouts the inter-peck interval is rather constant.

Bout length is very variable. Single pecks are not infrequent, and bouts of any length up to about ten pecks are common. This is by no means the maximum length however. The longest bout I have ever seen from a single chick was one of 307 pecks without a break at one stimulus, (a "correctly" oriented photograph of a hemisphere; see Appendix 2), at a very constant frequency of about 3 per second. At no time during the bout did it pause for very much longer than this interval, and certainly never as long as one second. After the bout, it paused for about 5 seconds, then gave another similar bout of 39 pecks, followed by another pause, and then another bout of 14 pecks. I have never seen anything else like this before or since. However it seemed to be only quantitatively different from other bouts, and I believe that in thinking of the mechanism of the Go/No go decision-maker it should be borne in mind that it must be potentially capable of such prodigious feats of repetition.

I have spoken of pecks as though they were all or none events. This was only for convenience because pecks are more amenable to counting than to measuring or timing. In fact however there is some vafiation in strength of pecking (Bousfield and Spear 1935). In long bouts of repetitive

pecking such as that described above, the intensity is indeed rather constant. However pecks may be very strong and decisive, or rather weak so that they scarcely work the microswitches. There is a characteristic pecking "intention movement", which presumably might be the result of low intensity activity of the Go/No go decision-maker. The movement I refer to in this case is a little jab of the bill towards the target which does not make contact. There is another form of behaviour which often precedes pecking and which might be called an intention movement. This is a lowering of the neck so that the bill is pointing nearly horizontally at the target, and the eyes seem to look along the bill at the target. It is often accompanied by a rapid side to side quivering of the head ("aiming"?).

Blindfolded chicks do not seem to give normal pecks, though they show drinking movements indistinguishable from normal ones. They occasionally show apparent pecks into the air, leaning far over backwards as they do so. Blindfolded chicks placed on a substrate completely covered with powdered food sometimes discover the food. This may be by accident: one chick made a bill-wiping movement, probably elicited by tactile stimuli from the little plastic ring round the eye used for blindfolding. This caused a little food to enter the bill, and the chick continued to feed for some time by bill-wiping. This is particularly striking in view of the fact that bill-wiping is normally a rejection movement which may be elicited by presumably noxious substances in the food such as strong mustard.

Another blindfolded chick discovered the food as a result of a preening nibble at its own foot, and continued to feed by a kind of ill-coordinated pecking in the general direction of the same foot.

Some blindfolded chicks appeared to be stimulated to show a form of pecking by auditory stimuli from other chicks feeding in the vicinity. This "pecking" was extremely clumsy and abnormal in appearance, and it did not occur very often.

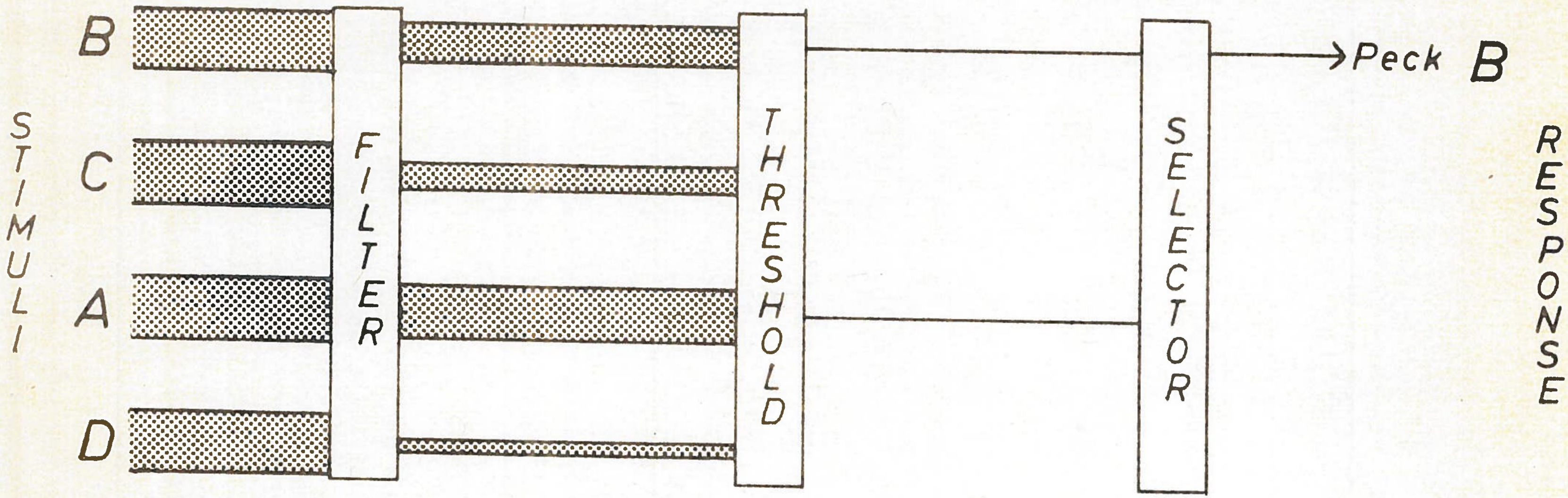
These observations suggest that visual stimuli are indispensable for normal pecking, but that possibly the Go/No go decision-maker is just capable of initiating a form of pecking without reference to the Threshold System.

THE STIMULUS EVALUATOR

This is the functional unit concerned with translating information from the stimuli received via the eyes, into quantities along some kind of "stimulating value continuum". It corresponds to Marler's "Filter", and his remarks apply to it (Marler 1961).

The quantities arrived at by the Stimulus Evaluator are used to determine the Threshold Values. In addition, in the two species studied in respect of absolute peck numbers, the stimuli exert an effect on the Go/No go decision-maker, and it is economical to think of the same Stimulus Evaluator as being implicated. In the gull chick the quantitative relationship between the two roles of the stimuli suggests that the same Stimulus Evaluator is indeed involved in both cases, inversely in one of them.

Figure 12 Inverted Threshold Model



The order of preference is A B C D, as indicated by thickness of lines leaving Filter (stimulus evaluator). On this occasion only A and B exceed Threshold, and B is chosen.

THE LEFT/RIGHT DECISION-MAKER

It is the main purpose of this thesis to argue that the mechanism which determines the direction of each individual choice is some kind of analogue of the Threshold Model. The model has so far been discussed with reference to one particular method of representation. The form of Figure 1 and other similar diagrams suggests a particular kind of structure which could be, and has been, used for physical simulation. The concepts of the fluctuating Variable X, and the thresholds with which it is supposed to interact, all belong to this particular picture. There are however other ways in which the fundamental properties of the model could be visualised. Which of them is to be preferred is partly a matter of individual taste. Three criteria by which they might be judged are generality, physiological feasibility, and graphical or physical representability. The form of the model so far discussed is good in the latter respect; I am not competent to judge its worth in the second. It is not the most general form as already mentioned, since it embodies assumptions not necessary for the deduction of the predictions tested.

A similar version of the model, which might be preferable to the original one in some respects, I call the Inverted Threshold Model (see Figure 12 and discussion below). It is formally the same and gives the same predictions, but is expressed in a different way which might be more realistic. Each stimulus is assigned a stimulating value by the Stimulus Evaluator, as in the original model. All the

values from the different available stimuli are compared or matched up against a single common "pecking threshold value" which varies from moment to moment If only one of them exceeds the threshold, only the stimulus concerned will be pecked. If more than one passes through the threshold barrier the stimuli will have an equal chance of being pecked. A possible way in which this equality of probability of being pecked is achieved will be mentioned below.

A more general statement of the properties of the class of models exhibiting all that is essential of the behaviour of the original form would be in terms of <u>states</u> with unspecified transition probabilities. Thus in the black-headed gull experiments (Impekoven), the birds are at any instant in one of seven possible states:

1. Equally likely to peck at all six colours.
2. Equally likely to peck at all colours except White.
3. Equally likely to peck at all colours except Black and White.
4. Equally likely to peck at all colours except Green, Black, and White.
5. Equally likely to peck at all colours except Yellow, Green, Black and White.
6. Pecking only af Blue.
7. Not pecking at all.

Expressed more generally without reference to a particular experimental situation, for any n stimuli presented in any combinations there are n+1 states, ranging from being equally likely to choose all

the stimuli through being equally likely to choose all except the least preferred, being equally likely to choose all except the two least preferred, etc., until the final state which is making no response at all.

The original form of the model is restricted in that the states are ordered such that it is impossible to pass from one to another without passing through specified intermediate ones. This restriction is of course entirely unnecessary for the deduction of the predictions tested, and the form with unspecified transition probabilities between states would be preferred on grounds of generality. I feel that the original form on the other hand is preferable on grounds of physical representability and perhaps physiological feasibility as well. However this is difficult to judge. The original form may lend itself better to crude physical simulation, for example the mercury column model mentioned in Chapter 3, but if a computer programme is used as a method of representation the more general form is at least as easy to deal with.

Does this general class of models (i.e. those having the properties listed on the previous page) include all those capable of yielding Prediction 1? Miss V. Cane (pers. comm.) has shown that Prediction 1 is/the only polynomial of second order or less which will satisfy the following common sense conditions:

1. If $P_1 = 50\%$, $P_2 = P_3$ (and if $P_2 = 50\%$, $P_1 = P_3$).

2. If P_1 or $P_2 = 100\%$, $P_3 = 100\%$

Other models, such as the Set Releasing Value Model, also satisfy these common sense conditions, and no doubt others give polynomial formulae of second order or less, but models of the Threshold type are the only ones known to me which are members of both these sets. In other words I do not know of any other models capable of yielding Prediction 1. On the other hand there may be very many models whose predictions are in practice very close to Prediction 1 even if they are formally different.

The two main problems to be solved in attempting to simulate or visualise physiological analogues of models of the type to which the Threshold Model belongs, are as follows:

1. There must be some source of variation which, in the terms of the general formulation, causes the animal to shift from one state to another. This was the role performed by Variable X in the original version. It was performed by the fluctuating mercury level in the physical model mentioned in Chapter 3; in a computer simulation the result was achieved by feeding in random numbers. I do not know what might provide this variation in the animal. The present evidence does not allow us to choose between a random or a non-random source, nor does it give much indication of the time-scale of the fluctuations. Evidence on the effects of hunger and thirst will be given in a separate section. Neurones, like all communication channels are "noisy" (Gerard 1960, Pringle 1951, 1963). This variation might contribute to the state changes.

In the more specific versions of the model, the Original and Inverted forms in which two hypothetical constructs are proposed, one can ask which of them provides the variation. For example in the original model, it was suggested that Variable X fluctuates rather than the threshold levels. Similarly in the Inverted model, the Pecking Threshold was thought to vary rather than the Stimulating Values. Both these suppositions are economical, because they imply fluctuations in only one variable, rather than parallel and synchronous fluctuations in many variables corresponding to the different stimuli. However, as mentioned in Chapter 2, there is no reason why the variables corresponding to the different stimuli should not also change. In the terms of the Original model, this would mean that the thresholds would have distributions, but, as also stated in that chapter the distributions must not overlap to any great extent.

2. The second major problem encountered in attempts to simulate or visualise physiologically the proposed mechanism, concerns the way in which choices are distributed equally between stimuli, when, in the general terms the animal is in one of the states of non-discrimination, or in the terms of the original Threshold Model, when Variable X exceeds more than one threshold. This state will be called "suprathreshold indecision". When only two stimuli are involved, the indiscriminate behaviour shown may be called "50/50 behaviour".

In the mercury column model the problem was solved by alternation. Alternation behaviour in choice situations is known in

rats (Glanzer 1953), but it does not seem to occur in chicks, at least in any simple form (Hayes and Warren 1963, and own observations). Whether chicks show a more complex type of alternation, perhaps alternation of bouts rather than of individual pecks may be shown by the study of continuous records of pecks on paper tape.

In a computer simulation of the model random numbers were used to provide this 50/50 behaviour. Random noise in the nervous system might play an equivalent role in the animal. One possible way in which this could occur is best illustrated with reference to the Inverted model (though an equivalent can be thought of for the Original one).

Suppose that the channels carrying the information about the "stimulating value" of the different stimuli pass to a "selector" mechanism which selects for a peck the stimulus with the highest "stimulating value" at a given moment (see Figure 12). If there were no "pecking threshold" barrier this would mean that virtually 100% of all the pecks would be directed at the preferred stimulus except in those cases where the "stimulating values" of two stimuli were so close together that variations due to noise in the system became significant. If a pecking threshold barrier is interposed as described above, on the other hand, a very different kind of result will be obtained. Since the threshold system postulated follows the all or none rule, the supposed continuous variation of the stimulating values "upstream" from the threshold barrier will be reduced to one

of two values "downstream". One of these values will be zero, and the other, whatever it is, will be constant for all stimuli. (In fact it is not necessary that the lower value should be zero. All that is necessary is that it should be consistently lower than the other value, and that the higher value should be equal for all stimuli.) If the stimulating values of two stimuli both manage to pass the test of the threshold barrier, both will start out in their channels from threshold barrier to selector with exactly equal values. Now noise in the channels leading from threshold to selector will play the decisive role in determining which is larger when they reach the selector, and therefore which stimulus will be pecked. If the stimulating value of only one stimulus penetrates the threshold barrier, only that stimulus can be pecked.

Clearly many other theories could be developed for a "50/50 mechanism" based on nervous noise. In making this kind of theory, one is not explaining the basic causation of the "randomness" in the system, but making use of the fact that such randomness is already known to physiologists. It is a different kind of "explanation" (Deutsch 1960).

An interesting possible basis for 50/50 behaviour is the concept of selective attention as developed by Sutherland and Mackintosh (e.g. Sutherland 1959, Mackintosh 1963; for a convenient summary see Sutherland 1964), and by others (Lawrence 1949, Zeaman and House 1962, Lovejoy 1965).

Let us suppose that the animal is at any one time attending to only one out of the many possible cues or stimulus dimensions by which stimuli might be distinguished: 50/50 behaviour occurs when it is attending to an irrelevant cue, that is one according to which the stimuli do not consistently differ.*1

For example in a colour preference test, the animal will, as far as colour is concerned, show 50/50 behaviour if it attends to the cue of position, and consistently chooses say the left hand stimulus, or the one it happens to be nearest. Thus if it shows an 80% preference for Orange over Green, the interpretation would be that, of the time spent attending to any cue, 60% was spent in attending to colour, and all the pecks were at Orange. During the remaining 40% of the time, it was attending to irrelevant cues such as position, and Orange and Green were equally likely overall to be pecked. Thus according to this theory, an animal's response to suprathreshold indecision is to switch its attention.*2

This gives rise to a development of the Threshold Model which, under the name of the Attention Threshold Model, will be discussed in more detail in the next chapter.

---

*1 Lovejoy (1965a and b), in his formal treatment of two attention models, makes precisely these assumptions.

*2 This could be related to McFarland's (1966) theory of displacement activities, according to which " 'frustration', which may result from conflict, thwarting or non-reward, diverts 'attention' ", thereby causing the switch to the behaviour called displacement. McFarland has some evidence for this.

THE EXECUTIVE MECHANISM OR "PECKER"

I have no information at all on the machinery responsible for actually guiding the bill toward the chosen target, executing the decisions of the Left/Right decision-maker. Hess (1956) has shown in domestic chicks that a relation between locus of stimulation on the retina, and peck direction, develops in the absence of visual feedback, and may be unalterable by visual feedback. From the present point of view, an interesting and difficult problem is that of how, through the stimulus evaluation and choice processes, the information about stimulus position remains tied to the information about stimulus value, and choice by the Left/Right decision-maker.

Facts which might be relevant to any future investigation of the executive mechanism, are those already mentioned about pecking intention movements and pecking in blindfolded chicks, and also facts about movements similar to, but slightly different from, true pecking. An example of these is "bill-pulling", resembling "bill-raking" in dust-bathing (Kruijt 1964), in which the bill strikes the substrate rather vigorously, and is then jerked or pulled towards the body. This may function like ground-scratching, to uncover food. It occurs in the same kinds of laboratory situation, for example during extinction in a Skinner Box. "Nibbling" resembles the first stage of drinking: the bill is slid around the substrate opening and closing. This movement certainly accounted for some of the "pecks" registered by my counters.

INFLUENCES ON THE FUNCTIONAL UNITS PROPOSED

Influences of the four functional units on each other have already been discussed. Thus the Stimulus Evaluator influences both the Left/Right and the Go/No go decision-makers in both the species studied, but there is no direct causal link between the activities of the two decision-makers. Other factors which might be expected to influence some of the functional units are learning; motivational state; and mechanisms of selective attention and interactions between stimulus elements - "heterogeneous summation". The last of these three factors will be considered in the next chapter.

Learning

A change in overall tendency to peck rather than a selective change in relative amount of pecking at different stimuli, would perhaps be due to a change in the behaviour of the Go/No go decision-maker, a change in K.

A change in relative tendency to peck at different stimuli, discrimination learning, could represent a change in the behaviour of Variable X or its equivalent; in the more general terms this would mean a change in the relative amounts of time spent by the animal in the various states. This type of change could affect percentage preferences in a quantitative way only: preference rank orders could not be reversed.

Alternatively discrimination learning might represent change in threshold levels. If threshold levels changed so much that they crossed each other, this would mean in the general terms that new states

would become possible. For example the list of states given above for the black-headed gull chick does not include the possibility that the animal might choose Red without being at least equally likely to choose Blue. If choice of Red were rewarded on the other hand, this state might become possible; in the terms of the Original model the threshold lines of Red and Blue would cross, and the preference rank order would change.

In the black-headed gull chick it might be possible to test whether discrimination learning acts on the Left/Right decision-maker alone, or on the Go/No go decision-maker as well. (If it acts by way of the Stimulus Evaluator we should expect the latter, since the Stimulus Evaluator affects both the decision-makers.) If discrimination learning affects both decision-makers the negative exponential relationship of Figure 11 should remain the same even though the actual values of K and T of the different stimuli would change. If it affects only the Left/Right decision-maker, T will change but not K, and the relationship expressed in Figure 11 will no longer hold.

Motivational state

In the earliest formulation of the Threshold Model the word Drive was used instead of Variable X. This was to emphasise the parallel between this model and others such as that of van Iersel and Bol (1958). Variable X is preferable, partly because in the light of a more general formulation of my model the parallel turns out to be a superficial one, and partly because Drive is a muddled and ambiguous

term (Hinde 1956, 1959).

However it remains possible that Variable X might indeed be closely associated with internal variables sometimes identified with the term Drive. These internal variables might also affect others of the functional units proposed here.

The experimental manipulations used here to define motivational state are deprivation of food and of water. A hungry chick is one deprived of food and/a thirsty chick is one deprived of water. These will be used only as relative terms, comparing different groups of chicks who have had different treatments.

If hunger and thirst influence the Go/No go decision-maker (K) they will change absolute peck numbers but not percentage preferences. If they influence Variable X they will change percentage preferences. In neither case will they affect preference rank order. This can only be done by causing threshold lines to cross over, or in the terms of the more general formulation, by rendering new states possible. This could be achieved by influencing the Stimulus Evaluator.

Effect of hunger and thirst on Variable X and K

Common sense, perhaps influenced by subjective experience, would expect that, in successive presentation tests, deprived animals should show lower percentage preferences than satisfied ones: a starving animal is unlikely to be fussy. Expressing it as the principle that generalisation gradients flatten out with deprivation, psychologists have confirmed this experimentally (e.g. Jenkins, Pascal and Walker 1958

on pigeons). Weidmann (1959) on the other hand, using black-headed gull chicks found an approximately linear increase with starvation time in peck-rate at different stimuli. The lines for the different stimuli diverged from a point, indicating a multiplicative interaction between the effects of starvation and external stimuli. That is to say percentage preferences did not change.

The Threshold Model even with Variable X positively related to hunger does not make any definite predictions about the effect of starvation on percentage preference in successive presentation tests, unless further assumptions are made. For the successive situation therefore, it seems best not to think in terms of predictions, but to use the experimental results to obtain ideas about the ways in which hunger and thirst affect pecking. For example Weidmann's finding could be explained on the assumption that starvation influenced the Go/No go decision-maker (K) in a multiplicative way.

However, the model with the additional assumption of the positive association between Variable X and deprivation, does make a definite prediction about the effect of deprivation on percentage preference in simultaneous presentation situations: since a raised Variable X will cause more 50/50 behaviour, percentage preferences should decrease with increasing deprivation. It is not obvious that this would be expected by common sense in the simultaneous situation.

I did experiments to test the prediction that hungry domestic chicks show lower percentage preferences in simultaneous choice tests

than less hungry ones, and that thirsty chicks show lower percentage preferences than less thirsty ones. In both cases the deprived animals were treated in the same way as all the animals used in the experiments previously described, never having had food or water. They were compared with animals given water (not thirsty) and with animals given food (not hungry). The experiment on the effect of watering will be described first, since it gave a more straightforward result.

Experiment on effect of watering

Four hundred and twenty chicks were tested in groups of 6, 70 groups of 6 in all. Half the chicks were given water ad-lib since the evening of day 1* when they were collected from the farm. The other half were never given any water. Neither group had ever been given food. Twenty-two of the groups of 6 were tested on day 2 and the rest on day 3.

The method of testing preferences was the same as in previous tests, using electric peck counters. Only two of the three chambers of the peck-counting apparatus were used so that in each 5-minute trial a group of 6 from both the deprived and the watered chicks were simultaneously tested. The preference tested was in all cases that for a blue hemisphere over a green one. Since I was interested not in the preference itself, which I already knew to exist, but in

---

* Day 1 was the first day of life for many of the chicks, but some were a little older, owing to the spread of hatching times.

how it would be affected by thirst, there was no need to vary the positions of the stimuli,and I did not do so. Thus in the left hand compartment blue was on the left, and in the right hand compartment green was on the left. On the other hand it was critical that the two groups of chicks, the deprived and the watered, should have equal and evenly distributed turns in each of the two compartments, and this was arranged.

The most striking result was the enormous reduction which watering caused on the overall tendency to peck. The mean number of pecks per trial in the deprived group was 41.7. In the watered group it was 4.7. The difference is highly significant ($P < 0.00006$ Mann-Whitney U test 2 tailed).

The percentage preferences also show a significant difference but it is not so striking. The mean percentage preference for blue over green in the deprived group was 82.4. In the watered group it was 87.0 ($P < 0.01$ Mann-Whitney U test 1 tailed). The prediction is therefore fulfilled.

Experiment on effect of feeding

Three hundred and sixty chicks were tested in groups of six, 60 groups in all. Half of them were given food ad-lib (Baby Chick Crumbs) from day 1 when they were collected, until they were tested on day 2 or 3. Thirty-two groups were tested on day 2 and the rest on day 3, the method of testing being the same as in the experiment on thirst. The same blue and green stimuli were used.

As in the previous experiment the deprived chicks gave a lower percentage preference than the others, the mean percentage preferences being respectively 61.8 and 74.3 ($P < 0.01$ Wilcoxon matched pairs test, 1 tailed). The prediction is thus again fulfilled.

However the effect of feeding is surprising in that it increased the total number of pecks. The mean number of pecks per trial of the unfed chicks was 72.3. That of the chicks given ad-lib food was 109, and the difference is significant ($P < 0.05$ Wilcoxon matched pairs test, 2 tailed).

Conclusion

The findings about percentage preferences are compatible with the theory that both food and water deprivation increase the overall level of Variable X. The effect of hunger on absolute peck numbers is rather strange. It would be expected if hunger decreases K, but this is the opposite conclusion to that drawn from Weidmann's result on black-headed gull chicks. This contradiction, together with the unexpected nature of the domestic chick result to common sense, suggests that any theoretical conclusions based on the effects of hunger on absolute peck numbers would be premature. It is possible that the hungry chicks pecked less as a result of general physical weakness from starvation. Alternatively, it may have been the result of a learning process, persistent lack of reward for pecking leading to a waning in general tendency to peck (see Appendix 2).

The findings about percentage preferences are compatible

with the theory that both food and water deprivation increase the overall level of Variable X. However unlike say Prediction 1 and Prediction 6, the prediction tested in this case was not a precise quantitative one, and its verification is only weak evidence for the theory from which it was deduced: it could be due to many other things, for example some kind of learning effect.

Effects of hunger and thirst on the Stimulus Evaluator

Effects on the Stimulus Evaluator could show themselves in the form of changes in preference rank order. There are cases known in which changes in motivational state have caused changes in order of preference between stimuli. This may involve a change in cue or stimulus dimension attended to (Sutherland 1964), rather than a change in preference within one stimulus dimension (e.g. Tinbergen, Meeuse, Boerema, and Variosseau 1943).

Psychologists have demonstrated ("Drive Discrimination") that animals can be trained to choose different stimuli when hungry and when thirsty (e.g. Bolles and Petrinovitch 1954 on rats).

Dr. Impekoven and I did experiments to try to train domestic chicks to approach different colours when hungry and when thirsty. They were kept in the coloured light apparatus described in Chapter 2, with food in cubicles of one colour, and water in cubicles of another colour. Half the chicks received food in red cubicles and water in blue ones, and the other half the reverse arrangement. They were then made hungry or thirsty and given preference tests between the two colours.

They showed strong preferences in the predicted directions. For example, in one experiment, out of 15 hungry chicks which made a choice, 12 chose the colour previously associated with food; and out of 16 thirsty chicks, 10 chose the colour associated with water. The formerly hungry chicks were then fed and made thirsty, and the formerly thirsty chicks were giveh water and made hungry. On retesting, of the 11 chicks now hungry which responded, all chose the colour associated with food, and of the 12 chicks now thirsty which responded, 11 chose the colour associated with water.

Several other experiments confirmed the conclusion that the colour preferences of chicks in this apparatus can easily be switched by changes in internal state. As mentioned in Chapter 2, control experiments with coloured and white light of different intensities suggested that in all cases the learned choice behaviour was not based on brightness discrimination.

It seems therefore, that in this approach situation hunger and thirst are capable of exerting an effect on the Stimulus Evaluator. It might be that this is a very artificial effect which does not occur in nature. However, for similar results on black-headed gull chicks in more natural conditions, together with a general discussion of this kind of phenomenon see Impekoven (in prep.).

CHAPTER 7 : INTERACTIONS BETWEEN STIMULUS DIMENSIONS

INTRODUCTION

The problem of how stimuli combine has interested both ethologists and psychologists, concerned respectively with absolute numbers of responses, and discrimination probabilities. The original "Law of Heterogeneous Summation" (Seitz 1940, Tinbergen 1951) was little more than a qualitative statement that stimuli can replace each other in contributing to a response, and that the probability or strength of response increases with the number of stimuli presented. Later authors have treated the law in a quantitative way, asking for example whether it is best described by the arithmetic operation of addition, or by that of multiplication (Weidmann 1959).

The related psychological concept of "Additivity of Cues" in discrimination learning is particularly relevant here because the formula called here Prediction 1 had previously been used as a quantitative expression of the Additivity of Cues effect (Hara and Warren 1961; Sutherland pers. comm., who has a theoretical rationale for it; McGonigle pers. comm.). My own interest in the formula was originally as a possible means of expressing the law of Heterogeneous Summation quantitatively. Though the Threshold Model led away from this subject for a time, it is gratifying that the version of it called the Attention Threshold Model is able to return to make predictions in the field of interactions between cues. This will be the main subject of this chapter.

The type of experimental situation with which we will be concerned may be illustrated in terms of an extension of Experiment 4. The three stimuli presented in all possible pair combinations were, it will be remembered, Blue Solid, Red Solid, and Red Flat. They were treated as discrete objects each with its own threshold value. There is of course another way of looking at the three pair combinations. Thus when Blue Solid is presented with Red Solid, the test could be called a colour preference test with solidity irrelevant.* Red Solid versus Red Flat could be called a solidity preference test with colour irrelevant. Finally when Blue Solid is presented with Red Flat, the animal could show either a colour preference or a solidity preference or both. This is an Additivity Test: both cues are relevant.

If we introduce a fourth stimulus object Blue Flat, the number of possible pair combinations is raised to six. Blue Solid with Blue Flat is a solidity test. Blue Flat with Red Flat is a colour test. The presentation of Blue Flat with Red Solid is called an Opposition Test since it pits the colour preference against the solidity one.

---

* The concept of "relevance" will be used in this sense. Thus an irrelevant cue is one according to which the stimuli do not consistently differ. This might mean either that the stimuli are identical with respect to the irrelevant cue, or that if they differ according to the irrelevant cue, they do so in a random manner with respect to the cue being considered by the experimenter, the relevant cue. In discrimination learning experiments, a relevant cue is one correlated with reward.

None of the simple versions of the Threshold Model we have discussed so far is able to make predictions relating the percentage preferences given in these six situations, other than Prediction 1 which incidentally applies to those combinations of choice test in which three stimuli are presented in all pair combinations. The simple versions of the model relegate interactions between cues, and combination of the effects of stimulus elements, to a role played inside the Stimulus Evaluator, determining threshold values in ways unknown.

However there are more complex versions of the Threshold Model, which in addition to yielding Prediction 1 and the other predictions so far discussed, make predictions about interactions between cues. These are versions of the Attention Threshold Model, mentioned in the last chapter in the context of mechanisms of 50/50 behaviour. It was suggested that an animal showed 50/50 behaviour when it ceased to attend to the relevant cue(s) or stimulus dimension(s) according to which the stimuli consistently differed, and instead attended to irrelevant cues such as position.

Before further predictions can be deduced from such a model, it must be expressed more formally than has been done so far. This will be done in the next section.

ATTENTION THRESHOLD MODELS

For convenience the language of the Original Threshold Model - Variable X, and threshold levels determined by external stimuli - will be used.

The basic idea of Attention Threshold Models is that there is not just one Variable X/threshold system, but many, corresponding to the different cues or stimulus dimensions by which stimuli might be distinguished. Thus there is a threshold system which makes decisions according to colour, another which makes decisions according to brightness, another for size etc. These separate threshold systems might correspond to Sutherland and Mackintosh's "Analysers" (Sutherland 1964). They will be called simply "Systems". Each System resembles the Original Threshold Model in that it has its own Variable X, and thresholds corresponding to the available external stimuli, in this case analysed according to the specific cue concerned. At any one instant of time, the animal attends to only one System, in the sense that at that moment only that System is potentially able to determine the direction of a choice: whether it actually does so will depend upon its Variable X (andalso on the Go/No go decision-maker but that can be ignored). The response to suprathreshold indecision is a switch in attention to another System.*

---

* A difficulty arises here if more than two stimuli presented together are considered. Is the response to suprathreshold indecision the same when three thresholds are exceeded as when only two are? The simple minded approach adopted above would suggest that it is, in which

(cont. on next page)

It is necessary for the deduction of Prediction 1, to suppose that after a switch in attention, a choice is as likely to be made as if the switch had not occurred. Perhaps the most economical way to embody this requirement in the model is to assume that one of the Systems called the Terminal System, plausibly that concerned with analysing the <u>positions</u> of stimuli, is always capable of reaching a definite decision: instead of going into the state of suprathreshold indecision, the animal, when attending to this System, might, say, choose the stimulus which it happened to be nearest, or consistently choose the right hand stimulus.

The simplest Attention Threshold Model which yields Prediction 1 then is one which assumes that whatever System it is attending to, the animal always responds to suprathreshold indecision by switching its

---

* cont. from previous page

case some unlikely consequences follow. For example, it is predicted that when more than two stimuli are presented together, the numbers of responses to all except the most preferred should be equal. For this reason it seems more probable that suprathreshold indecision leads to indiscriminate choice between only the stimuli whose thresholds are exceeded, rather than to general random behaviour. In this case Attention Threshold Models lose much of their attractiveness as explainers of "50/50 behaviour", since further complicating assumptions are necessary. One could assume either that an animal can only attend to 2 stimuli at a time, or that when it switches attention as a result of suprathreshold indecision, the information about which thresholds were exceeded is stored, and influences the final choice. For the present discussion there is no need to face up to this difficulty, since the experiments to be dealt with involve only pairs of stimuli.

attention directly to the Terminal System, supposedly that concerned with position. However this is a rather restricting assumption. A more general one would be that the animal does not necessarily switch its attention directly to the Terminal System, but may switch first to other Systems, and only necessarily switches to the Terminal System if all the others fail to reach a decision. One can picture a hierarchy of Systems, with waves of attention passing along it. Each attention wave ends either when one of the Systems is potentially able to make a decision because its Variable X lies above only one threshold, or when it reaches the Terminal System which can always make a decision.

This hierarchy model only yields Prediction 1 in the way given in Chapter 1, if the following additional conditions are met:

1. There is a dominant or, to borrow a word from the social hierarchy literature, Alpha System, which lies at the head of the hierarchy. Waves of attention do not necessarily have to begin in the Alpha System, but if they begin lower down in the series, they cannot travel back to the Alpha System. The three stimuli used to test Prediction 1 must differ consistently only according to the cue associated with the Alpha System.

2. If the animal attends to a sub-dominant System whose Variable X does not lie above the threshold of an available stimulus, it immediately switches its attention to another System.

One version of the model would suppose that the hierarchy of Systems is a rigid rank order, such that from any given System,

attention can only switch to the one below it. Alternatively one could consider more variable transition probabilities between the Systems, with the proviso (Condition 1) that for Prediction 1 to be deduced, the probability of transition from any other System to the one relevant to discriminating the experimental stimuli for a test of Prediction 1 be close to zero.

We can now deduce the consequences of an Attention Threshold Model, for experimental situations involving interactions between cues, such as the extension of Experiment 4 discussed above. For the sake of ease of calculation a rigid type of hierarchy will be assumed. To summarise the assumptions made: a wave of attention can originate in any System, but it can travel only one way along a rigid linear rank order of Systems. Once started, such a wave must end in one of two ways: either, one of the Systems is attended to when its Variable X is above only one threshold; or, the wave reaches the Terminal System. In either case a choice will be made (on condition that the Go/No go decision-maker permits it). A new attention wave cannot begin until the previous one has ended in one of these two ways. From now on, the name Attention Threshold Model will be used for the model having these assumptions.

Consider the six choice tests discussed above. They are listed in Table 34, using abbreviations B for Blue, R for Red, S for Solid and F for Flat.

TABLE 34

Test	Stimuli		Description
1	BS	RS	Colour test solidity irrelevant
2	BF	RF	" " " "
3	BS	BF	Solidity test colour irrelevant
4	RS	RF	" " " "
5	BS	RF	Additivity test both cues relevant
6	BF	RS	Opposition test both cues relevant

It will be assumed that the System concerned with colour is the Alpha system, that the Solidity System is higher in the hierarchy than the Terminal System of position, and that except with respect to these three cues the stimuli are identical.

It should be remembered that this particular hypothetical experimental situation is being discussed purely for simplicity. The conclusions drawn should be more widely applicable. Thus "colour" represents the Alpha System; "solidity" represents an intermediate System, and "position" represents the Terminal System. "Blue" represents the preferred quality on the Alpha System, "Solid" the preferred quality on an intermediate System, etc.

The model, and the calculations, may be better understood with reference to the flow diagram (McFarland 1965) in Figure 13, which happens to represent the situation in which both cues are relevant. The three nodes (circles) represent the states of attending to colour (C), solidity (D for depth), and position (P). The other Systems need

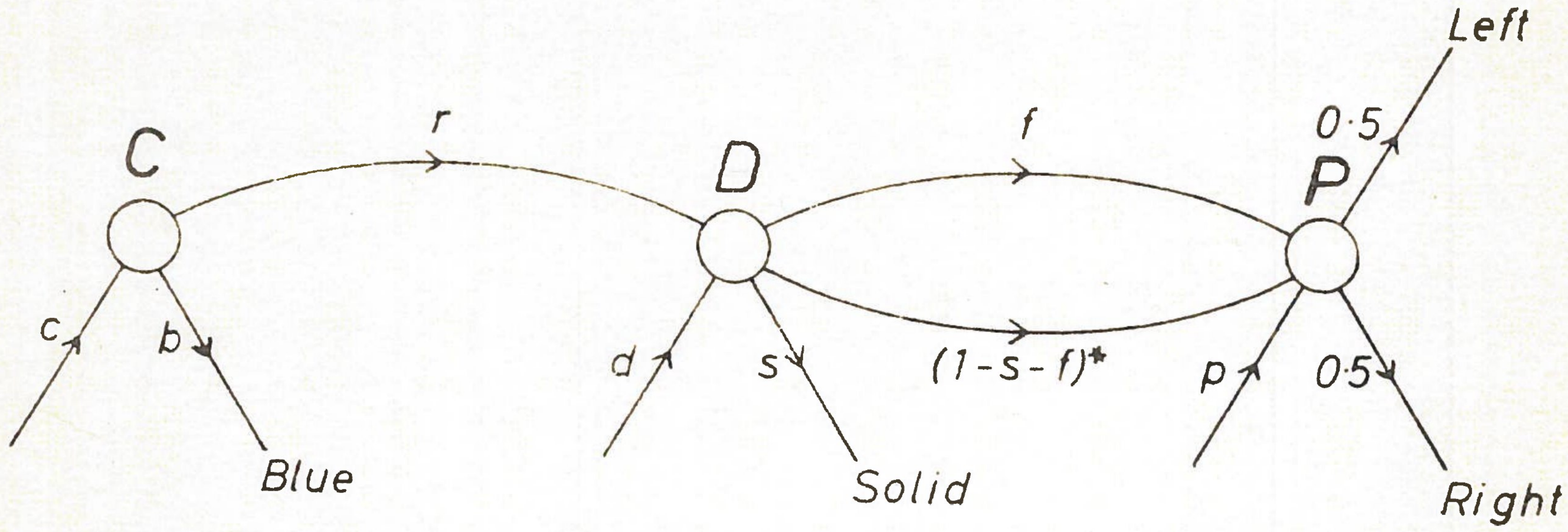
Figure 13 *Attention Threshold Model*

r ——— Red

b ——— Blue

f ——— Flat

s ——— Solid



*Branch absent if D begins

not be considered; since they are not Alpha, and their cues are not relevant they cannot affect the behaviour.

The transmittances (letters or numbers by lines) represent probabilities (Huggins 1957). Thus c, d, and p, are respectively the probabilities of a wave of attention beginning in Systems C, D, and P.* b is the probability that the Variable X in System C exceeds Blue's threshold but not Red's. That is, it is the Interthreshold Value between Blue and Red, and is written in as such in the threshold diagram above node C. r, the Total threshold Value of Red, is also the probability of a switch in attention from C to D, since we are considering both cues to be relevant. Similarly, s is the Solid - Flat Interthreshold Value, and f, the Total threshold Value of Flat, and the probability of a switch in attention to P provided that the chain of attention begins in D. If the chain of attention begins in C on the other hand, the probability of a switch to P is f + (1-s-f) = (1-s), because of Condition 2 above. Finally the probabilities of choosing Left and Right when the Terminal System P is attended to are both represented as/a half. (In fact, it might well be that one of these should be 1 and the other 0, but since we are labelling the stimuli only according to their qualities with respect to the other two cues, it is easy to see

---

* The simpler version of the model mentioned above, based on the assumption that all attention waves begin in the Alpha System, is obtained if d and p are made equal to zero. It is convenient to use this version for experimental examples where insufficient details are published to enable the more complex one to be used.

that in practice, these two transmittances can each be regarded overall as a half.)

Learning could act in the ways already mentioned in Chapter 6 - alteration of threshold values or of Variable X within the different Systems - but also by varying the transition probabilities of attention-switches between Systems, probabilities of attention waves beginning in different Systems, and relative positions of Systems in the hierarchy. All these could be represented as changes in the transmittances in flow diagrams such as Figure 13. Sutherland and Mackintosh's (Sutherland 1964) "two stages" in discrimination learning could of course be expressed in these terms. We will here not be concerned with the process of learning however, and will regard learning simply as part of the ontogenetic history of the animal leading up to its state - threshold levels, order of Systems in the hierarchy etc. - at the time of testing.

Table 35 gives the predicted numbers of pecks at each of the stimuli in the 6 tests of Table 34. Strictly these expressions should be multiplied by K, but since we are mainly concerned here with percentage preferences this can be ignored, as it will cancel out.

These expressions for peck numbers given in Table 35 may be combined to calculate percentage preferences. These are given in Table 36, each labelled with the number given to the test concerned in Tables 34 and 35. Thus for example P_4 is the percentage preference for RS over RF.

TABLE 35

Test Stimulus		Number of pecks					
1	BS	$c(b+\frac{r}{2})$	+	$d(\frac{s+f}{2})$	+	$p(\frac{1}{2})$	
	RS	$c(\frac{r}{2})$	+	$d(\frac{s+f}{2})$	+	$p(\frac{1}{2})$	
2	BF	$c(\frac{b+r}{2})$	+	$d(\frac{f}{2})$	+	$p(\frac{1}{2})$	
	RF	$c(\frac{r}{2})$	+	$d(\frac{f}{2})$	+	$p(\frac{1}{2})$	
3	BS	$c(b+r)(\frac{s+1}{2})$	+	$d(\frac{s+f}{2})$	+	$p(\frac{1}{2})$	
	BF	$c(b+r)(\frac{1-s}{2})$	+	$d(\frac{f}{2})$	+	$p(\frac{1}{2})$	
4	RS	$c(r)(\frac{s+1}{2})$	+	$d(\frac{s+f}{2})$	+	$p(\frac{1}{2})$	
	RF	$c(r)(\frac{1-s}{2})$	+	$d(\frac{f}{2})$	+	$p(\frac{1}{2})$	
5	BS	$c\left[b+r(\frac{s+1}{2})\right]$	+	$d(\frac{s+f}{2})$	+	$p(\frac{1}{2})$	
	RF	$c(r)(\frac{1-s}{2})$	+	$d(\frac{f}{2})$	+	$p(\frac{1}{2})$	
6	BF	$c\left[b+r(\frac{1-s}{2})\right]$	+	$d(\frac{f}{2})$	+	$p(\frac{1}{2})$	
	RS	$c(r)(\frac{s+1}{2})$	+	$d(\frac{s+f}{2})$	+	$p(\frac{1}{2})$	

TABLE 36

P	Stimuli	Percentage preference
P_1	BS RS	$\frac{c(2b+r)+d(s+f)+p}{2c(b+r)+2d(s+f)+2p}$
P_2	BF RF	$\frac{c(2b+r)+df+p}{2c(b+r)+2df+2p}$
P_3	BS BF	$\frac{c(b+r)(s+1)+d(2s+f)+p}{2c(b+r)+2d(s+f)+2p}$
P_4	RS RF	$\frac{cr(s+1)+d(2s+f)+p}{2cr+2d(s+f)+2p}$
P_5	BS RF	$\frac{c[2b+r(s+1)]+d(2s+f)+p}{2c(b+r)+2d(s+f)+2p}$
P_6	BF RS	$\frac{c[2b+r(1-s)]+df+p}{2c(b+r)+2d(s+f)+2p}$

A number of testable predictions relating these percentage preferences can be deduced. For example it follows that P_6 should equal $2(P_1P_4-P_4)+1$. These predictions will be considered in the next section, together with some others which follow from the Attention Threshold Model if not specifically from Table 36.

PREDICTIONS OF THE ATTENTION THRESHOLD MODEL

The predictions will be labelled Attention Prediction 7, 8, etc. Those that are deduced from Table 36 will be given first in terms of P_1 etc., and then in more general form. The details of the deductions of these predictions will not be given as they are rather tedious. Experimental evidence bearing on the predictions will be given.

Attention Prediction 7

P_2 should be greater than P_1 except in certain special cases such as when d = 0 in which case they should be equal (d = 0 is the special case in which all attention waves begin in the Alpha System.)

P_4 should be greater than P_3 except in certain special cases such as when d = 0 or when s+f = 1; in these cases P_4 should equal P_3. (s+f = 1 is the special case in which the Variable X of the solidity System is always above threshold.)

These can be combined into the single general prediction, Prediction 7, that a percentage preference involving a particular stimulus difference should be higher when both stimuli have a low stimulating value according to irrelevant cues, than when both stimuli have a high stimulating value according to irrelevant cues. (As mentioned above there are certain special cases in which this prediction will not be expected to hold: in addition to the two explicitly stated

above there are other more trivial ones such as when the percentage preference measured is 50%, i.e. not really a preference at all.)

Nissen and Jenkins (1943) trained chimpanzees on a simultaneous discrimination problem with two cues, brightness and size, relevant. That is to say they were trained in the equivalent of the Test 5 situation in Table 34. They were then tested with each cue separately relevant. The important fact from the present point of view is that in these single cue tests, the qualities of the stimuli according to irrelevant cues were varied. Thus the brightness preference was measured with both stimuli large and with both stimuli small, and the size preference was similarly tested at both brightness levels.

They tested 8 adult chimpanzees. In addition they quote the results of an earlier study by Nissen on 3 juvenile chimpanzees, each tested under two different conditions. There are therefore 14 separate sets of results. Table 37 gives the mean results from the adults and from the juveniles. Under the heading Irrelevant Cue, "both positive" means that both stimuli were at the preferred or previously rewarded level by the irrelevant cue; "both negative" means that the quality of both stimuli by the irrelevant cue was the non-preferred, previously unrewarded one. Attention Prediction 7 is then that the percentage preferences under "both positive" should be lower than the corresponding ones under "both negative".

TABLE 37

Subjects	Relevant cue	Irrelevant cue	
		Both positive	Both negative
Adults	Brightness	76.8	85.5
"	Size	75.5	79.5
Juveniles	Brightness	66.5	74.5
"	Size	67.8	85.5

If all the results are taken together in a Wilcoxon matched pairs test, the "both positive" figures are significantly smaller than the "both negative" ones ($P < 0.005$ 1-tailed). The prediction is therefore confirmed.

I tested Attention Prediction 7 on domestic chicks in the form of the hypothesis that the percentage preference for Blue over Red should be higher when both stimuli are Flat than when both stimuli are Solid; (Solid it will be remembered is preferred to Flat).

The method was the same as for Experiments 1 to 8 described in Chapter 2, except that instead of presenting three stimuli in all pair combinations, four stimuli were presented in only two pair combinations, Blue Solid with Red Solid, and Blue Flat with Red Flat. The experiment was repeated on two different batches of chicks. Table 38 summarises the results. The numbers are mean percentage preferences for Blue over Red.

TABLE 38

	Both Solid ("positive")	Both Flat ("negative")
First batch	82.6	90.3
Second batch	78.6	85.6

The differences are not very great, but if all the results are taken together in a Mann Whitney U test, the prediction is just significantly confirmed ($P < 0.05$, 1 tailed).

It is not surprising that the difference between the percentage preferences in the two cases is not very large: substitution of large numbers of different combinations of sample figures in the relevant expressions of Table 36 showed that the predicted differences would not be very great unless the preference for Solid over Flat were much stronger than other experiments have actually shown it to be.

Cue Additivity: Attention Prediction 8

P_5 should equal $2(P_1+P_4-P_1P_4)-1$. This is Attention Prediction 8.

Since it happens to be the same formula as Prediction 1, confusion will arise unless some terms are defined.*

Prediction 1 will be used as the name for the prediction as deduced in Chapter 1, that is with three thresholds all belonging to the same threshold system, and interacting with the same Variable X.

---

* Briefly, Prediction 1 is concerned with preference transitivity and Prediction 8 with cue additivity.

Thus according to the Original Threshold Model, Prediction 1 will be true when any three stimuli are presented in all possible pair combinations. When applied to this situation, it will be called Original Prediction 1. Prediction 1 can only be deduced from the Attention Model - "Attention Prediction 1" - when the three stimuli differ according to only one stimulus dimension, the System corresponding to this dimension being Alpha.

Attention Prediction 8 applies to an entirely different situation from Attention Prediction 1, and indeed the conditions under which they can be deduced do not overlap. The conditions for the deduction of Attention Prediction 8, which may be compared with those given above for Attention Prediction 1, are:

1. The differences between the stimuli in the additivity test should be a combination of the differences between the stimuli in the single cue tests. The stimulus differences in the single cue tests should therefore lie along different stimulus dimensions. (Though we are here considering a simple situation in which only two cues are relevant, expansions of the formula can be derived for the cases of three or any number of cues being relevant.)

2. Only three stimuli should be involved in the experiment, presented in all possible pair combinations.

3. The preference test along the stimulus dimension whose System is Alpha, should involve the most preferred of the three stimuli.

It happens that Condition 2 is also necessary for Prediction 1, and since it is the only condition necessary for Original Prediction 1, the latter is a more general prediction than Attention Prediction 8. This is not the case for Attention Prediction 1 however, which, as already mentioned, depends on conditions of its own which do not overlap with those for Attention Prediction 8.

According to the Attention Model therefore, Experiments 1, 2, and 3 in Chapter 2, were tests of Attention Prediction 1, but Experiments 4, 5, 6, and 7 were tests of Attention Prediction 8, the formula being the same in both cases. However since Experiments 4, 5, 6, and 7 could be, and in Chapter 2 were, regarded as tests of Original Prediction 1, it is not permissible to use these specifically as evidence for the validity of the Attention Model.

Attention Prediction 8 applies only to the case where the two single cue preferences combined are P_1 and P_4. The formula cannot necessarily be derived if say P_2 and P_4, or P_2 and P_3 are taken. However it is possible, by combining Attention Predictions 7 and 8, to predict the direction in which the Prediction 8 formula should err, when different combinations of the possible single cue preferences are used. Thus, except in the special cases mentioned above under Attention Prediction 7, P_5 should be smaller than $2(P_2+P_4-P_2P_4)-1$, and P_5 should be larger than $2(P_1+P_3-P_1P_3)-1$. It is also possible to prove that P_5 should be smaller than $2(P_2+P_3-P_2P_3)-1$. In special cases, P_5 may equal any of these expressions, but these predictions should under no circumstances be reversed.

Therefore for example if a worker followed the rule of keeping the preferred stimulus of each pair the same throughout the experiment, as in P_1, P_3, and P_5 we should expect Attention Prediction 8 to underestimate slightly. Substitution of large numbers of sample figures has shown that in this particular case the Prediction 1A formula $P_5 = \frac{P_1 P_3}{P_1 P_3 + (1-P_1)(1-P_3)}$ happens to give a reasonably close approximation, and is neither consistently too high nor too low. Thus for this situation, there are certain special cases in which a good fit to Attention Prediction 8 would be expected, but in general this formula would be expected to underestimate slightly, and the Prediction 1A formula, fortuitously, to give a closer approximation.

On the other hand, if the less preferred stimulus of each pair were kept constant throughout the experiment as in P_2, P_4, and P_5, we should expect Attention Prediction 8 to overestimate slightly. Again, substitution of sample figures has shown that this deviation is unlikely to be very great, but I have not found a formula to describe it.

If irrelevant cues are varied systematically in the single cue discfiminations, substitution of sample figures shows that Attention Prediction 8 is likely to be a fairly good approximation.

As already mentioned, where authors do not specify the qualities of their stimuli according to irrelevant cues, the most reasonable policy to adopt is to consider the simpler version of the model which does not need this specification, because it does not

differentiate P_1 from P_2, and P_3 from P_4. This will be done for the discussion of Hara and Warren's data.

As already mentioned, Hara and Warren (1961), Sutherland (in prep.) and McGonigle (in prep.) investigated cue additivity in mammals. I will discuss only the work of Hara and Warren in detail, since it is published. The other authors found essentially similar results. However they have their own interpretations, for which reference should be made to their forthcoming publications.

Hara and Warren trained cats on brightness, form, and size discriminations separately. Each cat was trained on all three discriminations, but at different times. For each animal, the differences between the stimuli in these initial single cue discriminations were manipulated so that it was known what differences yielded 70% and 80% discrimination success. In additivity tests, the differences according to the separate cues were combined as in Test 5, Table 35. As well as all possible combinations of two cues, Brightness with Form, Brightness with Size etc., they also combined all three cues. Both levels of stimulus discriminability, 70% and 80% from all three cues were combined in all possible combinations.

The additivity effect which they found, proved to be a regular predictable one, the increments in discrimination being equivalent no matter which cues were combined. So regular was it indeed that they were able to fit a formula to it empirically, and this formula, as already mentioned is identical to that of Attention Prediction 8 (and Prediction 1).

Cue Opposition: Attention Prediction 9

P_6 should equal $2(P_1P_4-P_4)+1$. This is Attention Prediction 9.

Qualitatively, the most significant fact about this Cue Opposition formula is that it is asymmetrical: if $P_1 = P_4$, P_6, the percentage preference predicted when the two preferences are pitted against each other is not 50% as common-sense might expect. It is biased in favour of the cue whose System is higher in the hierarchy. Substitution of sample figures shows that a qualitatively similar asymmetry is predicted if any other (i.e. other than P_1 and P_4) stimulus combinations are involved in the single cue tests. It also shows that the opposition effects predicted by the Attention Model are much more variable than the additivity effects. We should therefore not hope for very accurate fulfilment of Attention Prediction 9 unless large numbers of data are used.

Hara and Warren did indeed find an asymmetry of this kind when they opposed cues. Thus brightness was found to be "dominant" to size and form, and size dominant to form, when equally discriminable (70% or 80%) preferences were opposed. It is noteworthy that this dominance effect was obtained in spite of the fact that the percentage discrimination rates on the different cues separately had been carefully equalised, and in spite of the fact that the different cues contributed equally to the additivity effect. It is therefore very interesting that the Attention Threshold Model should predict

precisely this rather surprising combination of circumstances.

It is not necessarily very meaningful because of the variation, but for interest we can compare the actual quantitative results obtained by Hara and Warren with those predicted by the Attention Threshold Model. As above it will be assumed, in order to make definite prediction possible, that P_1 is in practice the same as P_2, and P_3 the same as P_4, or in other words that all, or nearly all attention waves begin in the Alpha System,

To predict the percentage preference when two preferences are opposed, we substitute 80% (or 70%) for P_1 and P_4 in the formula $P_6 = 2(P_1P_4-P_4)+1$. For the case of the 80% original discrimination rates the predicted opposition preference comes to 68%. The three observed figures, for Brightness against Size, Brightness against Form, and Size against Form are 68%, 67% and 58% respectively, with a mean of 64.3%. For the case of the 70% original discrimination rates, the predicted P_6 is 58%. The three observed figures, in this case more scattered, are 54%, 71%, and 49%, with a mean of 58.0%. As mentioned above, the variation is such that one should beware of taking these detailed quantitative results too seriously.

The model even predicts that a slight dominance effect in the same direction would be obtained if a 70% preference on a dominant cue were opposed to an 80% preference on a subordinate one. The preference in favour of the dominant cue should in this case be 52%. This has not been tested as far as I know.

Nissen and Jenkins (1943) in the study mentioned above also did cue opposition tests. It will be remembered that they trained chimpanzees with both brightness and size relevant. In opposition tests the positive size combined with the negative brightness was presented in a choice test with the negative size combined with the positive brightness. This is of course the P_6 situation of Table 34.

In this case, we know the values of P_1, P_2, P_3, and P_4, and are therefore in a position to test Attention Prediction 9 using P_1 and P_4 only. However, in this case we do not know which cue to assume is attended to first, and this is of course important. The most reasonable course therefore is to do the calculations separately on the assumption that the animals attend to brightness first, and on the assumption that they attend to size first. We should expect that in one case a good fit to Attention Prediction 9 will be obtained, and not in the other.

As mentioned above, data were obtained from 8 adult chimpanzees, and in addition the results of an earlier study by Nissen on juveniles, involving fewer data, are also quoted. Of the 14 independent sets of data available for testing Attention Prediction 9, any in which one of the single cue preferences was less than 50% are rejected from the present analysis. This is obviously necessary because under such conditions the "opposition" test ceases to be an opposition test and becomes an additivity test. Such rejection occured in only a few cases.

Figure 14 Attention Prediction 9: Cue Opposition. Chimpanzees (Nissen & Jenkins).

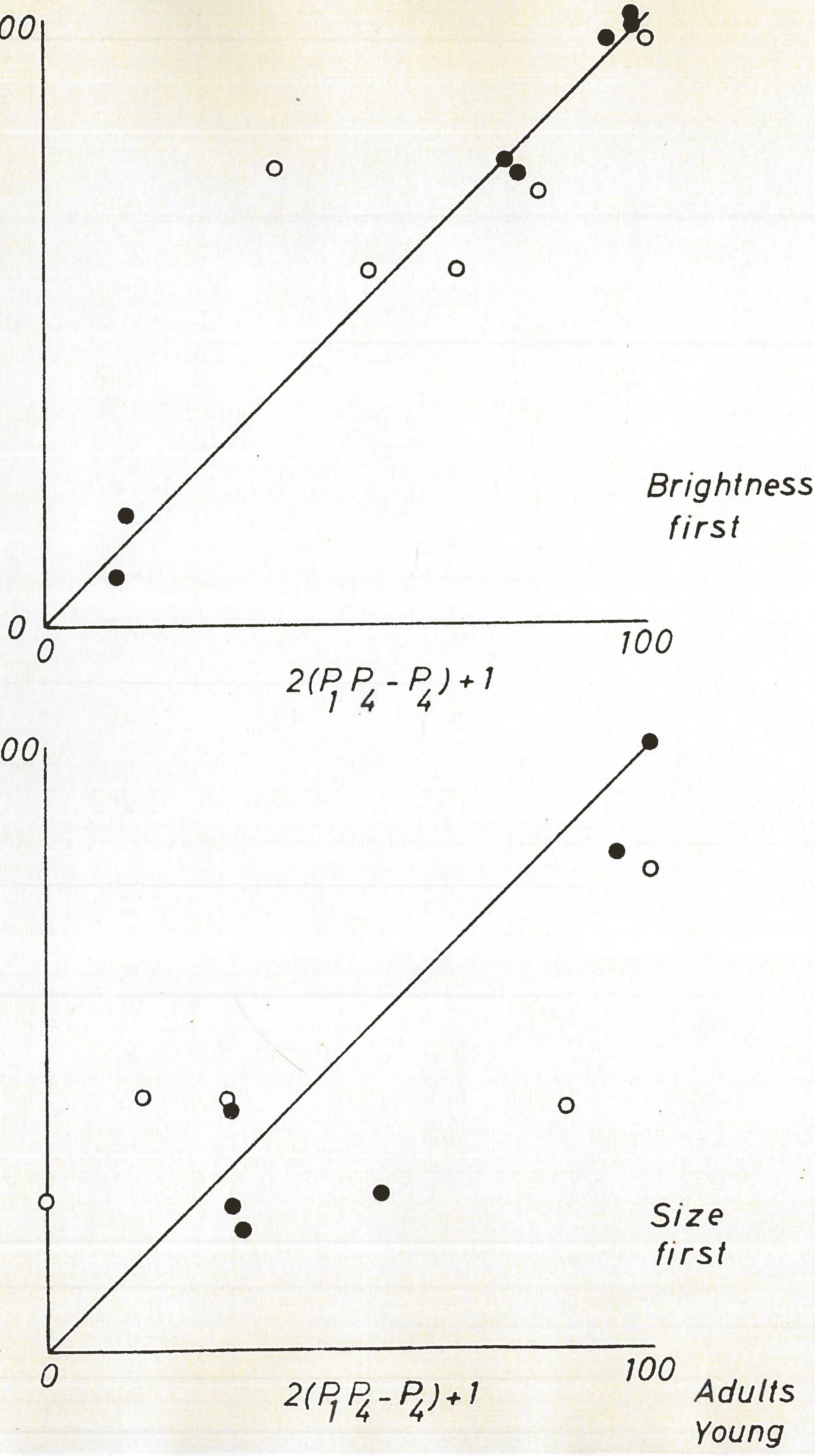


Table 39 gives the observed and predicted results on the assumption that brightness is attended to first. Table 40 is the equivalent for the assumption that size is attended to first. In both cases the predicted opposition preference, P_6 is calculated as $2(P_1P_4 - P_4) + 1$: the difference between the two cases is that different Ps are used. When brightness is assumed "first" P_1 is the brightness preference with both stimuli of the positive size, and P_4 the size preference with both stimuli of the negative brightness. When size is assumed "first", P_1 is the size preference with both stimuli of the positive brightness, and P_4 the brightness preference with both stimuli of the negative size. The observed P_6 when brightness is "first", is one minus the observed P_6 when size is "first".

The information from Table 39 and 40 is plotted in Figure 14. There are two graphs of observed against predicted P_6, in the upper graph brightness, and in the lower graph size, being assumed "first".

Just as expected, one of the two assumptions gives a poor fit to Attention Prediction 9, and the other gives a good one. This is especially well shown by the results from adults, (solid circles in Figure 14), for whom the number of data is much larger. The results from juveniles (open circles) are more scattered as would be expected from the small numbers involved, but they point in the same direction.

We may therefore conclude that in these Chimpanzees, the System concerned with brightness is higher in the hierarchy than that concerned with size, just as in Hara and Warren's cats, and that on this assumption Attention Prediction 9 is encouragingly well fulfilled.

TABLE 39 (Data from Nissen and Jenkins 1943)

Brightness assumed "first"

Subjects	P_1	P_4	P_6	$2(P_1P_4-P_4)+1$
Adult	98.0	56.0	98.0	97.8
"	98.0	66.0	100.0	97.4
"	88.0	88.0	74.0	78.9
"	84.0	74.0	76.0	76.3
"	94.0	54.0	96.0	93.5
"	56.0	100.0	8.0	12.0
"	56.0	98.0	18.0	13.8
Juvenile	83.0	93.0	58.0	68.4
"	88.0	75.0	71.0	82.0
"	75.0	92.0	58.0	54.0
"	100.0	67.0	96.0	100.0
"	63.0	83.0	75.0	38.6
Mean			69.0	67.7

TABLE 40 (Data from Nissen and Jenkins 1943)

Size assumed "first"

Subjects	P_1	P_4	P_6	Predicted P6 $2(P_1P_4-P_4)+1$
Adult	64.0	94.0	20.0	32.3
"	74.0	86.0	26.0	55.3
"	64.0	96.0	24.0	30.9
"	100.0	100.0	100.0	100.0
"	64.0	96.0	40.0	30.9
"	96.0	68.0	82.0	94.6
Juvenile	65.0	100.0	42.0	30.0
"	58.0	100.0	42.0	16.0
"	92.0	88.0	40.0	85.9
"	50.0	100.0	25.0	0.0
"	100.0	88.0	79.0	100.0
Mean			47.3	52.4

Other consequences of model

Assuming that attention waves take a measurable time to pass down the hierarchy of Systems, animals should take longer in reaching a decision when the System concerned in that decision is low in the hierarchy than when it is high. Now as we have seen, in theory the relative position of Systems in the hierarchy can be discovered by means of opposition tests. Therefore we should predict that decisions in which the relevant cue has shown itself to be dominant in opposition tests, should have shorter latencies than decisions involving subordinate cues, and this even if the percentage preferences are equal. For example, in Hara and Warren's experiments, the cats should have taken longer to make their choice in a size discrimination than in a brightness discrimination, even though the percentage discrimination performance on the two cues was equal at say 80%.

Hara and Warren do not quote latencies. However, McGonigle (in prep.) working on rats, found pronounced differences in latency in single cue discriminations equated for "discriminability" at 70% and 80%. The shorter latencies were shown for stimulus dimensions which showed themselves dominant in opposition tests. This is of course precisely the effect predicted here.

Other predictions about latency follow from the assumption that 50/50 behaviour is shown when animals attend to the Terminal System at the end of the hierarchy. Thus decisions between stimuli which are close to each other in the preference order, or which resemble each

other, should have longer latencies than decisions between very different stimuli. Most people would probably expect this on subjective or common sense grounds, and there is evidence for it from experiments on man (Dashiell 1937, Barker 1942, Guilford 1954).

For any given stimulus pair the mean latency of "wrong" decisions, i.e. choices of the less preferred stimulus, should be greater than the mean latency of "correct" choices of the preferred stimulus. This follows because wrong decisions are all "50/50 decisions", while only some correct decisions are. Such a result was obtained by Henmon (1911) in experiments on the judging of lengths of lines by man. Theoretically we should also predict that the latencies of correct choices should be bimodally distributed, the longer mode coinciding with the single mode of the distribution of latencies of wrong choices. However I think it unlikely that this latter prediction could be verified in practice: the variation is likely to be too great. Henmon's data do not provide any support for it.

From the assumption that suprathreshold indecision results in a switch in attention, it follows that animals should spend more time attending to a given cue if the stimuli available to it are far apart in the preference order by that cue, than if they are close. For example a chick should attend to colour more if presented with Orange and Green than if presented with Orange and Blue. The consequences of this for rates of discrimination learning are outside the scope of the present discussion, but one functional hypothesis which

follows from it is worth mentioning.

Much of the discussion of selective responsiveness, and of pecking preferences in young birds in particular, has been concerned with functional speculation (e.g. Quine and Cullen 1963). For some preferences, (see e.g. Appendix 2), a simple naturalistic explanation of function does seem plausible. In other cases, for example the colour preferences of the domestic chick, this is by no means the case. It seems possible that when we take a particular preference, say that for blue over green, and ask about its function we are asking the wrong question. Perhaps what we should be asking is not, "Why does it prefer blue to green?" but "Why does it show strong colour preferences?" It may be that there is little importance in which colours the animal happens to prefer, provided it prefers something.

The consequence of the Attention Threshold Model under discussion suggests a reason why this should be so. The chick, say, may be "programmed" (see Appendix 2) to acquire adaptive feeding preferences by discrimination learning. It may be advantageous that in this learning it should attend to colour. As we have seen, the Attention Threshold Model predicts that it will be more likely to attend to, and therefore learn about, colour if the thresholds of the available stimuli within the colour System are far apart. Thus paradoxically the animal might learn to prefer Green to Orange faster if it starts out with a strong preference for Orange over Green than if it starts out pecking almost equally often to both: in the former case

it will be more likely to attend to colour than in the latter. This explanation is, of course, obviously derived from attention theorists' accounts of the "Overtraining-Reveral Effect" (Mackintosh 1964, Lovejoy 1965a).

CONCLUSION

The Attention Threshold Model, conceived as an attempt at explaining the "50/50 behaviour" postulated by the Original Threshold Model, developed into something rather more complex, but also more powerful. Many of the detailed assumptions of the Attention model were necessary in order that it should yield Prediction 1 in the form deduced in Chapter 1. Such post-hoc contrivance may be justified on the grounds that it leads to further predictions in fields in which the Original Threshold Model could say nothing. To a fairly large extent these predictions have proved successful when tested against my own and published data. It is of course true that all the experiments used to test the "predictions" were done before the model was developed. However, the word "prediction" may still legitimately be used since the model's assumptions were not in any way adjusted to fit these facts: they were adjusted to fit only Prediction 1, and, it must be admitted, to fit in with the aesthetically attractive image of waves of attention sweeping down a hierarchy of threshold systems.

CHAPTER 8 : CONCLUSION

The Abstract summarises the work done, and since some of the other conventional functions of a concluding chapter have already been fulfilled in Chapter 6, this chapter will be brief.

The usefulness of a theoretical model for a mechanism of behaviour may be judged according to two main types of criterion, those concerned with its predictions, and those concerned with other aspects.

PREDICTIONS

In theory

A model may in part be evaluated according to the information content (Weaver 1949) of its predictions, or its Predictive Information Value. This is a measure of the extent to which it "commits itself" or "sticks its neck out", its improbability or vulnerability to disproof. Clearly a model whose predictions are so general as to be nearly obviously true, or which leaves very few alternatives, is of little interest.

Factors tending towards a high Predictive Information Value are:

1. Yielding of predictions which specify one or a few out of a wide range of possibilities. Thus a prediction that a quantity X should be larger than a quantity Y has low information value since the number of alternatives out of which it selects is low. Predictions which specify a precise relationship between measurable quantities have a higher information value, but this will depend in practice partly on the sensitivity of measurement.

Enough of the Threshold Models (including the Attention model) predictions are quantitatively precise to give the model a fairly high Predictive Information Value. It also yields some predictions with low information values, for example, Attention Prediction 7, and the prediction that hunger should lower percentage preferences.

2. Yielding of a large number of separate predictions. Again,

the Threshold Model is fairly prolific of predictions which are separate in the sense that they are not logically equivalent to each other. The ones mentioned in earlier chapters by no means exhaust the list that I know of, and I am hopeful that there are many more that I do not yet know of. The basic assumptions of the model can be applied to many different situations concerned with choice, and predictions can be deduced. Thus, for example, if P_1 is the percentage preference for A when it is presented together with B, and P_3 that when A is presented with C, the percentage of choices of A when all three stimuli are presented together should be $\frac{3P_1 + P_3 - 1}{3}$. If a fourth stimulus D is considered, and the percentage preference for A when presented with D is P_4, the percentage number of choices of A when all four stimuli are presented together should be $\frac{6P_1 + 2P_3 + P_4 -$

The Attention Threshold Model is especially productive of predictions. Interactions between any numbers of cues can be treated in the same kind of way as was the two cue situation discussed in Chapter 7.

3. There is also a sense in which the Predictive Information Value of a model depends on the unexpectedness of its predictions. If all the predictions of a model were expected, either through "common sense" or because they were predicted by other theories, somehow that model would seem less useful. This is not to say that compatibility with common sense or with other models is necessarily undesirable, far from it, but the value of a model is clearly greater if at least part

of the information it predicts is not expected on other grounds.

Some of the predictions of the Threshold Model are qualitatively expected by common sense or by other models, but not in quantitative detail. For example "strong stochastic transitivity" would be widely expected, but the precise formula of Prediction 1 would not. Part of the predictive information is shared by other models or by common sense, but, the information content of Prediction 1 being large (according to Factor 1 above), a considerable amount of it is unique to the Threshold Model. Thus out of the wide spectrum of possible predictions falling under the general heading of strong stochastic transitivity, the Threshold Model selects one. The Set Releasing Value Model selects another. "Common sense" does not select further than the general class.

Some of the individual predictions of the Threshold Model are expected on grounds other than the assumptions of this model. These include those with a low information content in the sense of Factor 1 above, but also more precise ones, for example Attention Prediction 8 (Sutherland: pers. comm., see Chapter 7). However, a model with a large Predictive Information Value in the sense of Factors 1 and 2 combined, is unlikely to share its whole complex of predictions with another model.

In practice

Clearly a model with a high Predictive Information Value is of little interest unless its predictions have a reasonably high

success rate: a good proportion of the "information" must prove itself to have some correspondence with reality. In assessing this, the problem mentioned above of accuracy of measurement arises; and it does so especially in connection with the other problem just discussed of the uniqueness of predictions. How accurately must we make our measurements in order to fulfil a quantitatively precise prediction; and/are our methods accurate enough to discriminate between different quantitatively precise predictions?

Some of the experimental results given here were just able to prove Prediction 1A of the Set Releasing Value Model significantly wrong: it might be that yet more sensitive methods would do the same for Prediction 1.

The question of whether other models could yield the same predictions has been mentioned above. A more difficult problem is whether other models could yield predictions theoretically different, but in practice virtually the same, and if so whether our methods are accurate enough to detect the difference. For example it would seem very difficult in practice to discriminate between Prediction 1A and the transitivity prediction which follows from Audley's (1960) model (with K = 2), though they are in theory different, and Prediction 1A always gives a slightly lower result. The second factor mentioned above as contributing to the Predictive Information Value of models may supply the answer to this problem: even if single predictions of models are so close as to be in practice indiscriminable, if the models

are of high Predictive Information Value, their total complexes of predicted information are unlikely to coincide in practice, just as (see above) they are unlikely to coincide in theory.

The success of the Threshold Model's predictions in fitting the facts to date is fair, and the failures do not justify its rejection since the predictions concerned depended on an additional assumption not essential to the basic ideas of the model. Much remains to be done: the evidence so far obtained suggests at least that it is worthwhile doing it.

OTHER ASPECTS NOT DIRECTLY CONCERNED WITH PREDICTIONS

Part of the usefulness of a model consists in its qualities as a framework for thought. It is of the essence of a model that rather than necessarily bearing a close resemblance to the reality it is supposed to represent, and which the human mind does not yet comprehend, it is specifically constructed by the human mind for the human mind, and simplicity is to some extent a desirable quality in a model. In so far as it yields a large quantity of predictive information which fits with observed behaviour within the limits imposed by methods of measurement, it may be inferred to have some analogous properties with the underlying reality. However its purely mental function as a framework for thought, and a generator of ideas should not be forgotten.

It may perform this function partly by breaking down the problem facing the thinker into manageable units which he can manipulate where before it was too large for him to deal with. For example the hypothetical mechanism controlling pecking was broken down into four units, and one of these units, the "Left/Right decision-maker" was broken down further into "Variable X", "Thresholds", and a "50/50 mechanism".

It seems that something akin to aesthetic appeal is also important. A model which makes a pleasing mental picture, which stimulates the imagination, may perhaps have an advantage as a begetter of ideas. The Threshold Model, to me, rates only moderately highly

in this respect. I mention it partly in justification for introducing, and largely discussing, the model in terms which are superfluous from the predictive point of view. The more general terms given in Chapter 6 happen to have stimulated my imagination less than "thresholds" and "Variable X", and this is partly what a model is for. Others no doubt have no need of these pictorial aids, and would prefer to talk in terms of states.

It would be a mistake to over-emphasise mental attractiveness as a desirable quality of a model, at the expense of its function in representing reality. A model for a behaviour mechanism should be more than just an attractive mental picture, and more than a blueprint for a machine which behaves in certain respects like an animal. Similarity of behaviour suggests similarity of underlying mechanism, and the higher the information content of the behaviour the two have in common, the more justifiable is the inference of common mechanism.

In this sense comparison between model and animal can be likened to comparison between two animals. If a chick and a Phyllobius beetle behave in the same way with respect to Prediction 1, we might cautiously suggest that the similarity in behaviour reflects a similarity in decision-making mechanism. We might be wrong. In the same way we would suggest, and again we might be wrong, that the similarity between the behaviour of the artificial machine called the Threshold Model and these animals is also due to a similarity of mechanism.

The comparative approach between animals may be useful to

the physiologist if, for example it happens to be easier to work with some animals than with others. Much medical research is conducted in the hope that information obtained from other animals may be generalised to man. Comparative studies between models and animals have a special usefulness in so far as, having made them ourselves, we know exactly how the models work. It is not very helpful to conclude that chicks and beetles might have a similar decision-making mechanism if we do not know how either of these mechanisms works. But it could be helpful to conclude that these animals have a similar decision-making mechanism to the Threshold Model, because we know exactly how the model works, (or at least a few versions of it).

There remains the question of what it meant by"similar". In comparing bird and insect, if we concluded that they shared a common type of mechanism, we would not necessarily be thinking of identical neural structures (Vowles, 1961). We would hope, however, that owing to some basic similarity in underlying principles, detailed knowledge of the nervous mechanisms in one animal might at least provide enough fruitful ideas to shorten considerably the labour of an investigation into the corresponding mechanisms of the other. It is my hope that the Threshold Model, through a cautious comparative approach, might in a more modest way make this kind of contribution to physiology.

A P P E N D I X 1

TESTING PREDICTION 1 WITH DATA ON HUMAN PREFERENCE

INTRODUCTION

When most of the main part of this thesis was written I was unaware that, mostly in the 1920s and 1930s, a number of studies of human preference had been carried out, in some of which the design of the experiments was incidentally such as to allow Prediction 1 to be tested. Stimuli were presented in all possible pair combinations. As in the case of the borrowed data of Chapter 2, in the present treatment these pairs have been combined into triplets, and Prediction 1 and Prediction 1A calculated for each triplet.

In one recent study (McLaughlin and Luce 1965) the authors' aim was specifically to test for "strong stochastic transitivity" (see Chapter 1), and in particular what they call the "product rule", which is the formula called here Prediction 1A. In this case therefore the design of the experiment was more like my own of Chapter 2 in that the pairs of stimuli were arranged in independent triplets.

Since the information necessary to assess the significance of preferences is not available, all percentage preferences have been included, except those of less than 50%.

BRIEF REMARKS ABOUT STUDIES USED

Dorcus (1926) investigated colour preferences of a wide variety of different types of subject. Variation in preference was very great, possible grounds for rejection of the data as a fair test of Prediction 1. They will, however, be included.

Hevner (1930) presented subjects with 20 samples of handwriting in all possible pair combinations. Most of the percentage preferences in this case were very high, i.e. there was considerable unanimity in preference. The number of data is large: 818 triplets were formed.

Folgmann (1933) studied the preferences for various composers of the members of four leading American orchestras. The names of the 19 composers were presented in all possible pair combinations to the subjects. He quotes separate mean figures for each of the four orchestras. Again the number of data is large, over 800 triplets for each orchestra.

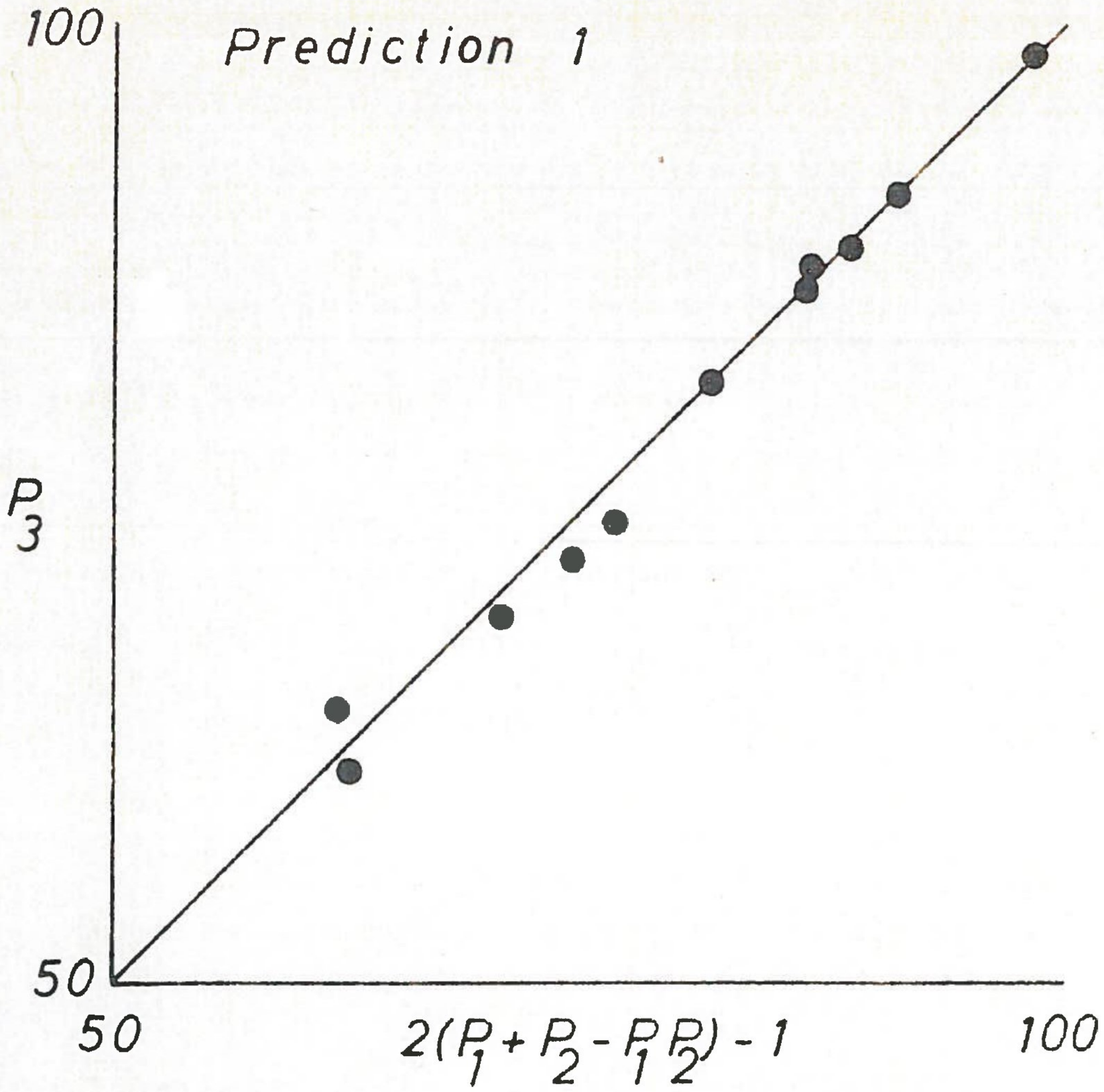
Shen (1937) investigated the colour preferences of 1368 Chinese students. Seven colours were presented in all possible pair combinations. The figures he quotes are the means from all the subjects.

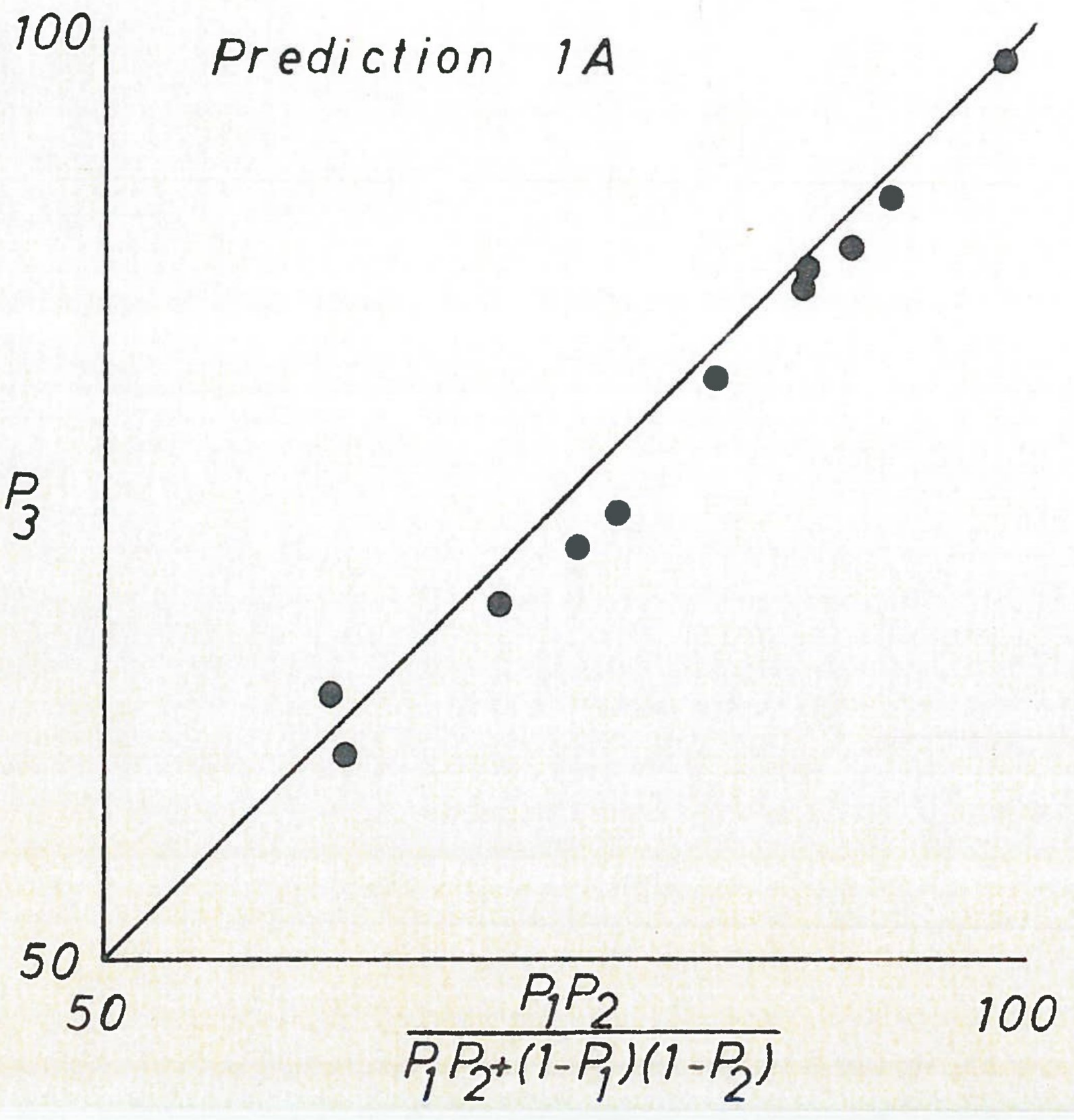
Guilford (reported in 1954) asked subjects which they preferred out of pairs of nine vegetables. The figures he quotes are means from all subjects.

McLaughlin and Luce (1965), who as already mentioned performed their study with the specific aim of investigating transitivity,

presented three individual subjects with pairs of solutions containing different quantities of sucrose and quinine. The subjects had to state which member of each pair they preferred. Nine separate triplet results were obtained from each subject.

Human preferences





RESULTS

The table summarises mean results for each of the studies. The figure gives the same information. The top graph is a plot of observed against predicted P_3 for Prediction 1, and the lower graph the same for Prediction 1A.

Author	Subject(s)	Mean P_3	Mean Prediction 1	Mean Prediction 1A
Dorcus	Various	69.0	70.4	71.4
Hevner	American students	98.2	98.2	98.5
Folgmann	Philadelphia Orchestra	90.8	91.2	92.3
"	N.Y. Philharmonic Orch.	88.1	88.7	90.1
"	Boston Symphony Orch.	86.0	86.3	87.6
"	Minneapolis Sym. Orch.	87.1	86.6	87.9
Shen	Chinese students	72.0	74.1	75.5
Guilford	American students	81.1	81.3	82.9
McLaughlin and Luce	R.S.	73.9	76.4	77.7
	C.P.	64.3	61.8	62.3
	T.C.	61.0	62.5	63.0

DISCUSSION

There seems to be a definite tendency for Prediction 1A to overestimate, just as in Chapter 2. In most cases we cannot do significance tests owing to non-independence of data. However, Dorcus tested large numbers of different types of subject independently. If the means from each of these independent tests are used in a Wilcoxon matched pairs test, Prediction 1A significantly overestimates ($P < 0.01$). Prediction 1 does not differ significantly from P_3.

McLaughlin and Luce also obtained independent data such that significance tests are possible. In this case neither prediction differs significantly from P_3, but the scatter is quite large.

However although it is not significant, in many of these studies, there is, unlike in the animal work, a suggestion of a tendency for Prediction 1 to overestimate slightly. This is especially marked in those triplets involving relatively low percentage preferences - close to 50%. These are presumably the triplets which would have been most likely to have been rejected had the significance of the preferences been known.

The possibility that the Threshold Model might be applicable to man as well as the other species discussed is an intriguing one. Looked at introspectively, it seems at first sight to be rather implausible: one is unwilling to believe that when faced with a choice between two alternatives, one either definitely chooses one or else chooses entirely at random. However it conceivably might apply in those cases

where the choice is a very difficult one to make, where both alternatives are almost equally desirable. Do we not sometimes, after a period of wavering between two alternatives, suddenly terminate our doubt by a wild choice, which may even be for a third alternative not previously considered?

Some form of Attention Threshold Model too might be applicable to man. Zeaman and House (1962) have applied an attention model to discrimination learning in children. A housewife, say, choosing food in a shop might "attend" successively to a number of separate preference dimensions, own taste, husband's taste, appearance of packet, price etc. However, this could not account for the present results unless some assumptions are made.

I am at present uncertain how to react to the possibility that the Threshold Model might apply to man. The main purpose of this appendix is simply to present the fact that human data give a reasonably good fit to Prediction 1.

A P P E N D I X 2

THE ONTOGENY OF A PECKING PREFERENCE IN DOMESTIC CHICKS

INTRODUCTION

Before beginning on the work which is described in the main part of this thesis, I did some experiments, also on pecking in domestic chicks, but with a different theoretical aim, and therefore they are best considered separately in an appendix.

Pecking in the domestic chick has been a favourite subject for students of behaviour ontogeny, and it has provided ammunition for both sides in the "nature or nurture" controversy (Spalding 1873 reprinted 1954, Breed 1911, Shepard and Breed 1913, Moseley 1925, Bird 1933, Cruze 1935, Padilla 1935, Kuo 1932, Lehrman 1953, Schneirla 1956, Hess 1956, Fantz 1957, 1958). One reason for this popularity as a subject may have been that the young of this species receive rather little help in feeding from the parents, and develop an efficient feeding behaviour of their own within a few hours of hatching. Certainly my own interest in the ontogeny of this response is a largely functional one. Pecking preferences are regarded as part of the animal's equipment for survival, and their ontogeny as the process by which the genes, in interaction with their environment, achieve this equipment.

In an omnivorous animal, the most functionally interesting visual feeding preferences are those involving properties which a wide range of food objects are likely to have in common, and of these the most promising seemed to be solidity or three-dimensionality. Some

work had been done before on the learned use of solidity cues by chicks (Benner 1938, Hess 1950, 1961), and it was known that within the first two days of life, chicks reared in darkness gave more pecks in the first five minutes of sighted life to hemispheres than to comparable flat circles (Fantz 1958).

The first experiments to be described here also involve choice between a hemisphere, called S (for Solid), and a disc called F (for Flat). Chicks given various different previous treatments were given a choice between these two stimuli. In later experiments photographs of hemispheres and discs were used.

THE ONTOGENY OF THE SOLIDITY PREFERENCE

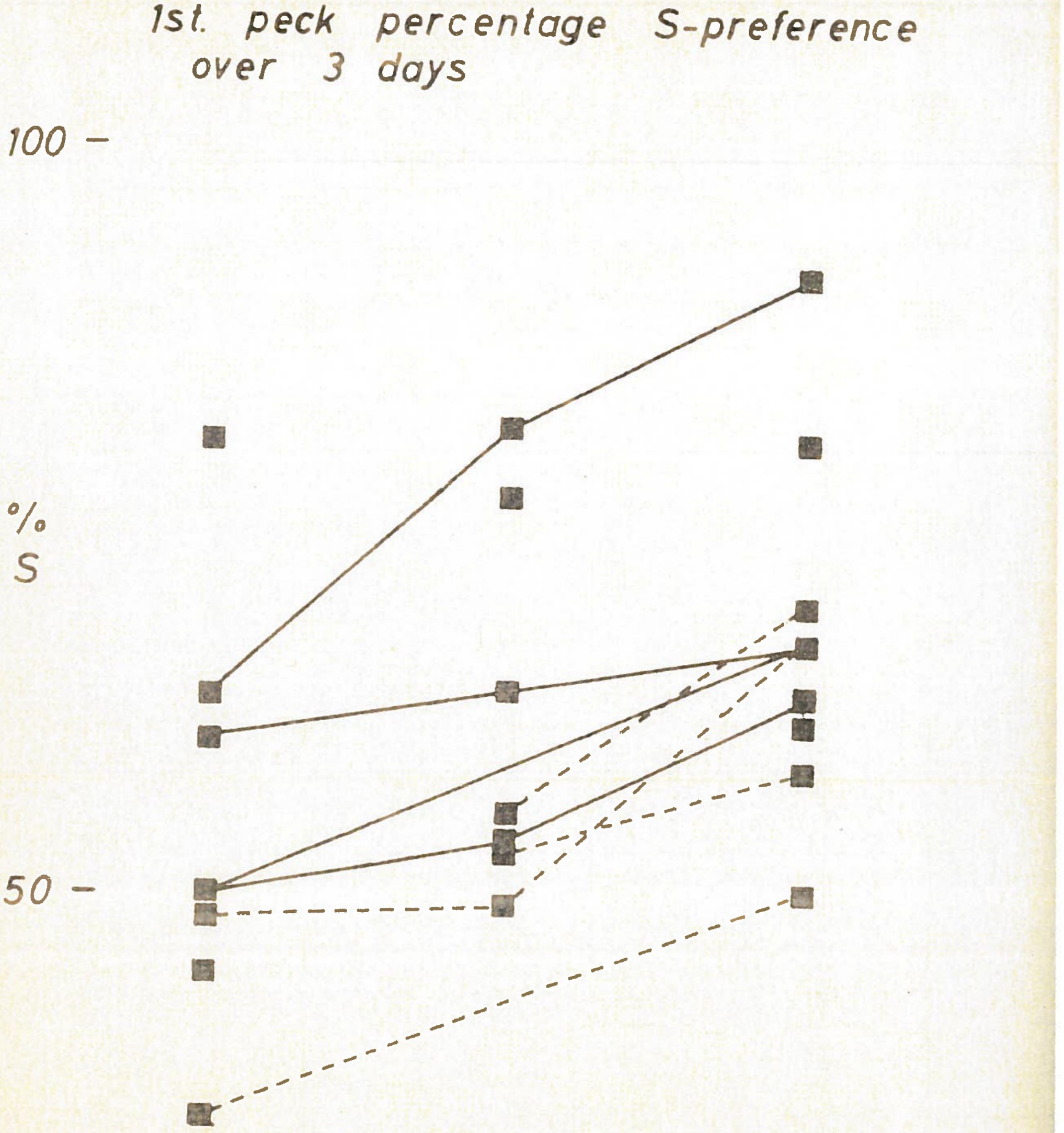
Preference testing method

Chicks were placed individually in a small cardboard box with two stimuli stuck to one wall, 9 cms. above the floor and 3 cm. from each other. They were a hemisphere (S) and a flat circle (F) of equal diameter, 6 mm., both painted white. Each chick was watched, and its pecks noted, for a standard time, usually one minute only since it was found that isolated chicks, if they had not pecked within this period, were unlikely to peck after it. In any case the number of pecks was low; typically about 50% of the chicks would not peck at all in the test period. At that time I did not appreciate the importance of familiarity of surroundings on the readiness of chicks to peck.

Temperature was found to influence pecking rate. After this effect had been noted, an attempt was made in subsequent tests to maintain the temperature in the testing box near the optimum of around 25 C.

In assessing the results, the total numbers of pecks given by different chicks to the stimulus objects were never used as such, though they were sometimes used in ranked form: pecks are very often given in rapid bursts, and cannot be considered as independent data. The basic figure used for analysis is the number of chicks out of a group showing a preference, preference being defined either in terms of the first peck given by each chick, or the majority of each chick's pecks. These two measures of preference give very similar results.

Figure (i)



"S-preference" or "Solidity preference" means preference for S over F. "1st Peck percentage S-preference" means number of chicks giving their first peck to S divided by total number of chicks pecking at either S or F expressed as a percentage.

"Maj. Pecks percentage S-preference" means number of chicks giving the majority of their pecks in the test period to S divided by total number of chicks pecking at S or F expressed as a percentage.

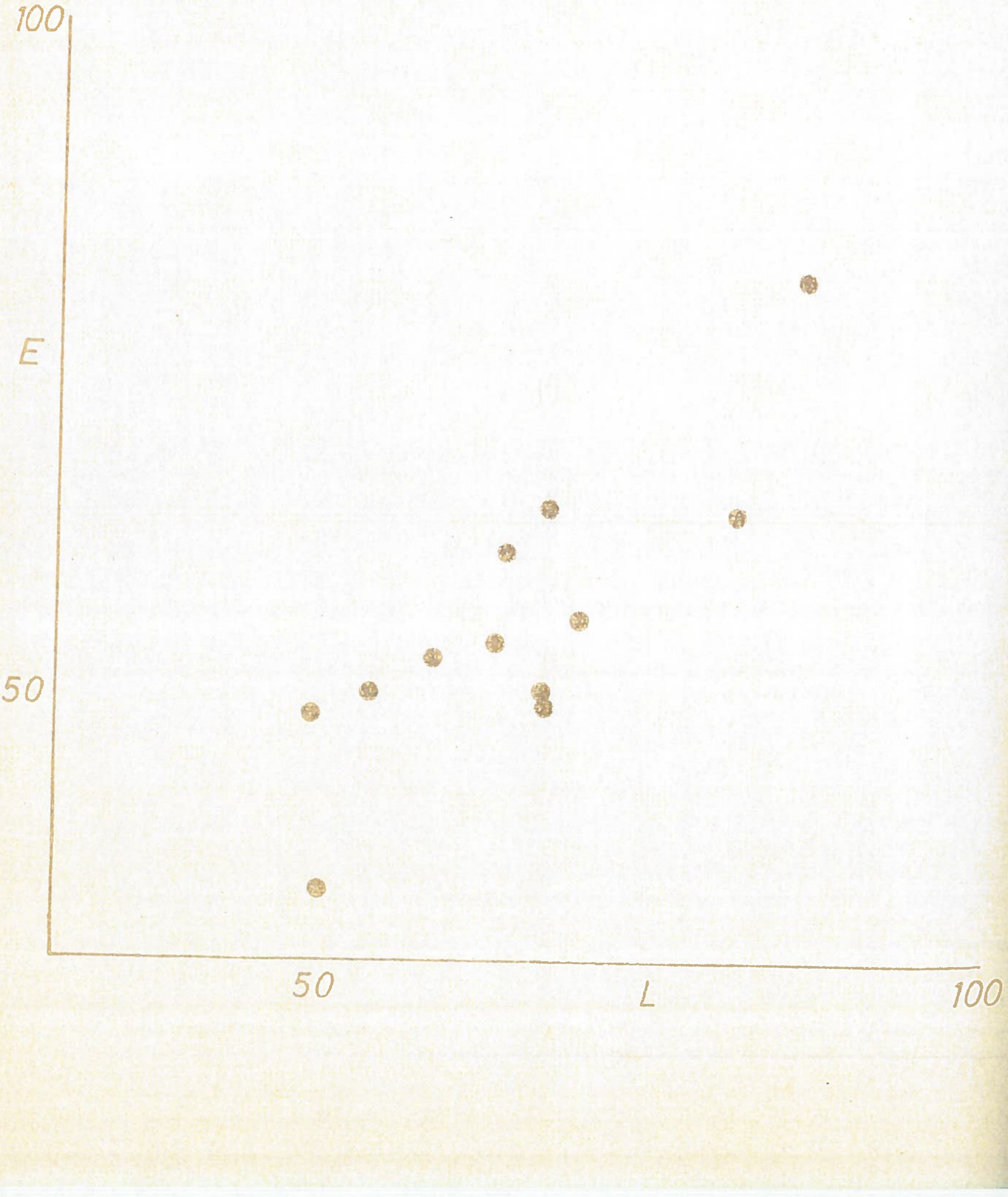
Changes in Solidity preference over three days

The chicks, were in most cases from the same supply as for the experiments described in the main thesis. They were kept in the light without food or water until testing, and were subjected to the preference test described above, on the day they were collected, called Day 1, or on Day 2 or on Day 3. In addition some were tested on more than one of these days. Most of the chicks had hatched the night before Day 1, but some were a little older. The exact ages of individual chicks were not known. A different batch of chicks was collected and tested each week. Nine batches in all were tested.

Figure (i) shows the first peck percentage S-preferences from groups of chicks tested on each of the three days. The lines joining the points signify that the chicks concerned belonged to the same batch. Absence of a line attached to a point indicates that members of the batch concerned were tested on one day only. Continuous lines join points from chicks which had never been tested before. Dotted lines join points from chicks with some experience of the

Figure (ii)

1st. peck percentage S-preference :
"Earlier"(E)/"Later"(L) correlation.



testing situation.

A number of conclusions can be drawn from the results:

1. Most of the points on Figure (i) lie above the 50% mark indicating that the S-preference does indeed exist, as we should expect from Fantz's finding. For most of the batches the preference was significant, in some cases very strongly so.

2. The lines on the graph tend to slope upward from left to right, indicating that the strength of the S-preference increases over the three days. In order to show this conclusively it would be better to test chicks of different ages at the same time, but this would introduce difficulties owing to the great inter-batch variation (3).

3. The gradients of the different lines are rather similar, or in other words the lines cross each other little, suggesting that there is considerable batch-specific variation in absolute level of S-preference, but that each batch shows the same rate of increase in the preference. The effect may be represented in terms of a correlation between earlier and later points from the same batch, counting Day 2 points as "earlier" when compared with Day 3 ones, and as "later" when compared with Day 1 ones. The correlation, shown as a scatter diagram in Figure (ii) seems to be a strong positive one. It is not legitimate to take all the points on the scatter diagram in determining the significance of the correlation, because some Day 2 results are represented twice. However if this duplication is eliminated, the Spearman Rank Correlation Coefficient is still reasonably high at +0.7,

and is significant ($P < 0.05$).

I call the batch-specific variation demonstrated by this correlation the "Batch Effect". It may or may not be genetic. An interesting feature of the Batch Effect is that although it can also be demonstrated if Maj. peck preferences are used, it is not shown by the figures for the absolute numbers of pecks given to both stimuli. This suggests that whatever causes the Batch Effect it influences the "Directing" decision-maker rather than the "Go/No go" decision-maker (see the main thesis).

4. In previously untested chicks there is a tendency for the total number of pecks given in the test period to increase over the three days, but in previously tested chicks there is a tendency for it to decrease. The difference between the two classes of chick is significant. Experience of the testing situation seems also to have a slight decreasing effect on Solidity preference, but it is not significant.

The waning in pecking tendency as a result of experience of the testing situation suggests a possible explanation of the ontogenetic increase in Solidity preference shown in Figure (i). This explanation will be discussed in the next section:

A possible explanation of the ontogenetic increase in S-preference

The explanation is based on the idea of waning or extinction mentioned above and depends on two conditions or assumptions.

A. The waning is stimulus specific.

B. Chicks generalise from marks on the flat walls of their living boxes to the flat stimulus F rather than to the solid one S.

In their cardboard living boxes the chicks spent much of their time pecking at grain-marks and other blemishes in the surface of the walls and floor. These marks have little in common except that they are seldom solid and are nearly always flush with the flat wall or floor. If waning is stimulus-specific then , and chicks can generalise between a wide variety of flat objects as against solid ones, we should expect that the longer chicks have had experience of these conditions before testing the more strongly should they have waned in their responsiveness to flat objects in general. Waning to solid objects should be less marked, and could easily be offset by the general ontogenetic increase in overall pecking tendency.

The stimulus-specificity of waning

An experiment was done to test the first condition directly. The testing method was the same as for the experiments described above. On the evening of Day 2, chicks were divided into 3 groups, 2 experimental groups containing 36 chicks each, and 1 control group of 12 chicks. (The latter control group was not crucial for the experiment.) They were kept overnight in small cardboard boxes, six to a box. The boxes in which the 12 control chicks were kept were ordinary plain cardboard boxes; the six boxes of one of the experimental groups of 36, each had 2 S stimuli stuck to the walls; the six boxes of the other group of 36 each had two F stimuli stuck to the walls. On the morning

after, all were given the normal standard S-F preference test as described above. Table (i) gives the results.

TABLE (i)

	A: S-experience	B: F-experience	C:"no" experience
No. chicks	36	36	12
No. pecking	10	23	9
% No. pecking	28	64	75
1st peck S / No. chicks	4	22	7
1st peck F / No. chicks	6	1	2
% 1st peck pref. S	40	96	78
Maj. S / No. chicks	5	23	7
Maj. F / No. chicks	5	0	1
% maj. pref. S.	50	100	88

Significance of results:

B pecked more in total than A did $P < 0.03$ (Wilcoxon)

If either the four 1st peck numbers or the four Maj. peck numbers from groups A & B are used in a 2X2 contingency table χ^2 is high and $P < 0.001$.

It is obvious that the waning effect is highly stimulus-specific. We may surmise that the F pecking score of group A and the S pecking score of group B are roughly equivalent to those of normally reared chicks, and that the enormous differences in their pecking results are due to selective waning in responsiveness to the stimulus with which they had been reared. The results from the control group

C are quite compatible with this, though the numbers are too small for direct comparison with A and B to be meaningful.

The first assumption or condition of the explanation outlined above is then confirmed.

"Flatness" generalisation

The second assumption or condition proposed above was that chicks would generalise in their selective waning from the flat walls and floor of their living environment to stimulus F rather than S. A prediction from this is that chicks reared in an environment where there are no flat walls should show a lower preference for S over F than "normally" reared controls, perhaps even reversed preference, but the latter would probably require almost perfect generalisation.

Experimental boxes were lined with corrugated cardboard all over the walls and floor so that chicks reared in these boxes had very little experience of flatness. Controls were reared in flat-walled boxes.

The experiment was repeated on several batches with minor differences in method which are not important: in all cases the experimental and control groups received the same treatment except of course with respect to the experimental variable of box lining. Some of the batches were tested on more than one day. In these cases the data from the different days are given separately in the table. The testing method was the same as before in all cases. The results are summarised in Table (ii).

TABLE (ii)

Rearing condition		1st peck nos. Flat S	Flat F	Corrugated S	Corrugated F	% 1st peck pref. S Flat	Corrugated
Batch	Day						
E	2	15	13	17	11	54	61
E	3	24	14	17	16	64	52
F	1	19	11	14	10	64	58
F	2	17	4	14	4	81	78
F	3	20	2	13	4	91	76
I	3	28	7	24	16	80	60
J	3	31	5	18	10	86	64
K	2&3	4	1	3	3	80	50

The corrugated environment has not reversed the S over F preference, but in seven out of the eight experiments the corrugated-reared group gave a lower S-preference than the flat-reared controls. Furthermore, in the case of the two batches E and F for whom results were obtained for more than one day, the control chicks show the normal clear ontogenetic increase in preference while the experimentals do not. If the 1st peck numbers themselves are considered rather than the percentage preferences calculated from them it will be seen that in seven out of eight cases more of the flat-reared chicks gave first pecks to S than of the corrugated-reared ones. Conversely in five out of seven cases (one tie), more of the corrugated-reared chicks pecked

first at F than of the flat-reared ones. Not surprisingly, the chicks which had had their S-pecks selectively reduced pecked less overall than those with reduced F-pecks. In two of the cases significant results from within individual experiments support the overall conclusion that experience of the corrugated environment leads to a lower preference for S over F than experience of a flat one.

It seems then that selective waning of responsiveness to flat objects is a result of rearing in a flat-walled environment, and generalisation to the flat stimulus F may be a major cause of the ontogenetic increase in preference for S over F in unfed chicks.

I feel that this finding about the causation of the ontogenetic increase in S preference is of little biological interest in itself, since it may well only apply to the artificial environment in which my chicks were reared. If it has any importance it is in showing two of the ways in which adaptive feeding preferences may develop in nature. The extremely strong stimulus-specific waning in responsiveness shown in Table (i), and the powers of generalisation demonstrated in the experiments just described are likely to be of significance in the development of adaptive behaviour in general.

The solidity preference in dark-reared chicks

Having found a learning process which causes an increase in the solidity preference in light-reared chicks, and knowing also that this preference is often rather weak in first day chicks, we are

naturally led to ask whether the preference is completely dependant on this process of flatness-specific waning. Fantz's results from dark-reared chicks suggest that this is not the case and that the solidity preference develops in the absence of experience of this kind. It seemed worth-while to confirm Fantz's findings using the method with which the above results were obtained, and also trying to limit the chicks' previous experience in light, even more than Fantz did.

Sixteen chicks were hatched in a totally darkened room. (The darkness was not measured. To the dark-adapted human eye there was no visible light.) They were kept in darkness until testing. The testing room was next-door, also dark though not quite so perfectly as the rearing room. The two rooms were separated by a light-tight door. Each chick was tested once only. They were transferred one by one in darkness into the testing room, and placed in the normal preference-testing box described above, in front of the two stimuli, the normal S and F. Each test lasted for five minutes initiated by the light over the box being switched on. Eight chicks were tested on their first day, but their responsiveness was so low that I postponed testing the rest until the following day which for most of the chicks was their second, on the basis of the results mentioned above showing an increase in responsiveness with time in untested chicks.

The behaviour of the chicks on their first experience of light was remarkable for its normality. Several of them jumped backwards as soon as the light was switched on in an apparently startled manner, but they showed no overt signs of dazzle, and within a few seconds most were looking

about them "attentively" giving the so-called "pleasure twitter" (Collias and Joos 1953). The only abnormal feature of their behaviour that I could see was the relatively great inaccuracy of their pecking. This would be expected from previous work, (Shepard and Breed 1913, Mosely 1925, Bird 1933, Cruze 1935, Padilla 1935.) They were also somewhat unsteady on their feet but probably not much more so than normal chicks of the same age. No light-reared controls were kept, as the number of eggs available was limited. The pecking figures for each individual chick are given in Table (iii).

TABLE (iii)

Day	Chick	1st. peck	No. pecks S	No. pecks F
1	1	F	2	1
	2	S	12	1
	3	-	0	0
	4	S	8	1
	5	-	0	0
	6	S	3	0
	7	-	0	0
	8	-	0	0
2	9	F	5	1
	10	S	10	0
	11	S	22	2
	12	S	41	14
	13	S	37	1
	14	S	5	0
	15	S	16	0
	16	S	11	0

Totals (both days):

No. chicks	16
No. pecking	12
1st pecks S	10
1st pecks F	2
Maj. pecks S	12
Maj. pecks F	0

The preference for S over F is of course highly significant if all the pecks are considered, and is significant ($P < .02$ Binomial test 1-tailed) if only first pecks are considered. Fantz's result is thus confirmed. However of my 12 chicks which pecked, 5 pecked at other objects - small specks of dirt, their own feet etc., before pecking at either S or F. Of the remaining 7 whose first peck was at either S or F, 5 pecked first at S and 2 at F. This difference is not significant. To be pedantic therefore the solidity preference has not been conclusively demonstrated in chicks with no previous experience of pecking in the light. For the 5 chicks which pecked first at other objects before pecking at S or F, the number of such "stray" pecks was respectively 5, 1, 7, 2, and 10. It seems therefore almost safe to conclude that no previous experience of pecking in the light is necessary for the solidity preference to develop.

The Solidity preference in monocular chicks

A number of possible cues might be used by the chicks in discriminating S from F, for example stereoscopy, movement parallax, shadow casting, and surface shading (Woodworth and Schlosberg 1954), and also rather less interesting ones such as apparent size when viewed from the side. Of these I was especially interested in surface shading which will be discussed in the next section, but before beginning experiments on it, I did one experiment to test the importance of stereoscopy.

Twenty-eight chicks were half-blindfolded by means of Elastoplast stuck over one eye, in 50% of the cases the left eye and in 50% of the cases the right. Four stimuli were used instead of the usual 2 in an attempt at

eliminating the effects of possible side preferences which might have resulted from the sidedness of the blindfolding. The 2 Ss and 2 Fs were arranged alternately in a horizontal row at the same height above the floor as in the normal 2-stimulus tests (9 cm.). The testing procedure was in other respects as usual. The two ways of arranging the stimuli, SFSF and FSFS were given equal numbers of times, the stimulus card being turned over every five tests. Twenty unblindfolded control chicks were also tested. The experiment was carried out over 2 days, the second and third in the lives of the chicks, which were unfed, and reared in the light in the usual way. Table (iv) gives the results.

TABLE (iv)

	Half-Blindfold		Control	
No. of chicks	28		20	
No. pecking	13		12	
1st peck S	10		9	
1st peck F	3		3	
Maj. pecks S	10	($P < 0.01$)	10	($P < 0.05$)
Maj. pecks F	2		2	

The half-blindfolded chicks show a significant preference for S over F, and it is apparently no weaker than that of the controls. This shows that binocular vision is probably of little if any importance in this discrimination.

THE ONTOGENY OF THE USE OF SURFACE-SHADING CUES OF SOLIDITY

Introduction

Solid objects may be distinguished from flat in directed light by means of the differences in amount of light reflected from different surfaces. Since light tends to come mainly from above, solid objects usually appear lighter on top than underneath. This is one of the main ways in which solidity is identified by man in photographs or drawings. A familiar illusion is the loss of solid appearance seen if photographs of solid objects are turned upside down, (Benner 1938, DeRuiter 1956, Hess 1961).

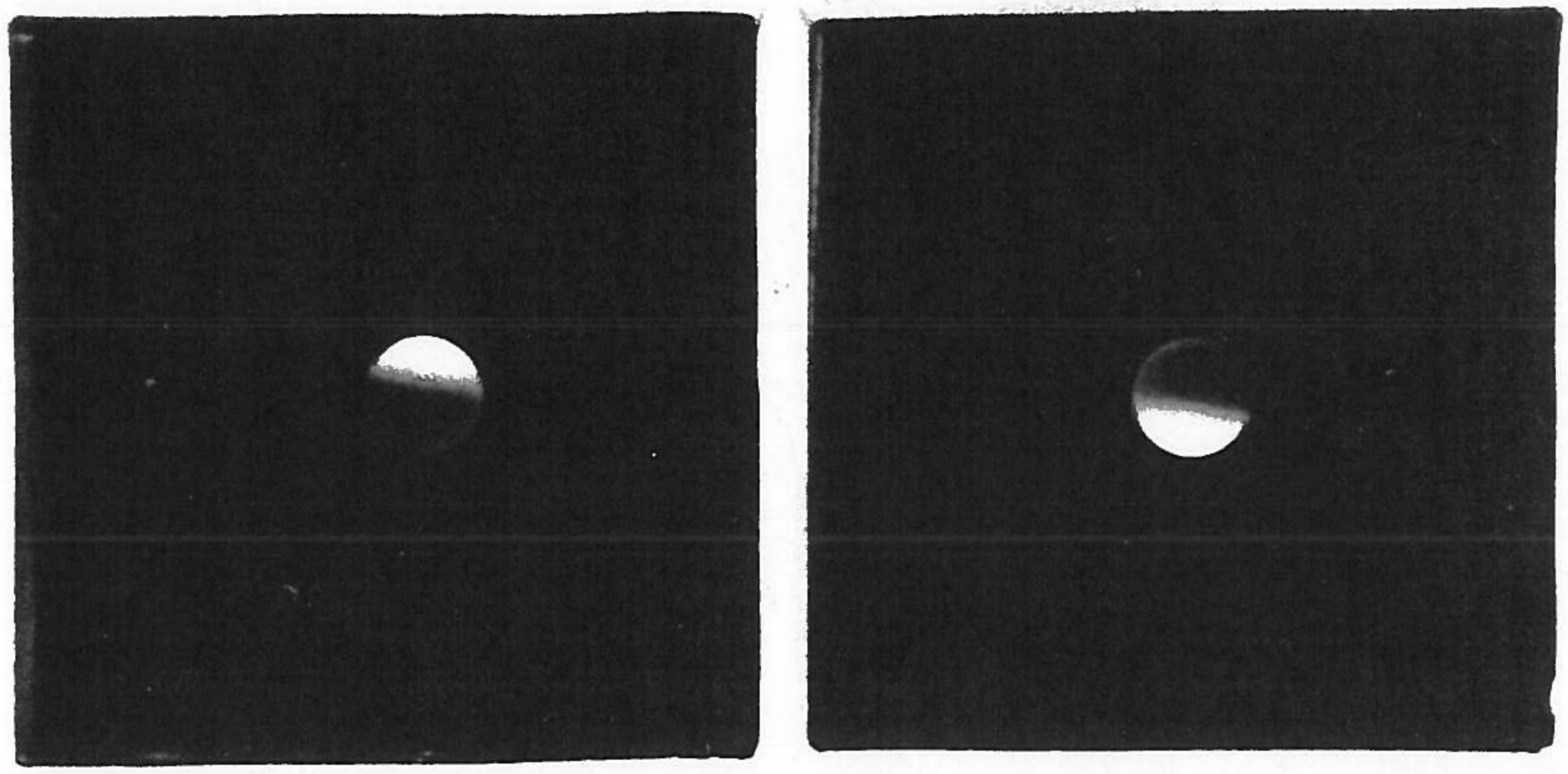
Hess (1950, 1961) presented chicks with photographs of wheat grains taken in directed light. Normal and inverted prints of the same negative were presented simultaneously. Two groups of chicks were used, one reared normally with overhead lighting, and the other in a special cage with light coming from below. The pecking preferences of the chicks in a choice test between the two orientations of the photographs were measured weekly for the first 8 weeks of their lives. In the first week, both groups of chicks showed a slight but non-significant preference for the "correctly" oriented photograph, i.e. the one in which the grains of wheat were lighter on their upper surfaces than on their lower surfaces. During the following weeks the control chicks showed a gradual increase in this preference, while the experimentals slightly more slowly came to prefer the inverted photograph, and by the seventh week did so significantly. Hess suggests that there may be an innate predisposition to learn to prefer the correctly

oriented photograph more easily than to learn to prefer the inverted one.

Since in Hess's photographs the grains cast very prominent shadows on the background, it is impossible to tell whether the cue being used in the discrimination is surface shading orientation or cast shadow orientation, or both. Furthermore the surface shading of Hess's photographs is not as prominent as it might be, and it could be that the chicks had difficulty in seeing it. The possibility therefore existed, and indeed was hinted at by Hess himself, that there is an unlearned preference for the surface shading qualities characteristic of solid objects. In spite of /Fantz's (1958) conclusion, on the basis of experiments varying the directedness of illumination on solid objects, that dark-reared chicks do not use surface shading cues, I decided to look into this matter further. It seemed a very interesting case from the point of view of the ontogenetic origin of adaptedness (Lorenz 1961), since the environmental feature to which a preference for a "correctly" oriented photograph is presumably adapted, namely the prevailing direction of light in nature, is easily defined, and it is easy to control the animal's experience of it.

Methods

In most of these experiments (except the final one) the apparatus used was the electric peck counter described in Chapter 2, the testing procedure was the same and groups of 6 chicks were normally used. It will be remembered that light in the peck-counting apparatus came from above. The data most commonly presented are the numbers of groups of 6 chicks giving the majority of their pecks in the time, to each of the stimuli. *1st peck



PSC and PSI

data give similar results.

The stimuli were as follows:

GS (Grey Solid): The same as S above, but painted grey.

PS (Photo Solid): A photograph of a hemisphere taken in directed light.

PSC (Photo Solid Correct): PS "correctly" oriented so that the lighter half was uppermost (see opposite left).

PSI (Photo Solid Inverted): PS inverted so that the darker half was uppermost (see opposite right).

PF (Photo Flat): A photograph of a flat disc.

The hemisphere and disc photographed were respectively half a ping-pong ball and a cardboard disc of the same diameter, both painted white. The background was a sheet of black cloth. In order to eliminate cast shadows both model objects were supported above the background. The final prints were made so that the stimulus objects had the same diameter as the original S and F, 6 mm. The prints were glued on to stiff black cardboard rectangles and presented as described in Chapter 2.

Choice between photographs of a hemisphere and a disc

Thirty-two groups of 6 chicks were each tested once only for 2 minutes. In all tests the choice was between the hemisphere photograph PS, and the disc photograph PF, but in half the cases PS was "correctly" oriented (PSC) and in the other half it was inverted (PSI). The chicks were tested on Day 3. Before testing they had been kept under normal lighting conditions, and had not been fed and watered.

The numbers of groups of chicks giving the majority of their

pecks at each of the stimuli in the two situations, PSC with PF, and PSI with PF, are given in Table (v).

TABLE (v)

	PS	PF	
Orientation of PS			
PSC ("Correct")	14	1	($P < 0.01$; Wilcoxon 2 tailed)
PSI (Inverted)	8	8	

There is a strong preference for PS over PF when PS is "correctly" oriented with the lighter side uppermost. When PS is inverted there is no preference between it and PF. A 2 x 2 test gives χ^2 of 5.109 for 1 degree of freedom, with a 1-tailed P value of less than 0.05. We can conclude therefore that inverting the photograph PS has an effect in the expected direction on pecking: it seems probable that chicks under 4 days old, and unfed, treat photographs of solid objects in the same kind of way as we do, responding only to correctly oriented ones as though they were solid.

Choice between a real hemisphere and photographs of a hemisphere and a disc

Since the correctly oriented photograph of a hemisphere PSC is so strongly preferred to a flat circle, (and to PSI), a reasonable question to ask is whether it is still inferior as a stimulus to a real hemisphere.

The main technical difficulty was in deciding how to paint the real hemisphere so that it matched the photographs in brightness. A shade of grey was chosen so that, subjectively, it seemed to approach the photographs

in brightness, but was still somewhat brighter. From previous work not described here, and also from Curtius (1954), it was known to be likely that if the chicks showed any brightness preference they would tend to choose the darker stimuli. Thus since the hypothesis being tested in these experiments was that the real Solid should be preferred to the photographs, it was arranged so that if a brightness preference were shown it should tend to favour the null hypothesis.

Three experiments, A, B, and C, were done, differing in minor details. In A, groups of 4 chicks were used instead of groups of 6, and were tested on Day 3. In B, the chicks were not from my usual supplier, and were of a different breed, Rhode Island Red X Light Sussex. They were tested on Days 1, 2, and 3. In C, the chicks were tested on Days 1 and 2. The chicks were reared in the light without food or water, as before.

In all three the same stimuli were used, GS real hemisphere painted grey as explained above, PSC, a correctly oriented photograph of a hemisphere, and PF, a photograph of a disc. They were presented in all possible pair combinations. The results, given in Table (vi), once again consist of the numbers of groups of 6 (or 4) chicks giving the majority of their pecks to each of the stimuli.

TABLE (vi)

	GS		PSC		PSC		PF		GS		PF
Experiment											
A	6		4		8	*	2		9	*	1
B	28	**	7		26	**	7		33	**	1
C	7		15		17	**	4		11		9

* $P < 0.02$)
** $P < 0.01$) Wilcoxon matched pairs

The three experiments do not all give the same result, but they agree in confirming the preference already found for PSC over PF. Experiment B also shows a significant preference for GS over PSC, (and also over PF), but experiment C shows no preference for GS over PSC, and even tends non-significantly in the other direction. I feel the most likely explanation for this discrepancy is batch-specific variation in tendency to attend to brightness, (Sutherland 1964). Both PS and PF, being slightly darker, should be preferred to GS if brightness alone were considered. If the batch of chicks used in Experiment C had a relatively strong tendency to attend to brightness the results actually obtained would be expected: a preference for PS over GS and a greatly increased tendency to peck at PF as opposed to GS. The batch used in Experiment B on the other hand perhaps tended to ignore brightness and attend to some other cue, perhaps movement parallax. I would tentatively expect therefore that if there were no brightness differences between a real S and a photograph of one, the real one would always be preferred.

In any case, whether or not shading cues are the only ones used in the solidity discrimination in my tests, there can be no doubt that they are important, and that orientation of brightness gradients is very important to chicks just as it is to ourselves. These experiments were all done on chicks reared in the light, who had had the opportunity for experience with solid objects seen with overhead lighting. The next question is whether these shading cues are used by chicks without the opportunity for such experience.

Photograph preference tests using dark-reared chicks

The arrangements for dark-rearing were the same as for the experiment described above. The chicks were hatched in an incubator in one dark room, and transferred for testing into another.

The preference testing apparatus with the microswitches was used, but I was mainly interested in observing the first peck which each chick gave, since I wanted them to have had as little experience as possible. They were each tested for an indefinite period. Tests were discontinued if it was clear to me that the chick was very unlikely to peck. This is not difficult to judge: when a chick has begun its long series of "distress" calls characteristic of isolation, it seldom breaks off to peck. Thirty-seven chicks were used, varying between 1, 2 and 3 days old at the time of testing. Only 19 pecked. (Typically 50% of isolated chicks do not peck in my testing situation.) Table (vii) gives the numbers of first pecks at each of the two stimuli, which were PF and a correctly oriented PS for all chicks.

TABLE (vii)

	PSC	PF
1st pecks	10	9

It should be remembered that in the previous experiment on dark-reared chicks, only 12 pecked, but this was enough to give a

strong preference for a real S over F, and also that all the 5 experiments so far done using these photographs, gave strong evidence of a preference for PSC over PF. It therefore looks as though dark-reared chicks really do not prefer PSC to PF. It seems that Fantz's conclusion (1958) that dark-reared chicks do not use shading cues in their solidity preference may indeed be true, though it would of course take many more experiments to be sure of this.

Discussion of results given so far on the use of shading cues

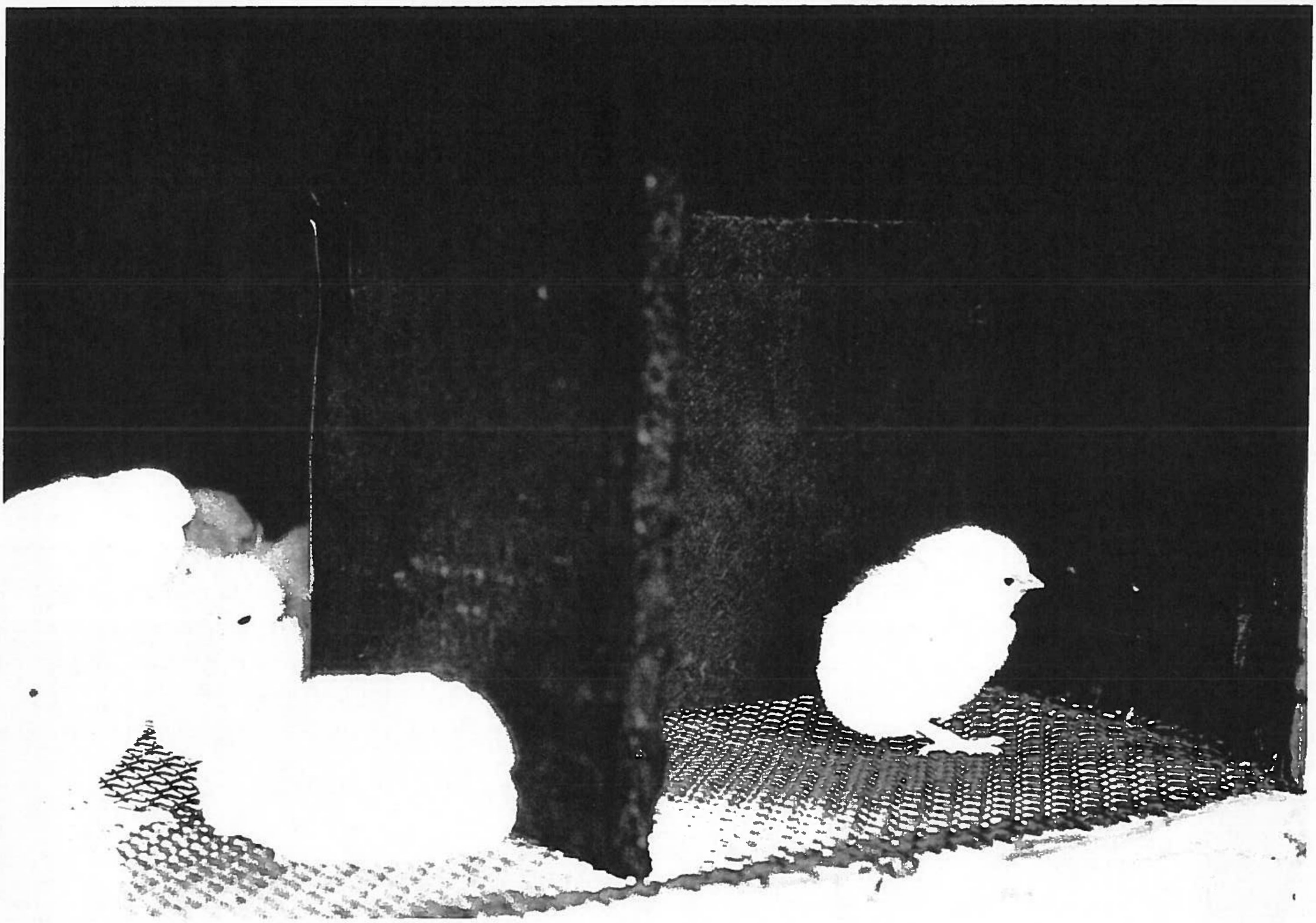
All chicks tested, whether reared in the light or in darkness prefer a real solid hemisphere S to a flat disc F. Light-reared chicks prefer a photograph of such a hemisphere to a photograph of a disc, but only if the photograph of the solid is oriented "correctly" so that it appears as a real solid object would appear lit from above, as in nature. If the photograph of the solid is inverted it receives significantly fewer pecks than if it is "correctly" oriented. Dark-reared chicks on the other hand do not prefer a "correctly" oriented photograph of a hemisphere to one of a disc.

One way in which these facts might be interpreted is in terms of learning. According to this chicks are hatched without any tendency to use shading cues of "solidity", but with the use of some other cue or cues, perhaps movement parallax. Within the few days of experience of overhead lighting that they have before testing, light-reared chicks come to learn the surface-shading properties of solid objects recognized by means of the other cue(s) which they can use

from the moment of hatching. In other words this theory is that the same learning process observed by Hess over 7 weeks, under circumstances of my experiments is shown to take place within a few days of hatching, and without food reinforcement. This was the theory which I thought the most plausible to account for my findings to date.

There is however another possibility. It could be that chicks are able to use shading cues of solidity without specific visual experience of solid objects in directed light, but that dark-reared chicks are unable to demonstrate this owing to the fact that light is necessary in order for their eyes to develop normally. Dark-reared chicks may in other words have some general defect in their vision, the result of light deprivation (Walk, 1965), which prevents them from performing the rather subtle discrimination which may be necessary for the "photograph preference", but which does not drastically impair their performance in discriminating a real hemisphere from a disc.

A critical experiment to decide between these two possibilities is fortunately easy to do: if chicks are reared with light coming from below for two or three days, and then tested with a choice between PSC and PSI, a "correctly" oriented and an inverted photograph of a hemisphere, the two theories should predict opposite results. The "learning theory" predicts that they should prefer the inverted photograph, or at least that they definitely should not prefer the "correctly" oriented one. The "built in" theory on the other hand



Testing compartment in underfloor lighting apparatus.

predicts with some certainty that they should show the usual strong preference for the "correctly" oriented photograph.

Experiment on chicks reared with underfloor lighting

The chicks were hatched in an incubator in a room which was kept completely dark from two days before the first chick hatched. Soon after hatching they were transferred in darkness into the next room, and placed in a cage with a wire netting floor, and with a black ceiling and black walls (see opposite). Three 40 watt lights underneath the wire floor were then switched on. The chicks were tested in a partitioned-off corner of this cage, so that they never had any experience of overhead light from two days before hatching until after testing. They were tested on Day 2 or 3.

The stimuli, PSC and PSI were presented behind windows in an aluminium screen, similar to those of the automatic peck-counting apparatus. The screen was painted black like the walls and ceiling of the cage.

The chicks were tested singly and observed usually for 5 minutes each. Their first peck was noted, and also their pecks were counted during the 5 minute test period. Probably because their surroundings were familiar they pecked much more than isolated chicks in previous experiments. Sometimes if a chick had not pecked within the 5 minute period, if I thought it might do so I left it in the testing compartment for a little longer. In such cases of course I only used first pecks in the analysis, and the results from such chicks do not

appear in the "majority of pecks" figures. Of the 31 chicks tested 15 pecked within the 5 minute period, and 6 more gave their first peck a short time later. Table (viii) gives the numbers of underfloor-lighting-reared chicks who gave their first pecks to each of the two stimuli, and also the numbers who gave the majority of their pecks in the 5 minute period to each of the two stimuli.

TABLE (viii)

	PSC (Correct)	PSI (Inverted)	
1st pecks	18	3	($P < 0.002$, Binomial 2-tailed.)
Maj. of pecks	13	2	($P < 0.01$, Wilcoxon 2-tailed.)

The prediction of the "built in" theory is strongly and significantly fulfilled, and that of the learning theory disproved. To this however must be added the reservation that the eggs were kept in the incubator for 18 days with overhead lighting. It is just conceivable that the chicks might have learnt an association between gravity and the prevailing direction of light while they were in the egg. However it seems almost impossible that they could use this information to learn a preference for PSC over PSI, and in any case there is physiological evidence that the visual system of chick embryos does not normally begin to function until around the eighteenth day of incubation (Peters, Vonderahe and Powers 1958).

GENERAL DISCUSSION

The use of deprivation experiments to determine whether a piece of behaviour should be called "innate" has been criticised (Lehrman 1953), partly on the grounds that it is impossible to deprive the developing animal of everything, and it is never obvious how much deprivation is needed to justify the use of the word "innate". On the other hand it is widely admitted that even if the word "innate" should not be used directly of behaviour itself, it can legitimately be used of an abstract quality of behaviour, individual difference (Dobzhansky 1962, Tinbergen 1965). It might be argued that the word "innate" could be used of other abstract qualities of behaviour such as complexity or information content (Thorpe 1963), species specificity, or adaptiveness (Lorenz 1961). The latter functional approach to the use of deprivation experiments is well exemplified by the last, and to me the most interesting of this series of experiments, that involving chicks reared with underfloor light. The argument is briefly that adaptiveness of behaviour implies the selective production, out of a wide range of possible behaviours, of those which "fit" with the environment in such a way as to favour the reproduction of the animal's genes, and that this in turn implies the possession by the animal of some kind of advance "information" about the part of the environment concerned (Young 1957, 1964, Fantz 1965). Such "information" must have come from the environment by a process of selection; two such processes are known, learning in the individual's own lifetime, and natural selection of

its ancestors (Pringle 1951). If one defines clearly the particular feature of adaptiveness in which one is interested, it might in principle be possible to deprive the developing animal of the corresponding particular relevant features of the environment, and so determine the extent to which each of the two selective processes is involved.

In the present case, if we assume that a tendency to peck at solid objects rather than flat is advantageous, the preference for PSC, the correctly oriented photograph of a hemisphere, over PSI the inverted one, relies for its correspondence with reality on the fact that in nature, light comes from above rather than from below. "Information" about this particular feature of the environment must have entered the chicks prior to the time when their preferences were tested. If this shorthand expression is found offensive, it can easily be restated: a selective agency, acting in this environmental condition of overhead light, has previously increased the chicks' relative tendency to peck at objects having the shading properties of solidity in overhead light. The simple deprivation experiment of rearing chicks in an environment in which the majority of light came from below, provided a means of removing the possibility of one of the two types of selective process, learning, causing the development of this particular behavioural selectivity.

It is irrelevant to say that learning, or other interactions with the environment were necessary in order for the preference to develop. For example, chicks reared in darkness apparently do not

differentiate PSC from PF. Environmental interactions of many kinds including learning were no doubt indispensable for the development of pecking. The point is so obvious it is trivial.

In this experiment, we are not concerned with the factors necessary for the development of pecking in general; nor with the factors necessary for the development of the PSC/PSI preference in common with all, or many other, preferences. We are concerned with the factors which might be expected to be specifically necessary for the development of this preference in particular, and we have seen that in this case the relevant environmental factor, overhead light, was not necessary during the lifetime of the individual.

This case has been made rather too straightforwardly, and some objections must be raised. The technical one that the chicks might conceivably have learnt something about the prevailing direction of light while in the egg, has already been mentioned, and more or less discounted as far-fetched. More serious objections concern the unproved assumptions about survival value, which are necessary for the argument. There are two such assumptions, firstly that a preference for solidity is advantageous, and secondly that the survival value of the PSC/PSI preference has any relevance to solidity: it is possible that PSC is preferred to PSI for an entirely different functional reason having no connection with the appearance of solid objects in overhead light. I feel that both these unproved assumptions are probably justified, and that the interpretation of this experiment

which I have given is a reasonable one.

Important though deprivation experiments inspired by such functional considerations may be, it is hard to see any advantage in using them as a device for the general rehabilitation of the word "innate" itself (Lorenz 1961). Though the functional approach to ontogeny may have ingeniously refuted cruder arguments against the use of the word, it has done nothing to allay the suspicion that the labelling of behaviour as "innate" may hinder research through appearing to explain, when really it only describes (Lehrman 1953).

Furthermore it is a dangerously ambiguous word which may mean different things in different special cases. Probably the best solution to the problem of how to label behaviour shown to develop in spite of deprivations of various kinds, is to use descriptive operational expressions containing a brief reference to the kind of deprivation employed (Jensen 1961). For example if chicks show a certain pecking preference after being reared in darkness, it should be called a "dark-reared preference", rather than an "innate" preference. This term will then distinguish it from "diffuse-light-reared preferences", "underfloor-light-reared preferences", "unfed preferences", "isolation preferences", etc., all of which would be confused if given the common label "innate". It might be possible to plead that, with a proper understanding of the functional definition of "innateness" it should be clear which of the many possible deprivations is the relevant one in each particular case. Even if this were so, which is doubtful, it

would still seem preferable to state, if only briefly, the precise operation performed in each deprivation experiment, and then allow the reader to form his own judgement whether he wishes to use the word "innate" for the case. The facts are no less interesting or important if they are stated simply and descriptively, than if they are condensed into the unclear conclusion that the behaviour is "innate". Let deprivation experiments inspired by an interest in the origin of adaptiveness continue to be performed. But let the conclusions drawn from them be operational, and unambiguous.

In this concluding discussion, I have stressed the significance of the final, underfloor lighting experiment, because its result seems to me particularly surprising and interesting. This does not mean of course that the type of behaviour development shown by this experiment is the only way, or even the most important way in which chicks acquire adaptive preferences. Experiments described earlier showed that selective waning in responsiveness to (presumably) inedible flat objects, and generalisation between flat objects probably play a part in the development of the Solidity preference. No doubt parallel processes are instrumental in the ontogeny of other preferences.

Other experiments using both food and radiant energy as reward in a Skinner Box (made in collaboration with Mr. Jan Adam), showed that chick preferences can easily be modified by operant conditioning, for example the Solidity preference can be readily reversed. Obvious and predictable though facts of this kind are, their importance

in the ontogeny of adaptive preferences should not be underestimated.

A number of vivid analogies have been put forward to characterise the role of the genes in development. Thus Lorenz (1961) for example speaks of the "Innate teaching machine". The genetic information has been compared to a computer programme (Lorenz 1961, Tinbergen, 1965). Young (1957) speaks of the organism making "predictions", and also (1957, 1964) of the organism containing a "representation" of the environment to which it is adapted, a concept which seems particularly appropriate when the adaptation concerned is one of selective responsiveness to an external stimulus situation.

In some cases the genes could be said to make detailed specific "predictions" about aspects of the environment of which the organism has had no previous experience. For example the chick's genes "predict" that light will tend to shine from above, and a selective responsiveness or preference for PSC rather than PSI develops even when the expefimenter engineers that the prediction is incorrect, by rearing the animal in an environment with light coming from below.

In other cases the genes may "predict" nothing so detailed, and, to pursue the computer-programming analogy mentioned above, some of the instructions are conditional upon data fed in from the environment, or such data may modify the programme. Thus the Solidity preference may be reversed if pecks at F are rewarded, or may be consolidated if persistent pecks at flat objects go unrewarded.

The extent to which each of these two general programming strategies are adopted by the organism will of course depend on which is the most advantageous in particular cases. Two of the factors likely to have a bearing on this are firstly how early in life the character concerned is important for survival, and secondly the predictability of the ecologically relevant environment. As already mentioned, chicks must develop adaptive feeding preferences very early because they receive little parental help, but being omnivores, the environment relevant to their feeding is probably in many respects unpredictable. It is therefore not surprising that their pecking preferences provide good examples of both types of programme/data relationship, and continue to be a promising subject for ontogenetic research.

References

Andrew, R. J. 1961 The motivational organization controlling the mobbing calls of the blackbird. 2. Quantitative analysis of changes in the motivation of calling. Behav. 17, 288-321.

Audley, R. J. 1960 A stochastic model for individual choice behaviour. Psych. Rev. 67, 1-15.

Baerends, G. P., Bril, K. A. & Bult, P. 1964 Versuche zur Analyse einer erlernten Reizsituation bei einem Schweinsaffen (Macaca nemestrina). Z. f. Tierpsych. 22, 394-411.

Barker, R. G. 1942 An experimental study of the resolution of conflict by children. In Studies in personality (ed. Q. McNemar & M. A. Merrill). McGraw-Hill, New York.

Bastock, M., & Manning, A., 1955 The courtship of Drosophila melanogaster. Behav. 8, 86-111.

Benner, J. 1938 Untersuchungen über die Raumwahrnehmung der Hühner. Z. wiss. Zool. Abt. A. 151, 382-444.

Bird, C. 1933 Maturation and practice: their effects upon the feeding reactions of chicks. J. Comp. Psych. 16, 343-366.

Bolles, R., & Petrinovitch, L. 1954 A technique for obtaining rapid drive discrimination in the rat. J. Comp. Phys. Psych. 47, 378-380.

Bousfield, W. A., & Spear, E. 1935 Influence of hunger on the pecking response of chickens. Amer. J. Psych. 47, 482-484.

Bradley, R. A. & Terry, M. E. 1952 Rank analysis of incomplete block designs. 1. The method of paired comparisons. Biometrika 39, 324-345.

Breed, F. S. 1911 The development of certain instincts and habits in chicks. Behav. Mon. 1, 1-78.

Cane, V. 1961 Some ways of describing behaviour. In Current problems in animal behaviour (ed. W. H. Thorpe & O. L. Zangwill) : 361-388. Cambridge University Press.

Collias, N., & Joos, M. 1953 The spectrographic analysis of sound signals of the domestic fowl. Behav. 5, 175-188.

Coombs, C. H. 1950 Psychological scaling without a unit of measurement. Psych. Rev. 57, 145-158.

Coombs, C. H. 1958 On the use of inconsistency of preferences in psychological measurement. J. Exp. Psych. 55, 1-7.

Coombs, C. H. 1964 A theory of data. Wiley, New York.

Cruze, W. W. 1935 Maturation and learning in chicks. J. Comp. Psych. 19, 371-408.

Curtius, A. 1954 Über angeborene Verhaltensweisen bei Vögeln, insbesondere bei Hühnerküken. Z. f. Tierpsych. 11, 94-109.

Dashiell, J. F. 1937 Affective value-distances as a determinant of esthetic judgments. Amer. J. Psych. 50, 57-67.

Davidson, D., & Marschak, J. 1959 In Experimental tests of stochastic decision theories (ed. C. W. Churchman & P. Ratoosh), Measurement: definition and theories: 233-269. American Association for the Advancement of Science, New York.

Deutsch, J. A. 1960 The structural basis of behavior. Cambridge University Press.

De Ruiter, L. 1956 Countershading in caterpillars. Arch. Néerl. Zool. 11, 285-341.

Diamond, S., Balvin, R. S., & Diamond, F. R. 1963 Inhibition and choice. Harper and Row, New York.

Dobzhansky, T. 1962 Mankind Evolving. Yale University Press, New Haven.

Dorcus, P. M. 1926 Color preferences and color associations. Pedagog. Sem. 33, 399-434.

Fantz, R. L. 1957 Form preferences in newly hatched chicks. J. Comp. Phys. Psych. 50, 422-430.

Fantz, R. L. 1958 Depth discrimination in dark-hatched chicks. Percept. Motor Skills. 8, 47-50.

Fantz, R. L. 1965 Ontogeny of perception. In Behavior of non-human primates (ed. A. M. Schrier, H. F. Harlow & F. Stollnitz) vol. 2, 365-401. Academic Press, New York.

Flament, C. 1960 Comportement de choix et échelle de mesure. 1. Étude théorique. 2. Étude expérimentale. Bull. Cent. Étud. Rech. Psych. 9, 165-186.

Folgmann, E. E. E. 1933 An experimental study of composer-preferences of four outstanding symphony orchestras. J. Exp. Psych. 16, 708-724.

Gerard, R. W. 1960 Neurophysiology: an integration (molecules, neurons & behavior). In Handbook of Physiology, Section 1, Vol. 3, 1919-1965. American Physiological Society, Washington D.C.

Glanzer, M. 1953 Stimulus satiation: an explanation of spontaneous alternation and related phenomena. Psych. Rev. 60, 257-268.

Guilford, J. P. 1954 Psychometric methods. McGraw-Hill, New York.

Hailman, J. P. 1964 Coding of the colour preference of the gull chick. Nature 204, 710.

Hara, K., & Warren, J. M. 1961 Stimulus additivity and dominance in discrimination performance by cats. J. Comp. Phys. Psych. 54, 86-90.

Hayes, W. N. & Warren, J. M. 1963 Failure to find spontaneous alternation in chicks. J. Comp. Phys. Psych. 56,575-577.

Henmon, V. A. C. 1911 The relation of the time of a judgment to its accuracy. Psych. Rev. 18, 186-201.

Hess, E. H. 1950 Development of the chick's response to light and shade cues of depth. J. Comp. Phys. Psych. 43, 112-122.

Hess, E. H. 1956 Natural preferences of chicks and ducklings for objects of different colors. Psych. Rep. 2, 477-483.

Hess, E. H. 1956 Space perception in the chick. Sci. Amer. 195, July, 71-80.

Hess, E. H. 1961 Shadows and depth perception. Sci. Amer. 204, March, 138-148.

Hevner, K. 1930 An empirical study of three psychophysical scaling methods. J. General Psych. 4, 191-212.

Hinde, R. A. 1956 Ethological models and the concept of 'drive'. Brit. J. Philos. Sci. 6, 321-331.

Hinde, R. A. 1959 Unitary drives. An. Beh. 7, 130-141.

von Holst, E., & von St. Paul, U. 1963 On the functional organisation of drives. An. Beh. 11, 1-20.

Honig, W. K. 1962 Prediction of preference, transposition, and transposition reversal from the generalization gradient. J. Exp. Psych. 64, 239-248.

Huggins, W. H. 1957 Signal flow graphs and random signals. Proc. Inst. Radio Engineers, 45, Part 1, 74-86.

van Iersel, J. J. A. & Bol, A. C. A. 1958 Preening of two tern species. A study on displacement activities. Behav. 13, 55-73.

Jenkins, W. O., Pascal, G. R. & Walker, R. W. 1958 Deprivation and generalization. J. Exp. Psych. 56, 274-277.

Jensen, D. 1961 Operationism and the question "Is this behavior learned or innate?" Behav. 17, 1-8.

Kear, J. 1964 Colour preference in young Anatidae. Ibis 106, 361-369.

Kruijt, J. P. 1964 Ontogeny of social behaviour in burmese red junglefowl. Behav. supp. 12.

Kuo, Z. Y. 1932 Ontogeny of embryonic behavior in Aves. 4. The influence of embryonic movements upon the behavior after hatching. J. Comp. Psych. 14, 109-122.

Lawrence, D. H. 1949 Acquired distinctiveness of cues. 1. Transfer between discriminations on the basis of familiarity with the stimulus. J. Exp. Psych. 39, 770-784.

Lehrman, D. S. 1953 A critique of Konrad Lorenz's theory of instinctive behavior. Q. Rev. Biol. 28, 337-363.

Lorenz, K. 1961 Phylogenetische Anpassung und adaptive Modifikation des Verhaltens. Z. f. Tierpsych. 18, 139-187.

Lovejoy, E. 1965a Analysis of the overlearning reversal effect. Psych. Rev. 73, 87-103.

Lovejoy, E. 1965b An attention theory of discrimination learning. J. Math. Psych. 2, 342-362.

Luce, R. D. 1959 Individual choice behavior. Wiley, New York.

MacCorquodale, K. & Meehl, P. E. 1948 On a distinction between Hypothetical Constructs and Intervening Variables. Psych. Rev. 55, 95-107.

Mackintosh, N. J. 1963 Discrimination learning in animals. D.Phil. Thesis, Oxford.

Mackintosh, N. J. 1964 Overtraining and transfer within and between dimensions in the rat. Q. J. Exp. Psych. 16, 250-256.

McFarland, D. J. 1965 Control theory applied to the control of drinking in the barbary dove. An. Beh. 13, 478-492.

McFarland, D. J. 1966 The role of attention in the disinhibition of displacement activities. Q. J. Exp. Psych. 18, 19-30.

McLaughlin, D. H. & Luce, R. D. 1965 Stochastic transitivity and cancellation of preferences between bitter-sweet solutions. Psychonom. Sci. 2, 89-90.

Marler, P. 1961 The filtering of external stimuli during instinctive behaviour. In Current problems in animal behaviour (ed. W. H. Thorpe and O. L. Zangwill), 150-166. Cambridge University Press.

Marschak, J. 1960 Binary choice constraints and random utility indicators. In Mathematical models in the social sciences (ed. K. J. Arrow, S. Karlin & P. Suppes), 312-329, Stanford.

Moseley, D. 1925 The accuracy of the pecking response in chicks. J. Comp. Psych. 5, 75-97.

Muntz, W. R. A. 1962 Effectiveness of different colours of light in releasing positive phototactic behavior of frogs, and a possible function of the retinal projection to the diencephalon. J. Neurophys. 25, 712-721.

Muntz, W. R. A. 1964 Vision in frogs. Sci. Amer. 210, March, 110-119.

Nissen, H. W. & Jenkins, W. O. 1943 Reduction and rivalry of cues. J. Comp. Psych. 35, 85-95.

Padilla, S. G. 1935 Further studies on the delayed pecking of chicks. J. Comp. Psych. 20, 413-443.

Papandreou, A. G. 1957 A test of a stochastic theory of choice. Univ. Calif. Pub. Econ. 16, 1-18.

Peters, J. H., Vonderahe, A. R. & Powers, T. H. 1958 Electrical studies of functional development of the eye and optic lobes in the chick embryo. J. Exp. Zool. 139, 459-468.

Pletnjev, A. W. 1937 Vitamin A, die Sehfunktion und Richtungsbewegungen von Küken. Z. f. Vitaminforsch. 6, 140-149.

Pringle, J. W. S. 1951 On the parallel betweeh learning and evolution. Behav. 3, 90-110.

Pringle, J. W. S. 1963 The two biologies. Inaugural lecture, Oxford Clarendon Press.

Quine, D. A. & Cullen, J. M. 1963 The pecking response of young arctic terns, Sterna macrura, and the adaptiveness of the "releasing mechanism". Ibis, 106, 145-173.

Schleidt, W. 1962 Die historische Entwicklung der Begriffe "Angeborenes auslösendes Schema", und "Angeborener Auslösemechanismus" in der Ethologie. Z. f. Tierpsych. 19, 697-722.

Schneirla, T. C. 1956 Interrelationships of the "innate" and the "acquired" in instinctive behavior. In L'instinct dans le comportement des animaux et de l'homme. Masson & Cie, Paris.

Seitz, A. 1940 Die Paarbildung bei einigen Cichliden. Z. f. Tierpsych. 4, 40-84.

Shen, N. C. 1937 The color preference of 1368 Chinese students, with special reference to the most preferred color. J. Soc. Psych. 8, 185-204.

Shepard, J. F. & Breed, F. S. 1913 Maturation and use in the development of an instinct. J. An. Beh. 3, 274-285.

Smedslund, J. 1960 Transitivity of preference patterns as seen by pre-school children. Scand. J. Psych. 1, 49-54.

Spalding, D. A. 1873, reprinted 1954. Instinct. With original observations on young animals.

Sutherland, N. S. 1959 Stimulus analysing mechanisms. N.P.L. Symp. 10. Mechanisation of thought processes, Vol. 2, 575-610. H.M. Stationery Office.

Sutherland, N. S. 1964 The learning of discriminations by animals. Endeavour 23, 148-152.

Thorpe, W. H. 1963 Ethology and the coding problem in germ cell and brain. Z. f. Tierpsych. 20, 529-551.

Thurstone, L. L. 1927 A law of comparative judgment. Psych. Rev. 34, 273-286.

Tinbergen, N., Meeuse, B. J. D., Boerema, L. K. & Variosseau, W. W. 1943 Die Balz des Samtfalters, Eumenis (=Satyrus) semele. Z. f. Tierpsych. 5, 182-226.

Tinbergen, N. 1951 The study of instinct. Oxford University Press.

Tinbergen, N. 1963 On aims and methods of ethology. Z. f. Tierpsych. 20, 410-433.

Tinbergen, N. 1965 Animal Behavior. Time Inc. New York.

Tugendhat Gardner, B. 1964 Hunger and sequential responses in the hunting behavior of Salticid spiders. J. Comp. Phys. Psych. 58, 167-173.

Vowles, D. M. 1961 Neural mechanisms in insect behaviour. In Current problems in animal behaviour (ed. W. H. Thorpe & O. L. Zangwill), 5-29. Cambridge University Press.

Walk, R. D. 1965 The study of visual depth and distance perception in animals. In Advances in the study of behavior (ed. D. S. Lehrman, R. A. Hinde & E. Shaw), 100-154, Academic Press, New York.

Weaver, W. 1949 The mathematics of communication. Sci. Amer. 181, 1, 11-15.

Weidmann, U. 1959 The begging response of the black-headed gull chick. Abst. 6th Int. Eth. Cong., Cambridge.

Wood Gush, D. 1955 The behaviour of the domestic chicken: a review of the literature. An. Beh. 3, 81-110.

Woodworth, R. S., & Schlosberg, H. 1954 Experimental psychology. Methuen, London.

Young, J. Z. 1957 The life of mammals. Oxford University Press.

Young, J. Z. 1964 A model of the brain. Oxford University Press.

Zeaman, D. & House, B. J. 1962 The role of attention in retardate discrimination learning. In Handbook of mental deficiency (ed. N. R. Ellis), 159-223. McGraw-Hill, New York.

Statistical methods from:

Siegel, S. 1956 Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.