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EFFECTS OF RELATIVE REINFORCER FREQUENCY ON COMPLEX COLOR DETECTION

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Pigeons were trained under a discrete-trials detection procedure in which one of a set of color stimuli was presented on the center key and a single response turned off the stimulus and illuminated two side keys. Single responses to one or the other side key produced occasional reinforcers depending on the value of the color stimulus. In Experiment 1, one color-stimulus set comprised 559, 564, 569, and 574 nm, and right-key pecks were occasionally reinforced following presentations of members of this set. The other stimulus set comprised 579, 584, 589, and 594 nm, and left-key pecks were occasionally reinforced following presentations of members of this set. Across seven experimental conditions, the left/(left + right) relative reinforcer frequency was varied from .1 to .9. In Experiment 2, one stimulus set contained only one member, 574 nm, and right-key responses were occasionally reinforced following its presentation. Over 12 experimental conditions, two manipulations were carried out. First, the number of stimuli comprising the other stimulus set was increased from one (579 nm) to two (579 and 584 nm) to three (579, 584, and 589 nm) and to four (579, 584, 589, and 594 nm), and left-key responses were reinforced occasionally following center-key presentations of members of this set. Second, for each stimulus combination, the left/(left + right) relative reinforcer frequency was varied from .1 to .5 to .9 across three experimental conditions. The principal finding of Experiments 1 and 2 was that reinforcers and stimuli interacted in their effects on behavior. In Experiment 3, pairs of adjacent stimuli (5 nm apart) in the range 559 to 594 nm were presented in each experimental condition, and the left/(left + right) relative reinforcer frequency was held constant at .5. The data from all three experiments were analyzed according to a detection model describing performance in multiple-stimulus two-response procedures. This model provided independent measures of stimulus discriminability, contingency discriminability, and bias. The analysis showed that (a) consistent with the color-naming function, pigeons were better able to discriminate between higher nanometer values than lower nanometer values; (b) their ability to discriminate between the stimuli was independent of the number of wavelengths comprising each stimulus set; (c) they allocated delivered reinforcers very accurately to the previously emitted response; and (d) no consistent biases emerged.

Key words: signal detection, multiple-stimulus control, stimulus discriminability, contingency discriminability, bias, key peck, pigeons

Research in the experimental analysis of behavior has traditionally fallen into two, historically distinct, major categories: experiments designed to measure reinforcer effects on behavior under constant (and, typically, maximally different) stimulus conditions and experiments designed to measure the degree to which the behavior–reinforcer relation is controlled by antecedent stimuli under constant (and, most often, maximally different) reinforcer conditions. In the former, schedule-control, experiments, quantification of response–reinforcer relations has been rife, and numerous mathematical expressions have been offered to describe the relation between behavior and its consequences (e.g., Baum, 1974; Herrnstein, 1970).

By contrast, quantification in stimulus-control experiments has been less frequent (but see D. S. Blough, 1975, and Heinemann, Avin, Sullivan, & Chase, 1969). Blough, for example, provided comprehensive data on steady-state generalization performance using a single-response procedure in which the probability of reinforcement for responding in the presence of each of 25 color stimuli (spaced equal subjective distances apart) was varied. He offered a dynamic model of performance under stimulus and reinforcer control using an approach similar to that offered for reinforcer effects by Rescorla and Wagner (1972). His

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model is as follows: If the current total associative strength (i.e., the strength of responding in the presence of a stimulus) of Stimulus S_i is v_{si}, and the maximum associative strength is λ, then the change in the associative strength of that stimulus on any trial is a function of $\gamma q_{si}(\lambda - v_{si})$, where γ_{si} are a set of weighted Gaussian generalization factors centered on the stimulus element activated most strongly by S_i. The model appeared to fit Blough's data very well and reproduced effects such as shoulders in absolute response rates around stimuli associated with lower reinforcer probabilities and effects analogous to peak shift.

Recent behavioral detection approaches (e.g., Davison & Jenkins, 1985; Davison & Tustin, 1978) have also stressed the need for a consideration of the *joint* effects of stimulus and reinforcer control on behavior. Such models have introduced stimulus discriminability measures into schedule-control experiments and have extracted the biasing effects of reinforcer parameters from detection-type experiments.

The first of these models was that described by Davison and Tustin (1978). It used the generalized matching law (Baum, 1974) as a model of reinforcer bias in signal detection and derived apparently independent measures of response bias (a measure of the subject's tendency to favor one response over another) and stimulus discriminability (the degree to which different stimuli control behavior). However, Davison and McCarthy (1987) showed empirically that this model could not account, at least with an invariant sensitivity to reinforcement (a) parameter, for performance on a complex, multiple-stimulus temporal-discrimination task. Davison and McCarthy trained pigeons to peck the left of two side keys given a fixed duration of center-key illumination (either 5 s or 20 s in different experimental procedures) and to peck the right key following center-key presentation of any of 12 other durations ranging from 2.5 s to 57.5 s in steps of 5 s. When they varied the left/right reinforcer ratio, they found that sensitivity to reinforcer rate was inversely related to the discriminability of the temporal stimuli. This finding is incompatible with the detection model offered by Davison and Tustin; thus, that model is clearly limited in its effectiveness for simple, two-stimulus detection procedures. Further, as Davison (1987) noted, it is unclear how that model could logically be generalized to the n-stimulus case.

The second model was that presented by Davison and Jenkins (1985). In this model, the generalized matching law in the Davison–Tustin (1978) formulation was replaced with an expression that described the degree to which differential reinforcer contingencies controlled differential responding. In this formulation, a contingency discriminability term, d_r, replaced the generalized matching law sensitivity-to-reinforcement term, a. But again, this model failed under certain conditions. In particular, Alsop (1987) showed empirically that increasing the discriminability of the stimuli produced an apparent decrease in the control exerted by the reinforcers.[1] Further, as Davison (1987) noted, this model, like its predecessor, is not easily and logically extended to the multiple-stimulus (or multiple-response) signal-detection procedure, a procedure that is the focus of the present paper.[2]

The present research extends our previous work on complex stimulus control in two major ways: first by using color stimuli and second by testing a new model developed to deal specifically with the multiple-stimulus, two-response situation (Davison, 1987).

The model tested here is that suggested by Alsop (1987) for the two-stimulus situation and simultaneously extended by Davison (1987) to the multiple-stimulus case. The basic ideas of stimulus discriminability and contingency discriminability are identical to those discussed by Davison and Jenkins (1985), and the theory of reinforcer bias is also the same as in the former case for procedures that do not include conditional stimulus control (e.g., concurrent schedules). But the structure of this latter model for performance controlled by conditional stimuli (as in signal-detection procedures) differs from that suggested by Davison and Jenkins.

The fundamental notion is that in any situation, reinforcers delivered for a response in

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[1] Alsop, B. (1987, June). *Behavioral models of signal detection and detection models of choice.* Paper presented at the 10th Harvard Symposium on Quantitative Analyses of Behavior, Cambridge, Massachusetts.

[2] Davison, M. (1987, June). *Stimulus discriminability, contingency discriminability, and complex stimulus control.* Paper presented at the 10th Harvard Symposium on Quantitative Analyses of Behavior, Cambridge, Massachusetts.

the presence of one stimulus generalize to other stimulus–response combinations as an inverse function of the discriminability of these other stimulus–response combinations from that in which the reinforcer was delivered. In this model, generalization occurs in two dimensions: across stimulus discriminability and across contingency discriminability. Thus, if a reinforcer is delivered in Cell (1,1) of the stimulus–response matrix shown in Figure 1 (call this $R_{1,1}$), then the effect of this reinforcer on performance in other cells is as follows: If the cell differs only on the stimulus dimension, then the effect of the $R_{1,1}$ reinforcer in Cell $(1,j)$ is given by $R_{1,1}/d_{s1,j}$; if the cell differs only on the response dimension (say Cell $i,1$), then the effect on performance in this cell is $R_{1,1}/d_{ri,1}$; if the cell differs on both stimulus and reinforcer dimensions, the effect is $R_{1,1}/d_{s1,j}/d_{ri,1}$. Figure 1 shows this process for a reinforcer in Cell (1,1). Reinforcers delivered in any cell have effects in other cells according to the same logic, and the model assumes that the ratio of responses between cells equals the ratio of summated reinforcer effects in the cells.

In this model, d_s and d_r are ratio measures that range from 1 (no discriminability) to infinity (perfect discriminability). They are thus antilogs of the measures used by Davison and Tustin (1978) and by Davison and Jenkins (1985), and have the same sort of properties as the η measure proposed by Nevin, Jenkins, Whittaker, and Yarensky (1977) for stimulus generalization or confusion effects in detection situations.[3] The measures used here easily can be conceived of as relative measures (e.g., as $d_s/[1 + d_s]$), in which case their interpretation is the proportion of instances of stimuli or contingencies exerting appropriate control. It is a moot point whether it is best to conceive of the measures as ratios or as relative numbers. The decremental effects across variations of stimuli or responses are best conceptualized with the ratio measure (as a reciprocal process), whereas the process of reinforcer reallocation according to stimuli and responses in the simple (two-stimulus two-response) signal-detection case is more easily thought of as proportions of correct identifications. Here, we shall report relative discriminability measures simply because they can be more easily displayed.

RESPONSES (i)

STIMULI (j)	1	2	3
1	$R_{1,1}$	$R_{1,1}/d_{r1,2}$	$R_{1,1}/d_{r1,3}$
2	$R_{1,1}/d_{s1,2}$	$R_{1,1}/d_{s1,2}/d_{r1,2}$	$R_{1,1}/d_{s1,2}/d_{r1,3}$
3	$R_{1,1}/d_{s1,3}$	$R_{1,1}/d_{s1,3}/d_{r1,2}$	$R_{1,1}/d_{s1,3}/d_{r1,3}$

Fig. 1. The matrix of stimulus–response events in the present experiment. *i* denotes responses, *j* denotes stimuli, *R* denotes reinforcers, d_s denotes stimulus discriminability, and d_r denotes contingency discriminability.

By the process outlined above, reinforcers delivered in each of the stimulus–response cells defined by the experimenter are distributed across all other cells (including those in which reinforcers are delivered and those in which they are not) as an inverse function of the discriminability of those target cells. Thus, in the simplest two-stimulus two-response case, with reinforcers delivered only for correct responses ($B_{1,1}$ and $B_{2,2}$), the effective reinforcers (primed R variables) in the four cells are, following the matrix in Figure 1:

$$R'_{1,1} = R_{1,1} + R_{2,2}/d_{s1,2}/d_{r1,2} \quad (1a)$$

$$R'_{2,1} = R_{1,1}/d_{r1,2} + R_{2,2}/d_{s1,2} \quad (1b)$$

$$R'_{1,2} = R_{1,1}/d_{s1,2} + R_{2,2}/d_{r1,2} \quad (1c)$$

$$R'_{1,1} = R_{2,2} + R_{1,1}/d_{s1,2}/d_{r1,2}. \quad (1d)$$

More generally, for any cell (m,n) of the matrix, when s stimuli and r responses are available:

$$R'_{m,n} = \sum_{r}^{i=1} \sum_{s}^{j=1} R_{i,j}/d_{sn,i}/d_{rm,j}. \quad (2)$$

Note, of course, that any particular cell is indiscriminable from itself (i.e., $d_{si,i} = 1$ and $d_{rj,j} = 1$).

The model fitted was:

$$\frac{B_{1,j}}{B_{1,j} + B_{2,j}} = \frac{cR'_{1,j}}{cR'_{1,j} + R'_{2,j}}, \quad (3)$$

where the R' values are obtained from Equation 2 for each of the i responses (=2, here) and j stimuli available. The bias parameter, c, measures any preference on the part of the subject for emitting one response rather than

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[3] Nevin, J. A., Jenkins, P., Whittaker, S. G., & Yarensky, P. (1977, November). *Signal detection and matching.* Paper presented at the meeting of the Psychonomic Society, Washington, D.C.

the other independent of the stimulus or reinforcer conditions prevailing (Baum, 1974). Thus, for an experimental condition in which eight stimuli were arranged, according to Equation 3, eight data points were available for analysis in the model.

The present paper reports the results of three color-discrimination experiments with pigeons in which stimulus parameters, membership of a stimulus class, and relative reinforcer frequencies were manipulated. The model defined by Equations 2 and 3 was fitted to the data, and measures of stimulus discriminability, contingency discriminability, and response bias were obtained. In this manner, the independence or otherwise of stimulus and reinforcer effects on performance in complex multiple-stimulus discrimination tasks could be assessed. The approach taken here differed from that taken by D. S. Blough (1975) in that the dependent variable was relative response rate, the metric commonly used in quantitative approaches to schedule choice, rather than absolute response rate. Also, we did not attempt to place the present color stimuli equal subjective distances apart. Rather, we wanted to measure the discriminabilities between stimuli comprising the set, both within an extended matching/signal-detection model and, independently, by explicitly measuring performance between pairs of color stimuli.

GENERAL METHOD

Subjects

Six homing pigeons, numbered 151 to 156, were maintained at 85% ± 15 g of their free-feeding body weights by feeding them mixed grain in their home cages after the daily experimental sessions. Water and grit were always available in the home cage. Bird 152 died before the experiment was complete.

Apparatus

All experimental contingencies were controlled by a remotely placed computer. Initially, this was a Digital PDP 8/e® running time-shared SuperSKED® software, but at Condition 21 this was replaced by a PDP 11/73® running SKED-11® software. The computer also controlled an Oriel Corp. Model 7240 monochromator equipped with a 100-W quartz-halogen lamp, 1,200 lines/mm grating, and 280 micron fixed slit providing an approximate bandpass of 2 nm. No attempt was made to control the intensity of the output of the monochromator for differing wavelengths, and this output was led through a 1-m light-fiber and terminated 2 mm behind the clear center key of the experimental chamber. The color patch was approximately 3 mm in diameter on a black background.

The experimental chamber, which was 310 mm wide, 340 mm deep, and 310 mm high, was fitted with three response keys set 115 mm apart and 250 mm from the floor on one wall of the chamber. The translucent side keys, when operative, were illuminated white. All three keys were 20 mm in diameter and required a force of about 0.1 N for operation. Beneath the center key and 70 mm from the floor was a food hopper containing wheat. During reinforcement, which was 3-s access to this grain, the hopper was illuminated and all other lights in the chamber were extinguished. A 0.1-A 24-VDC houselight provided general illumination throughout the session.

Responses on the center key when the color patch was presented, and on the side keys when these were illuminated white, were effective and were counted.

Procedure

The subjects used in these experiments had extensive experience on procedures similar to those used here for over a year prior to the start of this research. These previous conditions were used to refine the procedure and to discover an appropriate set of stimuli for the present experiment. They are not reported here. Prior to this, the subjects had extensive experience responding on multiple schedules (Charman & Davison, 1983). Thus, no magazine or key-peck training was required, and the subjects were placed directly on the first experimental condition (Table 1).

The subjects were initially placed in the darkened chamber. About 1 min later, the houselight was illuminated, a color patch was presented on the center key, and the experimental session commenced. A single peck on the center key turned the color patch off and illuminated both side keys white. A single peck on the right key was designated "correct" following presentation of a shorter, or one of a set of shorter, wavelength(s) on the center key and was occasionally reinforced. A single peck on the left key was designated "correct" following presentation of a longer, or one of a set of longer, wavelength(s) on the center key and was occasionally reinforced. All other combinations of stimuli and side-key responses were designated "errors," and these produced a 5-s offset of all keylights (a sufficient time to select the next color). Unreinforced correct responses produced the same consequences as errors. Reinforcers were delivered according to a variable-interval (VI) 30-s schedule, derived from an arithmetic progression with 12 intervals and a shortest interval of 2.5 s. Intervals were selected randomly from this set without replacement, and they timed throughout the session. When an interval had completed timing, a reinforcer was allocated to either the next left-correct or next right-correct response with a fixed probability that was changed across conditions (Table 1). This reinforcer remained available, and no more were arranged, until it had been taken, at which point a new interval was selected. The reinforcement procedure was thus a dependent concurrent VI VI schedule for correct responses (Stubbs & Pliskoff, 1969). Following a reinforced correct response (3-s grain), there was a 5-s blackout before the next trial commenced.

In each condition of the experiments, right-key responses were correct following the presentation of any of the colors comprising a set of colors (this set might have only one member), and left-key responses were correct following the presentation of any of the colors comprising a different set (again, this might have only one member). These sets were selected from eight color stimuli, 559 to 594 nm in steps of 5 nm. Before the start of each trial, one of the two sets was selected with a probability of .5, and then a particular member of that set was selected with each stimulus in the set being equally probable (i.e., sampled with replacement). Stimulus selection was not dependent on either the previous response or on the previous stimulus selected. Thus, a noncorrection procedure was used.

Sessions ended in blackout after 40 reinforcers had been obtained or after 45 min had elapsed, whichever event occurred first.

The general procedure in each of the three experiments reported here was as described above. The specific conditions for each experiment were as follows: In Experiment 1 (Table 1), the shorter wavelength set of stimuli included 559, 564, 569, and 574 nm, and right-key responses were reinforced occasionally following presentation of members of this set. The longer wavelength set comprised 579, 584, 589, and 594 nm, and left-key responses were reinforced occasionally following presentation of members of this set. Over Conditions 1 to 8, the reinforcer frequency for correct left-key responses relative to total reinforcers for correct responses was varied from .1 to .9. (The data from Condition 5 are not reported because of intermittent problems with the houselight during this condition.)

Table 1

Experiment 1. Sequence of experimental conditions and number of training sessions under each condition. A right-key response was correct following the presentation of 559, 564, 569, or 574 nm, and a left-key response was correct following 579, 584, 589, or 594 nm. p(Rft/L) denotes the probability of a reinforcer being assigned to a correct left-key peck. The data from Condition 5 are not reported because of intermittent problems with the houselight during this condition.

Condition	p(Rft/L)	Sessions
1	.1	18
2	.5	31
3	.8	31
4	.35	22
6	.9	23
7	.2	27
8	.65	30

In Experiment 2, the shorter wavelength set contained only one member, 574 nm, and right-key responses were reinforced occasionally following its presentation (Table 2). Over Conditions 9 to 22, two manipulations were carried out. First, the number of stimuli comprising the longer wavelength set was increased from one (579 nm, Conditions 9 to 11), to two (579 and 584 nm, Conditions 14 to 16), to three (579, 584, and 589 nm, Conditions 17 to 19), and finally to four (579, 584, 589, and 594 nm, Conditions 20 to 22). In all of these conditions, left-key pecks were reinforced occasionally following center-key presentation of members of this set. Second, for each stimulus combination, the relative reinforcer rate for left-correct responses was varied from .1 to .5

Table 2

Experiment 2. Sequence of experimental conditions and number of training sessions under each condition. A right-key response was correct following the presentation of 574 nm, and a left-key response was correct following the presentation of the other color or colors. p(Rft/L) denotes the probability of a reinforcer being assigned to a correct left-key response. The data from Conditions 12 and 13 are not reported because of a monochromator failure during these conditions.

Condition	p(Rft/L)	Sessions
574 versus 579 nm		
9	.5	24
10	.1	22
11	.9	25
574 versus 579 or 584 nm		
14	.9	24
15	.1	21
16	.5	29
574 versus 579, 584, or 589 nm		
17	.9	27
18	.1	29
19	.5	26
574 versus 579, 584, 589, or 594 nm		
20	.5	22
21	.1	28
22	.9	31

to .9 across three experimental conditions. (Data from Conditions 12 and 13 are not reported because of a monochromator failure during these conditions.)

In Experiment 3 (Conditions 23 to 32), pairs of adjacent stimuli were presented in each condition (i.e., 559 vs. 564 nm, 564 vs. 569 nm, etc.), and the relative left-correct reinforcer rate was kept at .5 (Table 3). Condition 28 (574 vs. 579 nm) replicated Condition 9 of Experiment 2, and this particular stimulus pair was again presented in Condition 32.

The data collected were the numbers of responses emitted on the left and right keys following the presentation of each of the wavelengths comprising each stimulus set and the numbers of reinforcers delivered for correct responses following the presentation of each wavelength.

Experimental conditions were changed when all subjects had met the following stability criterion. The first nine sessions' data of each experimental condition were discarded. Then, for each session, the overall discriminability (log d) between the stimulus sets and the overall bias (log B) between left- and right-key responses were calculated using the measures suggested by Davison and Tustin (1978):

Table 3

Experiment 3. Sequence of experimental conditions and number of training sessions under each condition. A right-key response was correct following the presentation of the shorter wavelength, and a left-key response was correct following the presentation of the longer wavelength. The probability of reinforcement for a correct left-key response was always .5.

Condition	Stimuli	Sessions
23	564, 589	50
24	569, 584	26
25	559, 564	28
26	564, 569	31
27	569, 574	28
28	574, 579	26
29	579, 584	26
30	584, 589	31
31	589, 594	21
32	574, 579	28

$$\log d = .5 \log\left(\frac{B_{1,j} \cdot B_{2,k}}{B_{2,j} \cdot B_{1,k}}\right),$$

and

$$\log B = .5 \log\left(\frac{B_{1,j} \cdot B_{1,k}}{B_{2,j} \cdot B_{2,k}}\right),$$

where B_1 and B_2 denote left- and right-key response counts and j and k denote the two stimulus sets. For each successive and nonoverlapping block of three sessions, the medians of these measures were calculated. If three such medians did not show a monotonic trend, then the performance was taken as stable *for that measure*. When both measures had achieved this criterion once, a subject's performance was judged stable. Finally, when all subjects' performances on these criteria were stable, the conditions were changed for all subjects. These criteria, then, required a minimum of 18 sessions for stability. The actual number of sessions required for stability are shown in Tables 1 to 3.

RESULTS

The numbers of responses emitted, and reinforcers obtained, following the presentation of each wavelength in all the conditions of the experiments are shown in the Appendix. These data have been summed over the last five sessions of each experimental condition. The Appendix shows that although the relative overall frequency of left- versus right-key reinforcers was controlled experimentally, it was not the case that equal frequencies of reinforcers were obtained for responses to each of the wavelengths comprising each stimulus set. For example, in Conditions 1 to 8, generally the lowest reinforcer frequencies were obtained by the subjects at the intersection of the stimulus classes (here, 574 and 579 nm). This is, as will be seen, the area in which the discriminability between the stimulus classes was lowest.

Because of the large amount of data collected in the present experiments, we shall focus mainly on the group data and present individual-subject data to support our interpretation of the group-data trends. Figure 2 shows the results of Experiment 1 averaged over the 6 subjects, but a caveat is in order: The functions shown in Figure 2 are not totally representative of the individual subjects, as we shall show. In Experiment 1, one stimulus set comprised hues of 559, 564, 569, and 574 nm, the other stimulus set comprised hues of 579, 584, 589, and 594 nm, and the relative reinforcer frequency for left-correct responses (relative to total reinforcers) was varied from .1 to .9 across seven experimental conditions. In Figure 2, log left-/right-key behavior ratios are plotted as a function of wavelength for each relative left-correct reinforcer frequency arranged. Generally, each function appears to be a relatively normal, ogival, psychophysical function. When left- and right-key reinforcers were equal (p = .5), the function was symmetrical around the horizontal indifference line drawn in the figure. The functions were ordered, with only five reversals, as a function of the relative probability of left-key reinforcers. The unusual feature of these data was, however, that the psychophysical functions were not parallel for different relative reinforcer frequencies, with the steepest functions arising from low left-key reinforcer probabilities and the least steep from high left-key reinforcer probabilities. This is clearly reflected in the different effects that changing the probability of left-key reinforcers had on behavior ratios in the presence of longer versus shorter wavelengths. Following the presentation of the 559-nm stimulus, changing reinforcer probabilities had strong effects on behavior, whereas following presentation of the 594-nm stimulus, reinforcers had a relatively attenuated effect on behavior ratios. There was, therefore, a difference in sensitivity to reinforcer-frequency variation across stimuli, and hence an interaction between relative reinforcer frequency and stimulus value on behavior. Most functions flattened at their left and right extremes, but they did so at different log behavior-ratio levels, suggesting that the data were not constrained by ceiling or floor effects on the behavior measure.

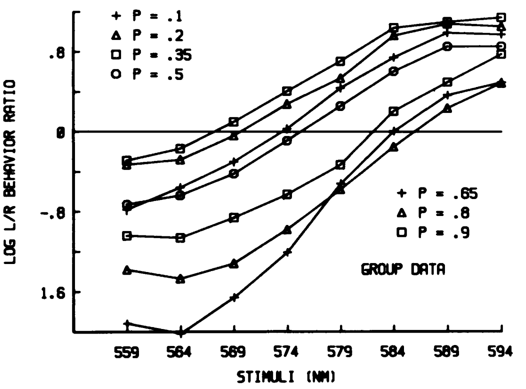

Fig. 2. Experiment 1: The logarithm of the left-/right-key behavior ratios as a function of wavelength (measured in nanometers, nm) for the group data. p denotes the probability of assignment of a left-key reinforcer.

Figure 3 shows individual-subject data plotted in the same way as in Figure 2. Not all of the individual data can be shown in Figure 3 because response-ratio measures were occasionally infinite. The convention was adopted that noninfinite data beyond infinite points (away from the intersection of the stimulus sets) were also not plotted. In comparison with Figure 2, only Birds 153, 154, and 155 showed the smaller distribution of data at longer wavelengths than at shorter wavelengths evident for the group data. Bird 152 showed a similar range of behavior ratios at all stimulus values. Bird 156 gave evidence of a reduced distribution around 579 nm, and Bird 151, a smaller distribution around 559 nm. The functions were not so clearly ordered as for the group data. In general, the functions for the left-key reinforcer probability of .9 were the highest or second highest functions, and frequently,

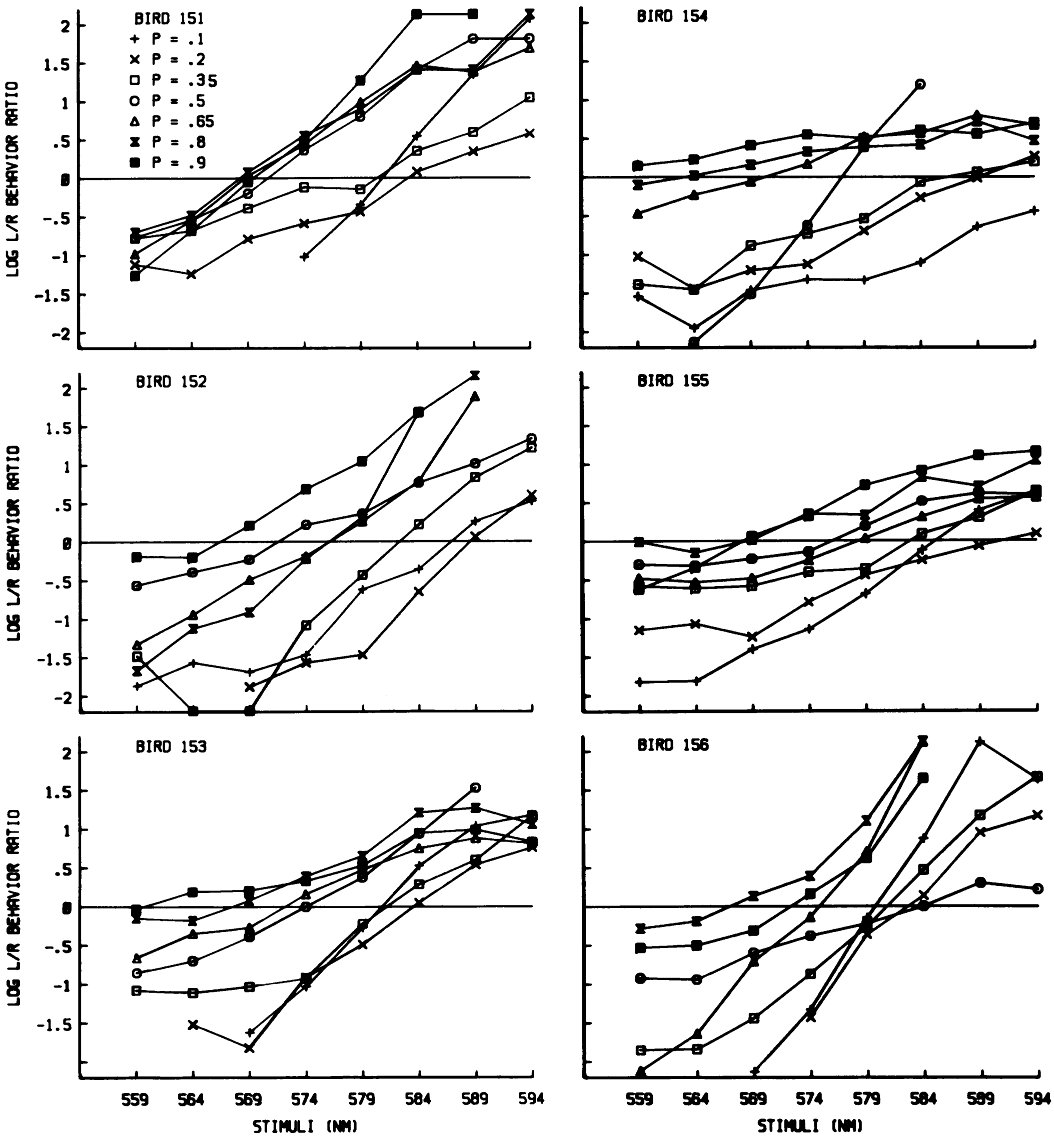

Fig. 3. Experiment 1: Individual-subject log left-/right-key behavior ratios as a function of wavelength (measured in nm). p denotes the probability of assignment of a left-key reinforcer.

but by no means invariably, the $p = .1$ function was among the lowest functions. The remaining functions were not particularly well ordered, and for many of the birds, in contrast to the group data (Figure 2), there was an apparently anomalous function. For example, for Bird 151, the $p = .1$ function was much steeper than the other functions and gave a higher log-response ratio at 594 nm than did $p = .2$, .35, .5, and .6. For Birds 153 and 155 also, the $p = .1$ functions were the steepest. For Bird 156, both the $p = .1$ and the $p = .65$ functions were steeper than the other functions. For Bird 154, the $p = .5$ function was considerably steeper than any other function. Were it not the case that 5 of the 6 birds showed one or more excessively steep function, and that they did so at different left-reinforcer probability levels, we would have assumed an equipment fault. To the contrary, it would seem that some left-reinforcer probability levels in combination, perhaps, with particular regions of color sensitivity produce either relatively steep or flat psychometric functions. It is also clear that, for at least 5 of the 6 birds, no monotonic transformation of the stimulus axis (i.e., a respacing of the distances between stimuli) could lead to a set of parallel psychometric functions.

Experiment 2 investigated the effects of increasing the number of stimuli comprising the longer wavelength set on performance following presentation of the single color comprising the shorter wavelength set (574 nm). For each combination, the reinforcer ratio was varied over three levels. The group results are shown in Figure 4 and are fully representative of the individual subjects. A change evidently did occur as the number of stimuli was increased, but it appears that the change was mainly one of bias rather than discriminability. That is, as the number of stimuli comprising the longer wavelength set was increased, there was a progressive decrease in the left/right response ratio and thus a relative increase in the frequency of emitting the response that was correct for the shorter wavelength (i.e., a right-key peck). To substantiate this group result, nonparametric trend tests were carried out on the individual-subject preference data for both the 574- and 579-nm stimuli across the increasing number of longer wavelengths at each reinforcer probability level. Significantly decreasing preferences were obtained at the .5 reinforcer probability level for 574 nm ($\Sigma S = -24$) and 579 nm ($\Sigma S = -20$), at the .9 reinforcer probability level for 579 nm ($\Sigma S = -16$), and at the .1 reinforcer probability level for 574 nm ($\Sigma S = -22$, all $N = 6$ birds and $k = 4$ conditions, $p < .05$). Collapsing across pairs of wavelengths, the decreasing trends were significant for both the .5 and the .1 reinforcer probability levels ($z = 2.61$ and 1.96, respectively; $p < .05$). The significant changes in preference, however, require careful interpretation because the numbers of reinforcers obtained in *each* stimulus in the longer wavelength set did not remain equal as the number of stimuli was increased.

The differences between the log response ratios for 574 nm and 579 nm in Figure 4 are, according to the Davison–Tustin (1978) model, measures of the discriminability of the stimuli (specifically, 2 log d). These measures were

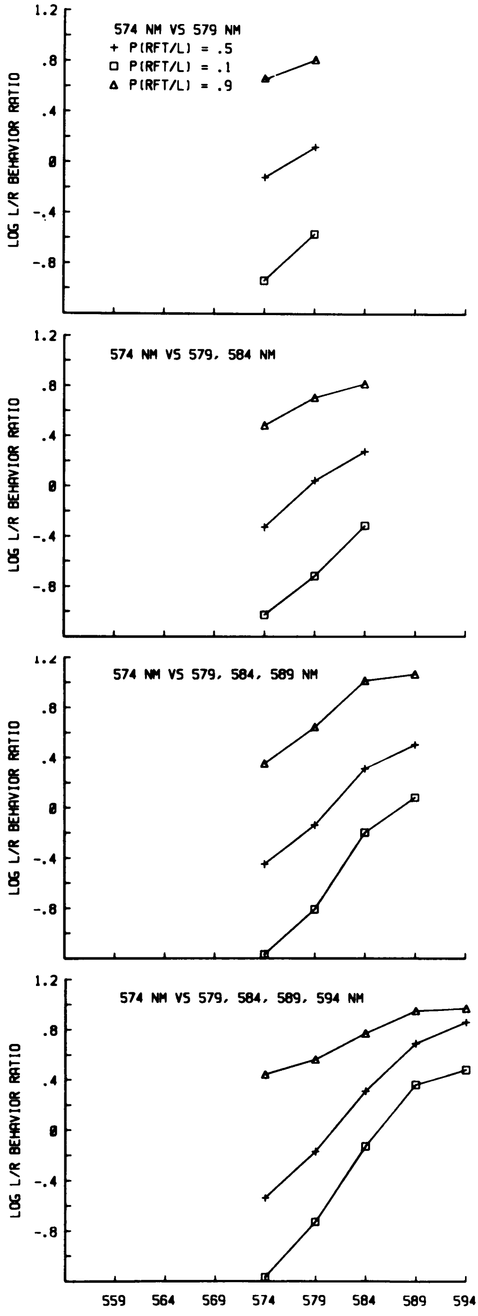

Fig. 4. Experiment 2: The logarithm of the left-/right-key behavior ratios as a function of wavelength (measured in nm) for the group data. p(Rft/L) denotes the probability of assignment of a left-key reinforcer.

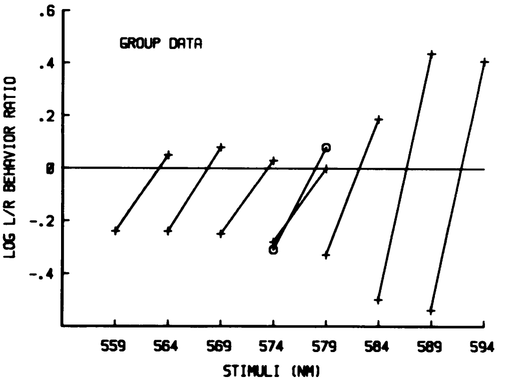

Fig. 5. Experiment 3: The logarithm of the left-/right-key behavior ratios as a function of wavelength (measured in nm) for the group data.

calculated for reinforcer probabilities of .1 and .9 for the individual subjects and then used in a nonparametric trend test. Neither of these estimates showed a significant trend as the number of stimuli comprising the longer wavelength set was increased.

Compared with the four- versus four-stimulus set (Experiment 1, Figure 2), the behavior ratios in 574 and 579 nm appeared to be more toward the left key in the one- versus one-stimulus set (Figure 4). However, binomial tests carried out with the individual-subject data showed that the differences were not statistically significant either within any reinforcer probability or across the three reinforcer probabilities arranged in Experiment 2.

Experiment 3 was carried out to measure the discriminability between successive pairs of the eight color stimuli. The group log left/right behavior ratios are shown as a function of wavelength in Figure 5. In this figure, the vertical distance apart of the pairs of data points measures discriminability (log *d*) according to the Davison–Tustin (1978) model. Clearly, discriminability was lower in the region 559 to 584 nm and higher in the region 584 to 594 nm. The group-data replication (Condition 32) was clearly satisfactory, in that discriminability decreased again to approximately its original level after exposure to higher discriminability stimulus pairs. Response bias is given by the mean of the connected data points. Clearly, there was a general bias toward emitting right-key responses. There was no clear trend in bias with increasing wavelength, but there was a suggestion that it was related to the level of discriminability. The relation between bias and discriminability is discussed below.

Figure 6 shows the individual-subject data from Experiment 3 plotted as in Figure 5. The individuals produced results similar to the group in that the response differential between pairs of stimuli increased from 559 versus 564 nm to 589 versus 594 nm for all subjects. Some subjects (e.g., Birds 153 and 155) showed very little response differential at the lower end of the color range, whereas others (Bird 156) showed relatively large response differentials throughout the color range, but still the largest differentials were seen at the longer wavelengths. The largest differentials were always at either 584 versus 589 nm or 589 versus 594 nm. Bias, measured by the mean of the connected data points, remained reasonably constant across experimental conditions for Birds 153, 155, and 156, but changed in differing ways for the other 3 birds. Response differentials were usually similar in the replication Condition 32 as in the replicand, Condition 28, though some increase occurred for Bird 153. Bias in the replicated condition was different (but in differing directions) for Birds 151, 153, and 154.

As we would hope, there was a similarity between the results shown in Figure 6 and those shown in Figure 3. Bird 156 showed the strongest control by color differences in both sets, and Bird 155 showed the weakest control in both.

Response Bias

Figure 7 shows group estimates of response bias (the mean of the response differentials shown in Figure 6) as a function of discriminability level (one half the difference between the response differentials shown in Figure 6) for each stimulus pair in Experiment 3. The best fitting straight line by the method of least squares is shown on the graph, together with its equation. Contrary to the assumptions of the Davison–Tustin (1978) model, there is an interaction between level of discriminability and bias as shown by the positive (0.20) slope. Specifically, the animals' behavior became more biased in favor of emitting a right-key response at shorter wavelengths where stimulus discriminability was lowest. Their behavior displayed little or no bias at the longer wavelengths, that is, in the region of best discriminability (Figure 6).

Figure 8 shows response bias as a function

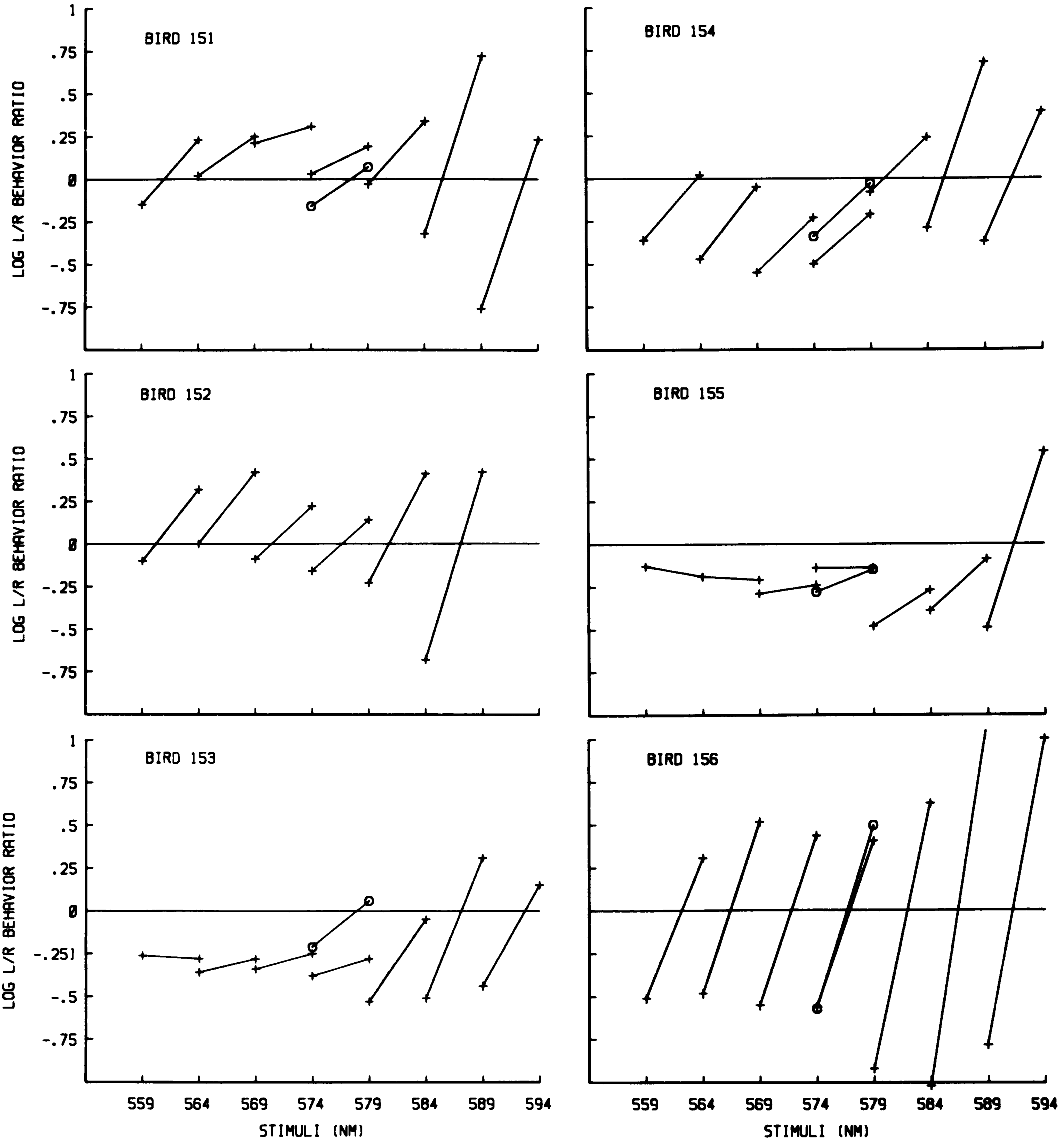

Fig. 6. Experiment 3: Individual-subject log left-/right-key behavior ratios as a function of wavelength (measured in nm).

of the overall left/right reinforcer-frequency ratio for the group data obtained in Experiments 1 and 2; that is, the two experiments in which relative reinforcer frequencies were manipulated. According to the generalized-matching-law based model of Davison and Tustin (1978), bias should be linearly related to changes in relative reinforcer frequency with a slope (sensitivity) of approximately 0.8. Clearly, although bias was positively related to reinforcer-frequency ratios, this relation was nonlinear. Further, similar degrees of response bias were shown at each reinforcer-ratio value, irrespective of the number of wavelengths comprising the stimulus sets.

DISCUSSION

The present research was designed to investigate the control exerted by color stimuli on the discriminative behavior of pigeons and to assess the effects of reinforcer-frequency variation on this control. Three experiments were reported in which pigeons were trained

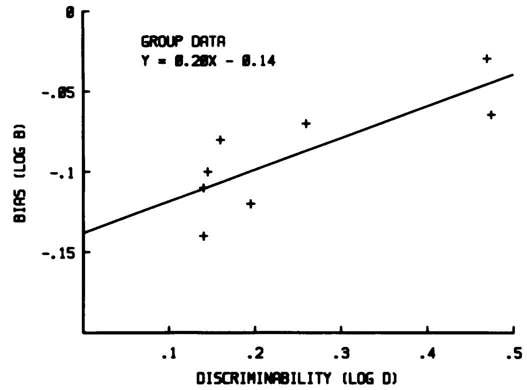

Fig. 7. Experiment 3: Group response biases as a function of stimulus discriminability. The best fitting straight line by the method of least squares is shown together with its equation.

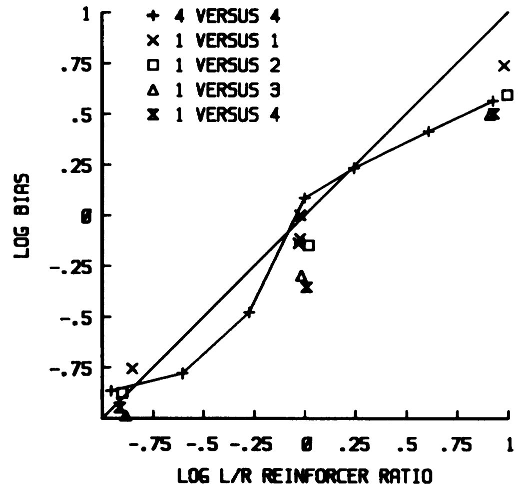

Fig. 8. Experiments 1 and 2: Response bias as a function of the logarithm of the obtained left-/right-key reinforcer ratio for the group data. The data points obtained in Experiment 1 are connected by a solid line. The number of wavelengths comprising each stimulus set are denoted as 4 versus 4 (Experiment 1) and 1 versus 1, 1 versus 2, 1 versus 3, and 1 versus 4 (Experiment 2).

to discriminate between different sets of wavelengths when the members of a particular stimulus set were varied (Experiments 2 and 3) and when reinforcer-frequency ratios were manipulated (Experiments 1 and 2).

The principal findings can be summarized as follows: First, within the range of wavelengths studied (i.e., 559 nm to 594 nm), discriminability was better the longer the wavelength (Figures 5 and 6). This result is consistent with previous color-discrimination experiments (e.g., D. S. Blough, 1961; P. M. Blough, 1979; Schneider, 1972; Wright, 1979; Wright & Cumming, 1971). Second, psychophysical functions were not parallel for different reinforcer-frequency ratios. Rather, sensitivity to reinforcer frequency varied as a function of wavelength, and hence, reinforcers and stimuli interacted in their effects on behavior (Figures 2 and 3). This result supports the similar findings of Davison and McCarthy (1987) obtained using complex temporal-stimulus sets. Third, these changes in reinforcer sensitivity with wavelength, together with the nonlinear relation between bias and reinforcer-frequency ratios displayed in Figure 8, render the Davison–Tustin (1978) model untenable as a descriptor of behavior in this situation. Clearly, an alternate model is needed, and we assess below the adequacy of the Davison (1987) approach in accounting for the present data.

The model defined by Equations 2 and 3 was fitted, using nonlinear multidimensional regression (Killeen, personal communication), separately to the data from Experiments 1, 2, and 3 to estimate the seven d_s parameters, d_r, and inherent bias. At least 5,000 iterations were carried out for each fit. The data used were relative responses emitted (left-key responses/total responses) in the presence of each stimulus summed over the last five sessions of each experimental condition (i.e., the data shown in the Appendix). The results of these fits are shown in Table 4, where d_s, d_r, and inherent bias values are all shown as relative numbers (i.e., $d_s/[1 + d_s]$, $d_r/[1 + d_r]$, and $c/[1 + c]$) for ease of understanding. Additionally, we calculated the percentage change in the error variance between predicted and obtained data when each parameter was varied ±25% additively from its best value (with all other parameters at their best values). The measure taken was the difference between the best fit error variance and the mean of the error variances produced by each 25% change, as a percentage of the best fit error variance. This measure gives some idea of the precision of estimation of each parameter. If the percentage is large, the estimate is precise because it came from a function that showed considerable variation around the estimate. If it is small, the function was relatively flat around the best estimate. Occasionally, in Experiment 3, rel-

Table 4

Best fitting parameter values (obtained from iterative nonlinear fits) for the detection model expressed in Equations 2 and 3 for the three experiments. The parameters are given as relative d_s values (that is, $d_{si,j}/(1 + d_{si,j})$, and as relative d_r and relative bias values. Shown in parentheses is the percentage change in the error sum of squares produced by varying the estimated parameters by 25% of their values while keeping the others at these best estimates. The larger the value of this measure, the more precise is the parameter estimation. (See text for details.)

	Subject						
Measure	151	152	153	154	155	156	Group
Experiment 1: Conditions 1–8							
$d_{s1,2}$	.70 (1)	.57 (4)	.66 (7)	.63 (8)	.57 (3)	.64 (1)	.59 (10)
$d_{s2,3}$	.83 (18)	.69 (18)	.59 (20)	.57 (20)	.65 (15)	.72 (7)	.66 (60)
$d_{s3,4}$	.81 (89)	.77 (88)	.67 (58)	.56 (46)	.63 (37)	.66 (15)	.67 (148)
$d_{s4,5}$	.57 (30)	.61 (88)	.62 (86)	.61 (116)	.61 (64)	.70 (40)	.62 (236)
$d_{s5,6}$	.80 (36)	.68 (65)	.82 (82)	.62 (63)	.72 (58)	.92 (249)	.72 (176)
$d_{s6,7}$	.88 (6)	.75 (39)	.80 (13)	.61 (28)	.68 (17)	.77 (2.8)	.72 (64)
$d_{s7,8}$	.72 (0)	.71 (8)	.62 (1)	.61 (6)	.73 (3)	.60 (0)	.66 (11)
d_r	.92 (424)	.98 (477)	.94 (527)	.97 (249)	.87 (315)	.93 (248)	.93 (1,065)
bias	.42 (40)	.57 (86)	.39 (54)	.56 (104)	.50 (116)	.48 (27)	.49 (240)
VAC	93	94	94	90	90	89	97
av. dev.	.08	.06	.07	.08	.07	.10	.04
Experiment 2: Conditions 9–11, 15–22							
$d_{s4,5}$	.65 (261)	.60 (136)	.58 (80)	.55 (87)	.55 (150)	.77 (347)	.61 (288)
$d_{s5,6}$	.84 (502)	.77 (199)	.70 (66)	.66 (69)	.61 (76)	.96 (4,130)	.79 (559)
$d_{s6,7}$	.77 (73)	.86 (260)	.84 (290)	.75 (61)	.77 (136)	.91 (2)	.77 (131)
$d_{s7,8}$	.10 (1)	.70 (4)	.16 (1)	.59 (2)	.78 (24)	.72 (0)	.62 (3)
d_r	.92 (1,087)	.96 (573)	.90 (410)	.92 (343)	.88 (623)	.97 (839)	.94 (1,048)
bias	.35 (138)	.54 (142)	.61 (203)	.49 (113)	.51 (303)	.35 (41)	.48 (323)
VAC	96	95	91	92	95	96	97
av. dev.	.04	.06	.07	.06	.04	.05	.04
Experiment 3: Conditions 23–32							
$d_{s1,2}$	.61 (80)	.70 (86)	.49 (47)	.65 (19)	.48 (116)	.73 (881)	.60 (985)
$d_{s2,3}$	.57 (67)	.69 (86)	.53 (45)	.65 (20)	.49 (120)	.78 (980)	.61 (1,022)
$d_{s3,4}$	.53 (58)	.65 (74)	.53 (54)	.60 (17)	.51 (136)	.77 (969)	.59 (980)
$d_{s4,5}$	.56 (130)	.65 (73)	.58 (113)	.62 (33)	.52 (271)	.78 (1,990)	.61 (2,052)
$d_{s5,6}$	.61 (77)	.82 (127)	.68 (89)	.63 (18)	.55 (160)	.87 (1,321)	.67 (1,245)
$d_{s6,7}$	.76 (130)	1.00 (186)[a]	.83 (139)	.89 (36)	.60 (154)	.95 (1,481)	.79 (1,745)
$d_{s7,8}$	.74 (119)	—	.74 (104)	.80 (29)	.78 (336)	.92 (1,390)	.79 (1,746)
d_r	1.00 (148)[a]	.79 (616)	.87 (243)	.85 (97)	1.00 (258)[a]	.97 (6,072)	.94 (3,169)
bias	.48 (335)	.46 (566)	.63 (1,119)	.58 (226)	.62 (1,621)	.51 (1,675)	.55 (7,696)
VAC	86	93	86	71	90	100	99
av. dev.	.05	.03	.04	.08	.03	.02	.01

[a] Parameter values limited to 1.00.

ative parameter values had to be limited to 1.0 (a d of infinity) in order to provide meaningful estimates. Note that $d_{s1,2}$ to $d_{s3,4}$ are not given for Experiment 2 because no data were collected for performance in the presence of 559 to 569 nm in this experiment. Similarly, because of the death of Bird 152, no parameter estimate for $d_{s7,8}$ is given for this subject in Experiment 3.

Precision of estimates of parameters was generally excellent in all three experiments, although they were lower for extreme upper and lower nanometer values in Experiment 1 and for upper values in Experiment 2. The reason for this is the relative flattening of the psychometric functions (Figures 2 to 4) at these extremes, which therefore provided little systematic variance in stimulus effects (although, of course, providing good systematic variance in reinforcer effects). For a similar reason, precision of estimates generally increased with wavelength in Experiment 3 because longer wavelengths produced more systematic variance (Figures 5 and 6).

Percentages of data variance accounted for in individual-subject data were between 89%

and 94% in Experiment 1 (56 data), between 91% and 96% in Experiment 2 (42 data), and between 71% and 100% in Experiment 3 (16 data). Group-data variances accounted for were 97% in Experiments 1 and 2 and 99% in Experiment 3. Individual-subject average deviations ranged from .10 (Bird 156, Experiment 1) to .02 (Bird 156, Experiment 3), and 8 of the 18 average deviations were .05 or less. The fits of the data to the model were, therefore, very good.

Contingency Discriminability Measures

Table 4 shows that d_r was estimated precisely in all three experiments. The values of relative d_r for the group data were .94 in Experiments 2 and 3 and .93 in Experiment 1, and generally similar values were obtained for each individual subject across the three experiments. The interpretation of these individual-subject results suggests that between 79% (Bird 152, Experiment 3) and 100% (Birds 151 and 155, Experiment 3) of the delivered reinforcers were allocated correctly to the previously emitted response.

Inherent Bias

Inherent-bias values were estimated precisely in all three experiments. Values were similar for the group between Experiments 1 and 2, but somewhat different in Experiment 3. Individual subjects usually showed biases in the same direction between Experiments 1 and 2 (but see Bird 153 for a clear contrary example), but again values were rather different in Experiment 3. The differing results from Experiment 3 may be due to the absence of any reinforcer-frequency ratio manipulation in that experiment.

Stimulus Discriminability Estimates

Like the analysis of the behavior ratios for Experiment 3 (Figures 5 and 6), the model analyses also indicated that higher sensitivity to color differences occurred at the longer wavelengths used here. Indeed, the results for the individuals from the model analysis of Experiment 3 gave the highest discriminability values at exactly the same wavelengths as those at which the largest response differentials occurred in Figure 6. Comparing the highest discriminability parameter estimates from Experiment 3 with those from Experiments 1 and 2, the latter occurred at the same value for seven cases and at an adjacent value for the remaining five cases. Thus, the model, applied to all three experiments, describes the higher color sensitivity at longer wavelengths very well. Within the range of wavelengths used here, this finding of greater color sensitivity at longer wavelengths accords very well with Wright and Cumming's (1971) description of the color-naming function in the pigeon. They did not describe individual differences, but there clearly are individual differences between pigeons in the present research, both in the location of the peak sensitivity (over the range studied), and, more surprising, some very large individual differences in the general degree of color sensitivity over the whole range (compare, for instance, Bird 156 with Birds 153 and 155).

Comparison of Models

The approach to modeling taken here differs from that of D. S. Blough (1975) in a number of ways. First, Blough's model is a dynamic one (though he did not assess its adequacy as such), whereas the present model is a molar, steady-state model. Second, Blough's model assumes a Gaussian weighting of trial effects around the affected stimulus element. In comparison, the present model assumes that such generalization effects fall off with the reciprocal of the distance, in discriminability terms, from the presented stimulus. Blough's approach appears to provide an effective description of such well-known effects as peak shift and shoulders (see also Catania & Gill, 1964; Farthing, 1974). The present model does not predict such effects, and shoulders were not obtained in the present data (Figures 2 and 3). Because shoulders seem to appear in free-operant measures but not in two-response detection measures, each model appears appropriate for each data set. One real possibility is that contrast-type effects are simply absent in discrete-trial choice measures and are products of the structure of the freely emitted operant.

The model advanced by Davison (1987) and used here seems to describe multiple-stimulus detection very well. It is a conceptually simple model that assumes that the effects of reinforcers are decremented as reciprocal functions of both stimulus and response–reinforcer contingency discriminability in two-dimensional space. Whether the assumed reciprocal decay is ultimately correct, or whether some other decay process is preferable (e.g., decay via a normal distribution as used by D. S. Blough, 1975), cannot be answered by the present research and must be left for future research explicitly designed to answer this question. Equally, the metric by which discriminabilities in two (assumed orthogonal) dimensions are to be combined remains to be determined. The present model is related to the "city block" metric (see, for example, Gregson, 1975) in which reinforcer effects decrement according to the distance around the periphery of a right triangle in two-dimensional space. Davison (1987) also assessed models in which the total decrement was a function of the hypotenuse of the right triangle (euclidean model) and in which the total decrement was affected only by the greater of d_s or d_r (supremum model). Although he found that the supremum model accounted for more of the data variance than did the other models, the benefits (a 1% increase in group variance accounted for) were quite small compared with the total amount of variance accounted for by the model used here. Tests between such models will require careful selection of experimental conditions to provide data that will discriminate between them.

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APPENDIX

Left- and right-key responses and reinforcers summed over the last five sessions of each condition for each bird. p(R/L) is the assigned probability of a reinforcer for a correct left-key response relative to all correct responses.

			Stimuli (nm)							
Condition	p(R/L)		559	564	569	574	579	584	589	594
Bird 151										
1	.10	Right	115	114	116	104	78	25	5	1
		Left	0	0	0	10	35	87	110	114
		Reinf	48	54	40	35	1	8	4	10
2	.50	Right	111	101	80	39	18	5	2	2
		Left	19	29	50	90	111	126	127	127
		Reinf	29	35	19	9	22	25	29	32
3	.80	Right	110	100	59	29	15	5	5	1
		Left	22	33	71	103	116	127	127	131
		Reinf	11	15	8	3	33	50	39	41
4	.35	Right	115	111	96	77	79	42	27	11
		Left	19	23	39	58	56	93	106	122
		Reinf	41	32	30	21	10	18	25	23
6	.90	Right	127	110	70	33	7	1	1	0
		Left	7	23	62	100	126	132	132	133
		Reinf	11	7	2	0	39	42	45	44
7	.20	Right	119	121	110	102	93	58	40	27
		Left	9	7	18	26	34	69	87	101
		Reinf	39	47	20	31	7	12	10	19
8	.65	Right	133	114	71	39	14	5	6	3
		Left	14	32	76	106	133	142	142	145
		Reinf	29	22	12	10	30	35	30	32
9	.50	Right	—	—	—	309	223	—	—	—
		Left	—	—	—	361	446	—	—	—
		Reinf	—	—	—	106	90	—	—	—
10	.10	Right	—	—	—	462	417	—	—	—
		Left	—	—	—	117	161	—	—	—
		Reinf	—	—	—	178	22	—	—	—
11	.90	Right	—	—	—	48	41	—	—	—
		Left	—	—	—	709	714	—	—	—
		Reinf	—	—	—	21	175	—	—	—
14	.90	Right	—	—	—	135	31	16	—	—
		Left	—	—	—	542	309	324	—	—
		Reinf	—	—	—	17	100	83	—	—
15	.10	Right	—	—	—	476	200	124	—	—
		Left	—	—	—	117	98	174	—	—
		Reinf	—	—	—	170	11	19	—	—
16	.50	Right	—	—	—	375	98	28	—	—
		Left	—	—	—	226	202	272	—	—
		Reinf	—	—	—	93	51	56	—	—
17	.90	Right	—	—	—	162	29	6	2	—
		Left	—	—	—	418	167	187	193	—
		Reinf	—	—	—	19	56	64	61	—
18	.10	Right	—	—	—	469	130	67	48	—
		Left	—	—	—	65	49	111	129	—
		Reinf	—	—	—	174	3	7	16	—
19	.50	Right	—	—	—	317	67	22	11	—
		Left	—	—	—	224	113	156	168	—
		Reinf	—	—	—	99	31	32	38	—
20	.50	Right	—	—	—	394	65	22	3	1
		Left	—	—	—	172	75	117	137	144
		Reinf	—	—	—	105	16	25	25	29

APPENDIX (*Continued*)

			Stimuli (nm)							
Condition	p(R/L)		559	564	569	574	579	584	589	594
21	.10	Right	—	—	—	441	93	42	17	13
		Left	—	—	—	86	37	87	115	117
		Reinf	—	—	—	180	2	3	11	4
22	.90	Right	—	—	—	92	16	9	8	6
		Left	—	—	—	546	144	152	151	154
		Reinf	—	—	—	18	45	48	50	39
23	.50	Right	—	545	—	—	—	—	101	—
		Left	—	55	—	—	—	—	496	—
		Reinf	—	103	—	—	—	—	97	—
24	.50	Right	—	—	483	—	—	112	—	—
		Left	—	—	110	—	—	486	—	—
		Reinf	—	—	91	—	—	109	—	—
25	.50	Right	360	226	—	—	—	—	—	—
		Left	255	385	—	—	—	—	—	—
		Reinf	106	94	—	—	—	—	—	—
26	.50	Right	—	324	237	—	—	—	—	—
		Left	—	338	425	—	—	—	—	—
		Reinf	—	90	110	—	—	—	—	—
27	.50	Right	—	—	269	229	—	—	—	—
		Left	—	—	434	472	—	—	—	—
		Reinf	—	—	86	114	—	—	—	—
28	.50	Right	—	—	—	327	266	—	—	—
		Left	—	—	—	352	412	—	—	—
		Reinf	—	—	—	105	95	—	—	—
29	.50	Right	—	—	—	—	287	176	—	—
		Left	—	—	—	—	265	381	—	—
		Reinf	—	—	—	—	89	111	—	—
30	.50	Right	—	—	—	—	—	311	73	—
		Left	—	—	—	—	—	149	387	—
		Reinf	—	—	—	—	—	82	100	—
31	.50	Right	—	—	—	—	—	—	456	200
		Left	—	—	—	—	—	—	80	336
		Reinf	—	—	—	—	—	—	105	95
32	.50	Right	—	—	—	338	265	—	—	—
		Left	—	—	—	233	309	—	—	—
		Reinf	—	—	—	92	107	—	—	—
Bird 152										
1	.10	Right	148	149	148	148	122	106	54	35
		Left	2	4	3	5	29	46	98	117
		Reinf	43	45	50	39	3	3	5	12
2	.50	Right	124	111	98	59	48	23	14	7
		Left	34	45	58	97	111	133	143	151
		Reinf	36	32	26	11	22	24	22	27
3	.80	Right	141	133	129	90	46	3	1	0
		Left	3	10	16	54	97	139	141	143
		Reinf	14	13	11	13	28	40	45	36
4	.35	Right	151	155	155	144	110	58	20	9
		Left	5	1	1	12	41	97	135	147
		Reinf	35	38	32	31	4	18	20	22
6	.90	Right	87	88	55	25	12	3	0	1
		Left	56	55	90	119	132	143	145	143
		Reinf	5	2	3	2	50	39	52	47
7	.20	Right	151	155	153	148	149	126	71	31
		Left	1	0	2	4	5	28	82	123
		Reinf	37	49	38	38	1	7	11	19

APPENDIX (*Continued*)

Condition	p(R/L)		Stimuli (nm)							
			559	564	569	574	579	584	589	594
8	.65	Right	149	138	117	94	54	22	2	0
		Left	7	16	38	60	98	132	151	153
		Reinf	21	21	18	22	25	33	32	28
9	.50	Right	—	—	—	405	312	—	—	—
		Left	—	—	—	305	403	—	—	—
		Reinf	—	—	—	108	92	—	—	—
10	.10	Right	—	—	—	629	571	—	—	—
		Left	—	—	—	71	122	—	—	—
		Reinf	—	—	—	169	31	—	—	—
11	.90	Right	—	—	—	34	27	—	—	—
		Left	—	—	—	742	752	—	—	—
		Reinf	—	—	—	13	187	—	—	—
14	.90	Right	—	—	—	247	45	32	—	—
		Left	—	—	—	428	290	305	—	—
		Reinf	—	—	—	30	79	91	—	—
15	.10	Right	—	—	—	619	302	259	—	—
		Left	—	—	—	13	17	57	—	—
		Reinf	—	—	—	186	4	13	—	—
16	.50	Right	—	—	—	488	183	76	—	—
		Left	—	—	—	210	164	271	—	—
		Reinf	—	—	—	89	45	66	—	—
17	.90	Right	—	—	—	311	48	9	1	—
		Left	—	—	—	326	164	204	213	—
		Reinf	—	—	—	15	55	59	71	—
18	.10	Right	—	—	—	618	202	163	102	—
		Left	—	—	—	14	9	46	109	—
		Reinf	—	—	—	182	1	2	15	—
19	.50	Right	—	—	—	576	159	82	34	—
		Left	—	—	—	96	65	144	191	—
		Reinf	—	—	—	96	19	34	51	—
20	.50	Right	—	—	—	616	134	95	34	19
		Left	—	—	—	43	32	74	135	143
		Reinf	—	—	—	97	16	18	32	37
21	.10	Right	—	—	—	584	130	103	39	25
		Left	—	—	—	14	20	48	113	126
		Reinf	—	—	—	178	3	4	7	8
22	.90	Right	—	—	—	249	53	19	7	4
		Left	—	—	—	413	112	148	159	161
		Reinf	—	—	—	26	28	52	53	41
23	.50	Right	—	555	—	—	—	—	104	—
		Left	—	71	—	—	—	—	521	—
		Reinf	—	101	—	—	—	—	99	—
24	.50	Right	—	—	436	—	—	104	—	—
		Left	—	—	235	—	—	560	—	—
		Reinf	—	—	93	—	—	107	—	—
25	.50	Right	393	228	—	—	—	—	—	—
		Left	313	477	—	—	—	—	—	—
		Reinf	99	101	—	—	—	—	—	—
26	.50	Right	—	351	193	—	—	—	—	—
		Left	—	352	507	—	—	—	—	—
		Reinf	—	96	104	—	—	—	—	—
27	.50	Right	—	—	404	276	—	—	—	—
		Left	—	—	326	455	—	—	—	—
		Reinf	—	—	100	100	—	—	—	—

APPENDIX (*Continued*)

			Stimuli (nm)							
Condition	p(R/L)		559	564	569	574	579	584	589	594
28	.50	Right	—	—	—	416	295	—	—	—
		Left	—	—	—	286	409	—	—	—
		Reinf	—	—	—	107	93	—	—	—
29	.50	Right	—	—	—	—	412	183	—	—
		Left	—	—	—	—	242	472	—	—
		Reinf	—	—	—	—	86	114	—	—
30	.50	Right	—	—	—	—	—	501	167	—
		Left	—	—	—	—	—	104	440	—
		Reinf	—	—	—	—	—	92	108	—
31	.50	Right	—	—	—	—	—	—	—	—
		Left	—	—	—	—	—	—	—	—
		Reinf	—	—	—	—	—	—	—	—
32	.50	Right	—	—	—	—	—	—	—	—
		Left	—	—	—	—	—	—	—	—
		Reinf	—	—	—	—	—	—	—	—
Bird 153										
1	.10	Right	128	132	126	119	83	30	11	8
		Left	1	0	3	11	45	102	120	120
		Reinf	49	52	39	41	3	5	5	6
2	.50	Right	120	116	99	68	41	14	4	0
		Left	17	23	40	68	98	123	135	138
		Reinf	29	33	26	13	21	21	29	28
3	.80	Right	81	82	63	40	25	8	7	11
		Left	58	54	75	98	111	129	131	127
		Reinf	11	15	8	11	33	31	42	49
4	.35	Right	131	130	128	125	90	48	28	9
		Left	11	10	12	15	54	93	112	133
		Reinf	38	30	29	34	11	14	16	28
6	.90	Right	72	55	53	44	32	14	13	18
		Left	67	86	85	95	108	124	127	122
		Reinf	6	6	2	5	41	43	49	48
7	.20	Right	137	132	133	122	104	65	31	20
		Left	0	4	2	15	34	73	107	116
		Reinf	39	32	42	41	5	11	13	17
8	.65	Right	119	100	95	59	37	22	17	20
		Left	26	45	51	86	112	123	130	128
		Reinf	17	25	16	13	34	33	33	29
9	.50	Right	—	—	—	428	350	—	—	—
		Left	—	—	—	198	273	—	—	—
		Reinf	—	—	—	101	99	—	—	—
10	.10	Right	—	—	—	664	636	—	—	—
		Left	—	—	—	27	56	—	—	—
		Reinf	—	—	—	175	25	—	—	—
11	.90	Right	—	—	—	246	200	—	—	—
		Left	—	—	—	375	423	—	—	—
		Reinf	—	—	—	22	178	—	—	—
14	.90	Right	—	—	—	167	95	81	—	—
		Left	—	—	—	461	222	233	—	—
		Reinf	—	—	—	17	89	94	—	—
15	.10	Right	—	—	—	687	339	335	—	—
		Left	—	—	—	25	17	22	—	—
		Reinf	—	—	—	177	9	14	—	—
16	.50	Right	—	—	—	557	240	234	—	—
		Left	—	—	—	146	115	120	—	—
		Reinf	—	—	—	104	50	46	—	—

APPENDIX (*Continued*)

Condition	p(R/L)		Stimuli (nm) 559	564	569	574	579	584	589	594
17	.90	Right	—	—	—	220	75	59	56	—
		Left	—	—	—	416	136	150	156	—
		Reinf	—	—	—	28	53	61	58	—
18	.10	Right	—	—	—	583	185	147	118	—
		Left	—	—	—	7	10	52	80	—
		Reinf	—	—	—	179	2	7	12	—
19	.50	Right	—	—	—	457	123	74	57	—
		Left	—	—	—	158	87	131	150	—
		Reinf	—	—	—	98	32	36	34	—
20	.50	Right	—	—	—	521	102	63	30	32
		Left	—	—	—	89	52	89	120	121
		Reinf	—	—	—	94	15	24	30	37
21	.10	Right	—	—	—	575	135	94	56	62
		Left	—	—	—	8	13	52	91	82
		Reinf	—	—	—	179	—	8	7	6
22	.90	Right	—	—	—	156	28	34	18	18
		Left	—	—	—	420	115	109	125	124
		Reinf	—	—	—	22	45	43	43	47
23	.50	Right	—	487	—	—	—	—	138	—
		Left	—	78	—	—	—	—	426	—
		Reinf	—	102	—	—	—	—	98	—
24	.50	Right	—	—	432	—	—	177	—	—
		Left	—	—	182	—	—	441	—	—
		Reinf	—	—	91	—	—	109	—	—
25	.50	Right	492	502	—	—	—	—	—	—
		Left	270	261	—	—	—	—	—	—
		Reinf	96	114	—	—	—	—	—	—
26	.50	Right	—	511	479	—	—	—	—	—
		Left	—	223	250	—	—	—	—	—
		Reinf	—	112	88	—	—	—	—	—
27	.50	Right	—	—	498	465	—	—	—	—
		Left	—	—	226	260	—	—	—	—
		Reinf	—	—	97	103	—	—	—	—
28	.50	Right	—	—	—	534	498	—	—	—
		Left	—	—	—	224	261	—	—	—
		Reinf	—	—	—	115	85	—	—	—
29	.50	Right	—	—	—	—	494	339	—	—
		Left	—	—	—	—	145	305	—	—
		Reinf	—	—	—	—	101	99	—	—
30	.50	Right	—	—	—	—	—	465	201	—
		Left	—	—	—	—	—	144	408	—
		Reinf	—	—	—	—	—	100	100	—
31	.50	Right	—	—	—	—	—	—	469	263
		Left	—	—	—	—	—	—	169	371
		Reinf	—	—	—	—	—	—	96	104
32	.50	Right	—	—	—	414	310	—	—	—
		Left	—	—	—	253	358	—	—	—
		Reinf	—	—	—	97	103	—	—	—
Bird 154										
1	.10	Right	173	177	174	169	172	164	144	132
		Left	5	2	6	8	8	13	33	48
		Reinf	44	47	43	50	1	3	6	6
2	.50	Right	134	134	128	109	39	8	0	0
		Left	0	1	4	26	96	127	136	135
		Reinf	27	21	21	28	19	22	28	34

APPENDIX (*Continued*)

			Stimuli (nm)							
Condition	p(R/L)		559	564	569	574	579	584	589	594
3	.80	Right	98	86	72	56	51	48	28	44
		Left	77	90	103	120	126	127	147	131
		Reinf	13	10	6	7	41	45	35	43
4	.35	Right	167	169	153	146	135	94	80	67
		Left	7	6	20	27	40	82	95	107
		Reinf	26	37	35	27	8	21	27	19
6	.90	Right	74	66	50	40	43	36	39	30
		Left	105	112	130	142	135	145	141	151
		Reinf	6	7	10	3	38	49	43	44
7	.20	Right	156	164	160	158	141	110	86	59
		Left	15	6	10	12	29	60	84	111
		Reinf	37	43	41	36	6	4	18	15
8	.65	Right	124	106	89	68	39	36	23	29
		Left	42	62	77	101	128	133	144	135
		Reinf	23	15	11	15	37	33	37	29
9	.50	Right	—	—	—	398	351	—	—	—
		Left	—	—	—	380	423	—	—	—
		Reinf	—	—	—	101	99	—	—	—
10	.10	Right	—	—	—	716	709	—	—	—
		Left	—	—	—	45	52	—	—	—
		Reinf	—	—	—	170	21	—	—	—
11	.90	Right	—	—	—	110	128	—	—	—
		Left	—	—	—	594	575	—	—	—
		Reinf	—	—	—	14	186	—	—	—
14	.90	Right	—	—	—	135	50	69	—	—
		Left	—	—	—	544	291	267	—	—
		Reinf	—	—	—	17	96	87	—	—
15	.10	Right	—	—	—	671	332	314	—	—
		Left	—	—	—	78	43	61	—	—
		Reinf	—	—	—	179	8	13	—	—
16	.50	Right	—	—	—	477	213	194	—	—
		Left	—	—	—	266	158	173	—	—
		Reinf	—	—	—	103	43	54	—	—
17	.90	Right	—	—	—	116	33	24	25	—
		Left	—	—	—	655	222	234	229	—
		Reinf	—	—	—	22	58	68	52	—
18	.10	Right	—	—	—	645	206	184	141	—
		Left	—	—	—	40	25	42	88	—
		Reinf	—	—	—	174	5	8	13	—
19	.50	Right	—	—	—	525	160	118	106	—
		Left	—	—	—	233	90	135	144	—
		Reinf	—	—	—	112	20	30	38	—
20	.50	Right	—	—	—	415	88	49	35	25
		Left	—	—	—	306	93	130	146	152
		Reinf	—	—	—	112	21	22	20	25
21	.10	Right	—	—	—	547	132	118	77	57
		Left	—	—	—	56	18	31	75	92
		Reinf	—	—	—	172	2	5	9	9
22	.90	Right	—	—	—	163	31	21	35	37
		Left	—	—	—	520	138	152	135	133
		Reinf	—	—	—	16	55	44	42	43
23	.50	Right	—	644	—	—	—	—	216	—
		Left	—	60	—	—	—	—	489	—
		Reinf	—	105	—	—	—	—	95	—

APPENDIX (*Continued*)

Condition	p(R/L)		Stimuli (nm)							
			559	564	569	574	579	584	589	594
24	.50	Right	—	—	567	—	—	187	—	—
		Left	—	—	134	—	—	514	—	—
		Reinf	—	—	93	—	—	107	—	—
25	.50	Right	557	391	—	—	—	—	—	—
		Left	244	412	—	—	—	—	—	—
		Reinf	106	94	—	—	—	—	—	—
26	.50	Right	—	569	407	—	—	—	—	—
		Left	—	195	360	—	—	—	—	—
		Reinf	—	90	110	—	—	—	—	—
27	.50	Right	—	—	612	495	—	—	—	—
		Left	—	—	174	289	—	—	—	—
		Reinf	—	—	109	91	—	—	—	—
28	.50	Right	—	—	—	632	509	—	—	—
		Left	—	—	—	199	316	—	—	—
		Reinf	—	—	—	97	103	—	—	—
29	.50	Right	—	—	—	—	392	264	—	—
		Left	—	—	—	—	327	457	—	—
		Reinf	—	—	—	—	90	110	—	—
30	.50	Right	—	—	—	—	—	431	112	—
		Left	—	—	—	—	—	219	536	—
		Reinf	—	—	—	—	—	101	99	—
31	.50	Right	—	—	—	—	—	—	474	196
		Left	—	—	—	—	—	—	204	482
		Reinf	—	—	—	—	—	—	94	106
32	.50	Right	—	—	—	519	389	—	—	—
		Left	—	—	—	238	365	—	—	—
		Reinf	—	—	—	119	81	—	—	—
Bird 155										
1	.10	Right	132	129	127	125	110	77	39	25
		Left	2	2	5	9	23	58	95	109
		Reinf	45	37	53	45	0	5	11	4
2	.50	Right	102	105	99	90	60	37	30	32
		Left	51	50	58	65	93	119	122	124
		Reinf	21	31	31	23	16	30	25	23
3	.80	Right	73	84	71	44	46	19	24	12
		Left	72	60	72	99	99	125	120	132
		Reinf	7	10	10	7	25	39	49	53
4	.35	Right	115	117	115	104	100	64	48	27
		Left	30	29	30	41	44	78	96	117
		Reinf	38	35	33	29	9	17	14	25
6	.90	Right	108	94	62	44	22	15	10	9
		Left	26	43	72	91	116	121	125	126
		Reinf	14	6	7	2	46	43	35	47
7	.20	Right	140	140	140	129	111	97	81	67
		Left	10	12	8	21	40	54	69	82
		Reinf	42	48	47	36	4	2	7	14
8	.65	Right	114	116	114	96	74	49	34	33
		Left	38	34	38	54	79	101	118	121
		Reinf	16	21	24	11	31	30	33	34
9	.50	Right	—	—	—	368	316	—	—	—
		Left	—	—	—	289	341	—	—	—
		Reinf	—	—	—	111	89	—	—	—
10	.10	Right	—	—	—	499	464	—	—	—
		Left	—	—	—	134	169	—	—	—
		Reinf	—	—	—	172	28	—	—	—

APPENDIX (*Continued*)

Condition	p(R/L)		Stimuli (nm)							
			559	564	569	574	579	584	589	594
11	.90	Right	—	—	—	182	124	—	—	—
		Left	—	—	—	454	513	—	—	—
		Reinf	—	—	—	30	170	—	—	—
14	.90	Right	—	—	—	138	54	41	—	—
		Left	—	—	—	471	252	266	—	—
		Reinf	—	—	—	18	83	99	—	—
15	.10	Right	—	—	—	515	248	242	—	—
		Left	—	—	—	90	55	58	—	—
		Reinf	—	—	—	176	7	17	—	—
16	.50	Right	—	—	—	362	144	155	—	—
		Left	—	—	—	304	187	182	—	—
		Reinf	—	—	—	96	61	43	—	—
17	.90	Right	—	—	—	163	35	14	15	—
		Left	—	—	—	461	176	199	194	—
		Reinf	—	—	—	29	54	51	66	—
18	.10	Right	—	—	—	496	157	147	132	—
		Left	—	—	—	100	41	54	69	—
		Reinf	—	—	—	176	7	8	9	—
19	.50	Right	—	—	—	417	130	107	93	—
		Left	—	—	—	235	89	108	126	—
		Reinf	—	—	—	95	30	33	42	—
20	.50	Right	—	—	—	434	104	75	59	38
		Left	—	—	—	187	49	80	102	119
		Reinf	—	—	—	92	16	25	33	34
21	.10	Right	—	—	—	547	132	118	77	57
		Left	—	—	—	56	18	31	75	92
		Reinf	—	—	—	175	2	5	9	9
22	.90	Right	—	—	—	196	46	39	24	26
		Left	—	—	—	409	105	112	128	123
		Reinf	—	—	—	18	43	44	47	48
23	.50	Right	—	377	—	—	—	—	196	—
		Left	—	207	—	—	—	—	390	—
		Reinf	—	106	—	—	—	—	94	—
24	.50	Right	—	—	397	—	—	272	—	—
		Left	—	—	211	—	—	338	—	—
		Reinf	—	—	102	—	—	98	—	—
25	.50	Right	394	418	—	—	—	—	—	—
		Left	289	267	—	—	—	—	—	—
		Reinf	98	102	—	—	—	—	—	—
26	.50	Right	—	417	425	—	—	—	—	—
		Left	—	269	263	—	—	—	—	—
		Reinf	—	100	100	—	—	—	—	—
27	.50	Right	—	—	427	415	—	—	—	—
		Left	—	—	221	239	—	—	—	—
		Reinf	—	—	98	102	—	—	—	—
28	.50	Right	—	—	—	361	363	—	—	—
		Left	—	—	—	262	260	—	—	—
		Reinf	—	—	—	93	107	—	—	—
29	.50	Right	—	—	—	—	502	434	—	—
		Left	—	—	—	—	166	234	—	—
		Reinf	—	—	—	—	103	97	—	—
30	.50	Right	—	—	—	—	—	452	351	—
		Left	—	—	—	—	—	186	286	—
		Reinf	—	—	—	—	—	112	88	—

APPENDIX (*Continued*)

Condition	p(R/L)		Stimuli (nm)							
			559	564	569	574	579	584	589	594
31	.50	Right	—	—	—	—	—	—	462	138
		Left	—	—	—	—	—	—	149	480
		Reinf	—	—	—	—	—	—	87	113
32	.50	Right	—	—	—	445	398	—	—	—
		Left	—	—	—	232	281	—	—	—
		Reinf	—	—	—	101	99	—	—	—
Bird 156										
1	.10	Right	135	137	134	129	77	16	1	3
		Left	0	0	1	6	55	118	133	130
		Reinf	57	36	47	42	1	3	5	9
2	.50	Right	158	157	138	124	108	87	59	66
		Left	19	18	35	52	65	88	118	109
		Reinf	24	30	22	23	20	21	29	31
3	.80	Right	89	83	59	40	10	1	0	1
		Left	47	54	79	98	127	136	138	137
		Reinf	11	12	7	3	41	35	49	42
4	.35	Right	140	139	137	125	92	36	9	3
		Left	2	2	5	17	50	107	134	141
		Reinf	30	32	40	30	6	19	21	22
6	.90	Right	109	105	94	57	27	3	0	0
		Left	32	33	46	83	112	134	138	138
		Reinf	5	6	8	1	40	49	45	46
7	.20	Right	138	141	140	136	98	58	14	9
		Left	0	0	0	5	43	80	126	132
		Reinf	30	42	48	46	6	7	11	10
8	.65	Right	133	130	113	78	22	1	0	0
		Left	1	3	22	56	109	133	132	135
		Reinf	23	24	12	15	25	31	34	36
9	.50	Right	—	—	—	380	192	—	—	—
		Left	—	—	—	215	401	—	—	—
		Reinf	—	—	—	86	114	—	—	—
10	.10	Right	—	—	—	537	284	—	—	—
		Left	—	—	—	9	270	—	—	—
		Reinf	—	—	—	180	20	—	—	—
11	.90	Right	—	—	—	97	16	—	—	—
		Left	—	—	—	416	494	—	—	—
		Reinf	—	—	—	13	187	—	—	—
14	.90	Right	—	—	—	128	44	19	—	—
		Left	—	—	—	444	241	264	—	—
		Reinf	—	—	—	11	90	99	—	—
15	.10	Right	—	—	—	558	201	25	—	—
		Left	—	—	—	5	80	255	—	—
		Reinf	—	—	—	181	2	17	—	—
16	.50	Right	—	—	—	438	66	3	—	—
		Left	—	—	—	101	204	266	—	—
		Reinf	—	—	—	101	36	63	—	—
17	.90	Right	—	—	—	189	15	1	1	—
		Left	—	—	—	334	156	172	175	—
		Reinf	—	—	—	18	58	60	64	—
18	.10	Right	—	—	—	529	149	18	0	—
		Left	—	—	—	1	26	157	173	—
		Reinf	—	—	—	177	4	8	11	—

APPENDIX (*Continued*)

Condition	p(R/L)		Stimuli (nm)							
			559	564	569	574	579	584	589	594
19	.50	Right	—	—	—	491	91	6	0	—
		Left	—	—	—	35	82	170	177	—
		Reinf	—	—	—	112	18	42	28	—
20	.50	Right	—	—	—	532	67	5	0	0
		Left	—	—	—	45	78	139	141	145
		Reinf	—	—	—	94	15	38	26	27
21	.10	Right	—	—	—	560	112	20	2	1
		Left	—	—	—	1	32	120	138	140
		Reinf	—	—	—	185	1	6	8	2
22	.90	Right	—	—	—	163	30	16	3	0
		Left	—	—	—	476	130	143	157	159
		Reinf	—	—	—	26	42	50	46	36
23	.50	Right	—	515	—	—	—	—	41	—
		Left	—	62	—	—	—	—	536	—
		Reinf	—	99	—	—	—	—	101	—
24	.50	Right	—	—	516	—	—	77	—	—
		Left	—	—	94	—	—	529	—	—
		Reinf	—	—	97	—	—	103	—	—
25	.50	Right	463	199	—	—	—	—	—	—
		Left	144	410	—	—	—	—	—	—
		Reinf	109	91	—	—	—	—	—	—
26	.50	Right	—	479	149	—	—	—	—	—
		Left	—	159	490	—	—	—	—	—
		Reinf	—	101	99	—	—	—	—	—
27	.50	Right	—	—	501	170	—	—	—	—
		Left	—	—	142	468	—	—	—	—
		Reinf	—	—	98	102	—	—	—	—
28	.50	Right	—	—	—	505	183	—	—	—
		Left	—	—	—	140	465	—	—	—
		Reinf	—	—	—	104	96	—	—	—
29	.50	Right	—	—	—	—	510	109	—	—
		Left	—	—	—	—	62	461	—	—
		Reinf	—	—	—	—	110	90	—	—
30	.50	Right	—	—	—	—	—	540	43	—
		Left	—	—	—	—	—	51	548	—
		Reinf	—	—	—	—	—	103	97	—
31	.50	Right	—	—	—	—	—	—	502	52
		Left	—	—	—	—	—	—	84	537
		Reinf	—	—	—	—	—	—	106	94
32	.50	Right	—	—	—	531	160	—	—	—
		Left	—	—	—	143	511	—	—	—
		Reinf	—	—	—	104	96	—	—	—