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The reaction-time/luminance relationship for pigeons to lights of different spectral compositions

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Pigeons learned to peck a key when it was illuminated during a 2-sec trial. A white-noise ready signal preceded the onset of the light; a response terminated the trial and occasionally produced reinforcement. For every trial, reaction time was recorded as the temporal interval between light onset and keypeck response. The initial experiment used "white" light; subsequent experiments used monochromatic lights of 525 and 625 nm. Within each session, the luminance of the light stimulus varied randomly over a three-log-unit range. For white light, overlapping ranges were used to extend the total luminance variation to six log units. Resulting reaction-time/luminance functions for white light were decreasing over most of the range. However, a rise in reaction time with increasing luminance was seen in the midluminance region and again at very high values. At 625 nm, the function decreased rapidly at low luminances and then leveled off or rose; at 525 nm, it was relatively flat at low luminances, where reaction times were lower than they were to photopically matched 625-nm values. Sensory and nonsensory factors might contribute to the shapes of these functions, which may be too complex to be used for psychophysical scaling.

Reaction time (RT) is the time interval between the onset of a stimulus and a specified response. It varies with a number of external factors, such as the nature of the stimulus, the response requirement, and the instructions to the subject. Yet, with suitable controls, it has proven useful in assessing a variety of phenomena, ranging from the speed of the nervous impulse (Helmholtz, 1850) to the manner in which complex information is processed (e.g., Sternberg, 1969).

One variable that clearly and systematically affects RT is the intensity of the stimulus. Early studies (Cattell, 1886, Piéron, 1920) showed an inverse RT-intensity relationship in the visual and auditory modalities as well as in those concerned with taste and electric shock. Such studies used a behavioral response, but the relation also holds for physiological measures; for example, the latency of the visual evoked potential increases as a power function of light intensity (Vaughan, Costa, & Gilden, 1966). The relation between RT and psychophysical estimates of stimulus magnitude has been of special concern. Studies have shown that the reciprocal of RT increases with auditory loudness (McGill, 1961) and with the brightness of a flash of light (Bartlett & MacLeod, 1954). Aikin (1973) compared the RT-intensity relationship to magnitude estimations of the same stimuli in both the visual and auditory modalities. She found linear relationships between log RT and magnitude estimates when a correction for irreducible minimum RTs was used.

The RT-intensity relationship may be particularly useful to animal psychophysicists. While there are many effective procedures for assessing sensory thresholds in nonhuman subjects, measurement of suprathreshold processes is more difficult (Blough & Blough, 1977). However, a number of investigators have used RT as a method of scaling suprathreshold stimuli. Using monkeys as subjects, Stebbins (1966) showed an inverse relationship between RT and auditory intensity for a wide range of sound frequencies. From these data he derived "equal loudness contours" describing the intensities of various tone frequencies required to yield criterion RT values. Moody (1969) performed a similar experiment using rats as subjects and lights of various wavelengths as stimuli.

In addition to varying with stimulus intensity, RTs to light appear to be sensitive to other features of the visual system. In measuring RT to a wide range of light intensities, for example, Kohfield (1971) found a break in the function in the region of the photopic threshold; that is, following an initial decline and leveling off of RT as intensity increased, a second portion of the curve showed further decline at higher intensities. Kohfield suggested that the two portions of the function represented the separate activity of rod and cone systems. A study by Pollack (1968) examined the RT-intensity relation for different wavelengths of light. These lights, matched by flicker

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photometry for photopic luminance, yielded similar RTs at the higher luminances studied. At lower luminances, however, the functions diverged, with RTs being longer for the longer wavelengths. Since photopically equated lights are scotopically unequal, the RT-intensity relation can explain this divergence; that is, in the intensity region where rods primarily were activated, the longer wavelengths were effectively less intense.

Although there is a large body of data concerning visual psychophysics in the pigeon, the RT measure has been infrequently used. Where measured, the RT of the pigeon keypeck has proven surprisingly insensitive to stimulus parameters. Studies by D.S. Blough (1978), Heinemann (1974), and Mulvanny (1976) have shown this measure to be invariant with varying difficulties of visual and auditory discriminations. On the other hand, the keypeck RT does vary systematically in a more complex situation requiring birds to respond to the correct stimulus in a spatially organized visual array (D.S. Blough, 1977).

Since the RT-intensity relation is so well known in human psychophysics and since the pigeon's keypeck is a widely used indicator of visual function, we felt it was important to explore the effect of luminance on the keypeck's RT. The present experiments showed that this measure reflected interacting effects of luminance and spectral composition of the stimulating light.

METHOD

Subjects

Three White Carneaux pigeons, 3 to 5 years of age, served as subjects in these experiments. They had had extensive experience on tasks that required them to peck at "white" lights and to withhold pecks when monochromatic lights were added to the stimulus field (e.g., P.M. Blough, 1975). The birds were maintained at approximately 80% of their ad-lib weights and were not run on days when their weights exceeded that amount by 15 or more grams.

Apparatus

The apparatus consisted of three subject chambers, a common optical system, and associated control equipment. The chambers were Lehigh Valley Electronics pigeon boxes whose interiors were painted flat black. The front panel was modified by lowering the pecking key from its original location to a position 10 cm above the opening for the food hopper. Behind the key was a fiber-optics cable, 4 mm in diameter, leading to an optical system in an adjacent room. The end of this cable was covered by a diffusing glass, which, in turn, was positioned so as to be as close as possible to the key without interfering with its operation. Just above this key were two additional response keys, unilluminated and not used in this experiment. The houselight was always turned off, and the 6-W food hopper lamp was painted flat black to reduce the illumination of the food hopper and thus to minimize light adaptation from this source. A speaker supplied a white-noise warning signal. Ventilating fans provided masking sounds.

A two-channel optical system supplied the stimulus lights. Its source was an Osram 150-W high-pressure xenon arc lamp operated by a voltage-regulated power supply. Light from one side of the lamp housing passed through a heat filter, lenses, and neutral density filters to form a "white" path. Light from the opposite side of the housing passed through a Bausch and Lomb grating monochromator whose entrance and exit slits were set at 3 and 2 mm, respectively, and whose nominal half band width was 6.6 nm/mm. Beyond the monochromator, the light passed through a second set of lenses and neutral density filters. Separate neutral density wedges in each path controlled within-session luminance changes, and a quietly operating shutter in each path helped to control stimulus presentations. The two paths combined just before the light reached the ends of the three fiber-optics cables that led to the pigeon chambers. Individual shutters, one in front of each of the fiber optics cables, permitted independent control of light entering the three chambers. Operation of these shutters made a noise that may have been audible in the subject chambers, but this noise did not signal stimulus onset (see below).

A LINC computer (Clark & Molnar, 1964) and associated relay equipment controlled stimulus presentations, performed timing operations, sensed responses, and recorded and analyzed data.

A UDT Model 10A photometer provided both absolute and relative luminance values for the stimulating lights. A microphotometer attachment, having the photopic spectral sensitivity of the human eye, read the luminance of the monochromatic path at 550 nm. To specify the luminances at other wavelengths, we applied the spectral sensitivity data of D.S. Blough (1957) and corrections for the spectral characteristics of the lamp and monochromator.

Procedure

The pigeon's task was to peck at the response key whenever it was illuminated. This task was similar to previous ones performed by the birds. However, a small amount of retraining was necessary to accustom them to working in a dark box and to the lowered position of the pecking key.

The final procedure consisted of series of sessions occurring most week days. A single session was preceded by at least 45 min of dark adaptation and included 384 trial presentations of the light stimulus. A white-noise warning signal preceded each trial by a variable amount of time, ranging from 1 to 1.5 sec. The white noise remained on during the trial and through reinforcement when it occurred. Following each stimulus presentation was an intertrial interval lasting 20 sec. Keypecks by any bird during the last 2 sec of the intertrial interval delayed onset of the white noise for all three subjects. Similarly, any responses during the warning signal, but preceding stimulus onset, reset the timer that programmed the white-noise duration for all subjects. Responses during a trial turned off the light and operated a food hopper with a probability of .125. If a bird failed to respond during a trial, the shutter associated with its box closed 2 sec after stimulus onset. Response contingencies during trials were controlled independently for the three subjects.

Stimulus presentations were controlled by both the quiet shutter in the common optical path and the three individual shutters associated with the three fiber optics cables. All three of the individual shutters opened at the onset of the white-noise warning signal. The common shutter remained closed until time to stimulus presentation had elapsed, when it opened and illuminated the response keys in the three boxes simultaneously. Offset of the stimulus was controlled by the individual shutters so that this event could be contingent on a keypeck. Thus, the noise associated with the operation of the individual shutters could not be a cue to stimulus onset, although it was added to the stimuli associated with its offset.

A randomized blocks design determined within-session stimulus luminances. There were 16 values covering a 3.0-log-unit range in approximately 0.2-log-unit steps. A single block of presentations consisted of all 16 luminance values; order of these values within a block was determined randomly. A session consisted of 24 such blocks; however, the data from the first block were not included

in any analysis. The experimental program set up reinforcements equally often for each luminance value. With this constraint, the assignment of reinforcements to trials was random.

The experiment consisted of series of such sessions run under a number of conditions. Three of these used white light and varied the luminance range covered by the test stimuli. One white-light condition used relatively dim lights, ranging from −2.91 to 0.09 log cd/m². A second condition used lights of intermediate luminances, ranging from −1.91 to 1.09 log cd/m². The third condition used relatively intense stimuli, ranging from 0.26 to 3.26 log cd/m². The intermediate condition preceded and followed the dim and intense series. Finally, two additional conditions assessed RT to monochromatic lights whose wavelengths were 525 to 625 nm. The procedure was the same as it was for the conditions using white light; however, there was only a single set of luminances. They ranged from −1.96 to 1.03 log cd/m² and occurred again in 0.2-log-unit steps over the 3.0-log-unit range. Series at each wavelength alternated. Figures 1 and 2 indicate the number of series for each condition.

For each condition, a single series was run until the bird had completed at least 11 sessions. Such sessions included only those in which the bird responded on at least 87% of the trials. The median RT at each luminance was computed for each of these sessions. From the 11 sessions, 9 were selected as the basis for final data analysis. The 2 sessions dropped were those in which the mean median RT across all stimuli showed the greatest deviation from the grand mean for that bird of all RTs over all 11 sessions. Further data analysis used only those session medians based on 12 or more responses. Most of the final data analysis, performed on sessions selected by the rule stated above, was based on the means of these medians.

RESULTS

The birds pecked at the lighted key on most trials, except that response probability declined at the lowest and highest luminances. A preliminary analysis concerned the effect on median RT of including trials that followed reinforcement. It seemed possible that light adaptation caused by exposure to the dim feeder light during reinforcement might affect the subsequent RT. However, excluding those trials did not affect medians, so all trials were included in the subsequent analysis.

Figure 1 describes the RT-luminance relationship for white light. The upper three panels show individual data for three birds. Each point represents the mean of medians from nine sessions; thus, these graphs show the data obtained for the various series at each of the three luminance ranges. The lines trace the mean of the two series run at the intermediate and high-intensity levels. It is evident that, while the shape of the functions replicated rather well across series within birds, a rather large shift in overall RT sometimes occurred between replications. The reason for such shifts is not known; it may be related to the adoption by the bird of different postures or "waiting behaviors" prior to stimulus onset.

The grand mean of the white-light data appears in the bottom panel of Figure 1. It represents most of the features found, to a greater or lesser extent, in each of the birds. As expected, RT was greatest at low luminances. However, the function is more complex than might have been anticipated. It falls at first with increasing luminance, but an inflection appears in the region between −2 and −1 log cd/m²; beyond this region, RT increased with luminance for Bird 676 and possibly for Bird 487, before falling again to a minimum at about 1.2 log cd/m². This rise in the function occurred consistently across replications in both low and middle luminance ranges. The rise was further confirmed by analyzing the RT distributions for each subject across the relevant luminance range. This analysis (not shown) related the frequency of short (less than 0.6 sec) RTs to luminance. For all subjects, the number of short RTs increased with

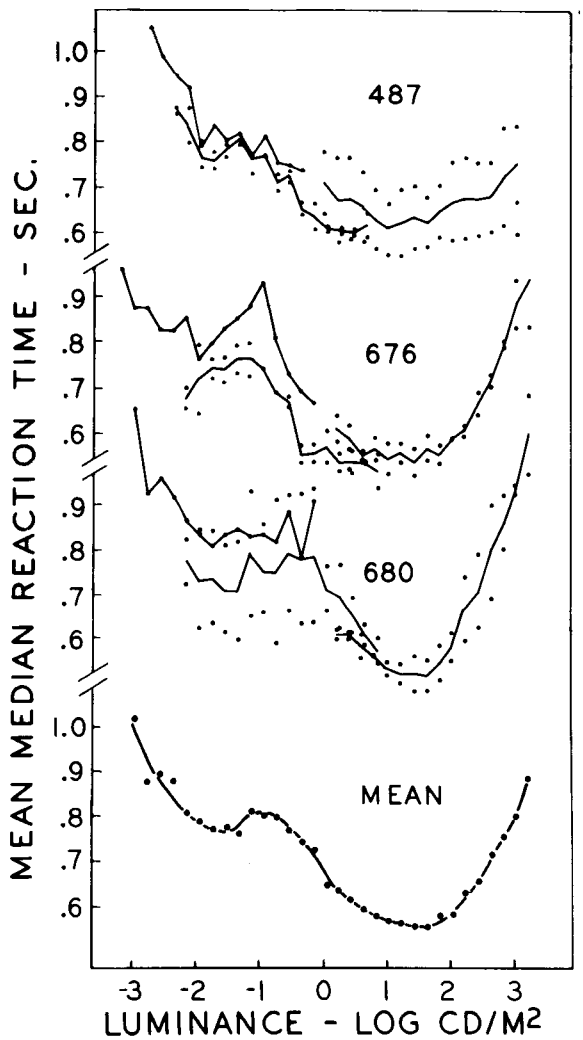

Figure 1. Mean median reaction times for white-light sessions. Each data point for an individual bird is the mean of a median RT at one luminance from each of nine sessions. The lines connect means of corresponding points for a series. Two series were run at intermediate and high luminances, one at low luminances. Each point in the bottom graph is the mean of all corresponding points above. Points are omitted where response frequency fell below criterion (see text).

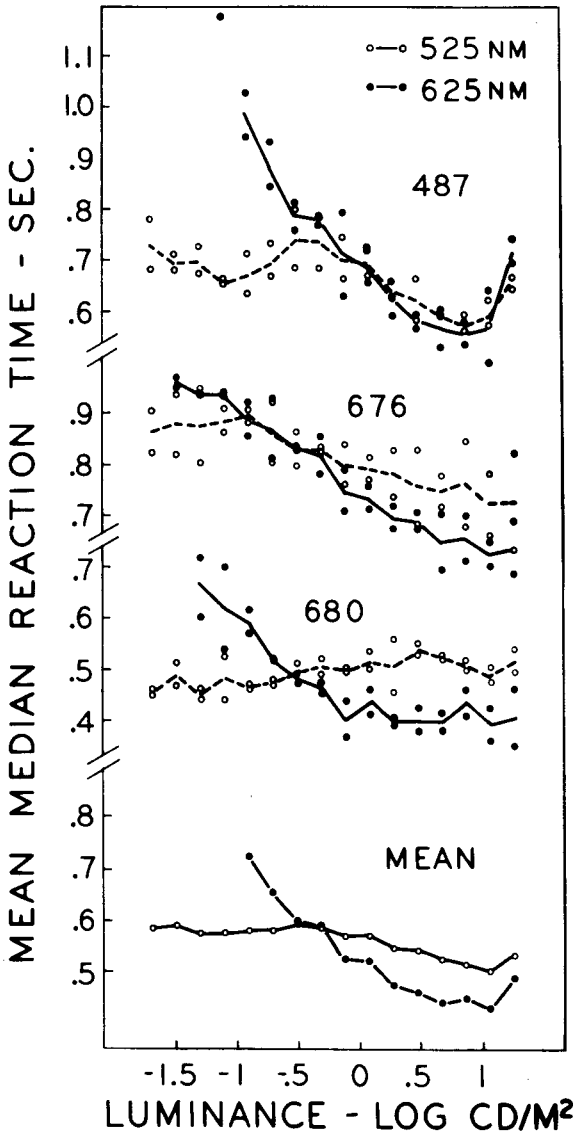

Figure 2. Mean median reaction times for monochromatic-light sessions. Two series were run at each wavelength; otherwise, plot is as in Figure 1.

luminance, then decreased, then increased again in this midluminance region.

A second striking feature of these data is the pronounced increase in RT with luminance at high luminances. For Birds 676 and 680, RT became almost as great to these intense lights as it was at the dimmest stimuli. All three birds showed the increase at high luminances.

Figure 2 summarizes the RT-luminance relationship for the two monochromatic lights. The luminance values are adjusted for photopic equality on the basis of a previous study that used the same apparatus (P.M. Blough, 1978). Again, the individual data points in the upper three panels are the means of medians across nine sessions; the lines join the means of corresponding data points. The grand means for the three birds appear in the bottom panel of Figure 2.

The form of the RT-luminance relationship clearly depends on the wavelength of the stimulating light. At 625 nm, RT generally decreased with luminance over most of the range; for Bird 680, the function flattened out at higher luminances, and for Bird 487, it increased at the highest luminances tested. There is no indication of the inflection seen in the midrange of the white-light data. At 525 nm, luminance had much less effect on RT and the data were less uniform across subjects. For Bird 487, the function was nonmonotonic and showed a marked rise at about -0.5 log cd/m^2, followed by a minimum at about 0.85 log cd/m^2 and a rise at the highest luminances tested. For Bird 676, the function was flat or slightly rising at low luminances; it then decreased, rapidly at first and then more slowly with increasing luminance. For Bird 680, RT changed little with luminance over much of the range, though it increased somewhat at higher luminances. Not only did wavelength affect the shape of the function, it also was associated with different RT levels. At lower luminances, RTs were lower to 525 nm than to 625 nm. The functions for the two wavelengths crossed in the midluminance region; this crossover and the relative flatness of the 525-nm function are reflected in the mean data shown in the bottom panel of Figure 2.

The 625-nm data points in Figure 2 do not extend as far into the low-luminance region as do the 525-nm data. Points were omitted because the birds failed to respond to dim 625-nm lights on many of the trials. Such failures probably resulted from failures to detect the stimulus and reflect the probable elevation of the absolute threshold for 625 nm over that for 525 nm.

Figures 3 and 4 show RT frequency distributions for one bird. In Figure 3, smoothed distributions of RTs to white light are shown at 0.4 log unit intervals across most of the stimulus range. Most striking is emergence with increasing luminance of a marked peak. The position of this peak moved first to the left and then to the right, reflecting the increase and subsequent decrease in median RT with increasing luminance. A close look will reveal the decrease and subsequent increase in short RTs with increasing luminance starting at about -0.6 log cd/m^2. As noted above, this decline in short RTs happened with all the birds. The rise in RT at high luminances appears due not only to the shift of the RT peak to the right, but to the addition of long RTs as well.

Figure 4 shows RT distributions for monochromatic stimuli from the bird shown in Figure 3. The two stimulus wavelengths produced markedly different distributions. At 525 nm, a mode appears throughout the tested range of luminances. Though this mode shifts somewhat to the left with increasing

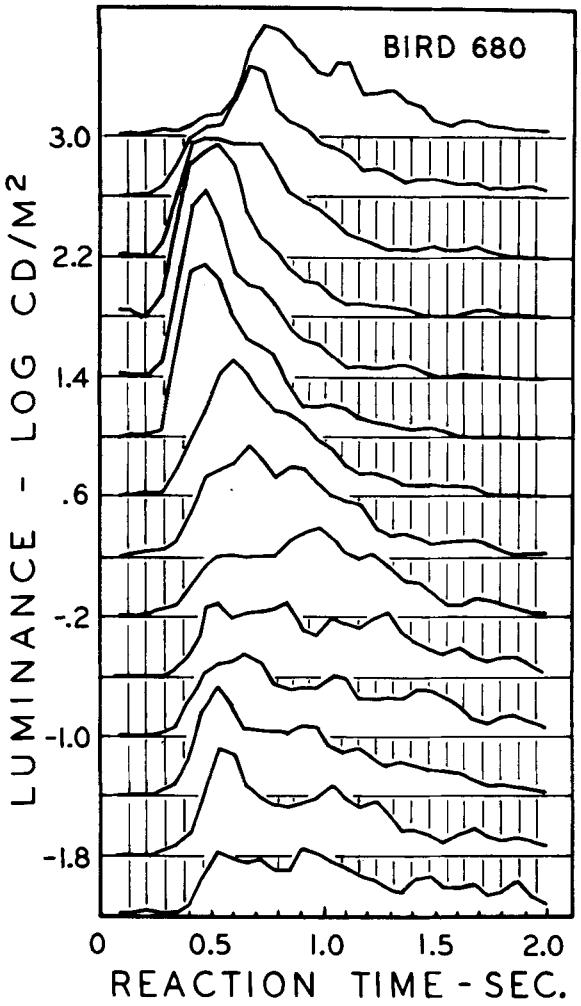

Figure 3. Frequency distributions of reaction times emitted by Bird 680 to white lights across much of the luminance continuum studied. The curves are smoothed by averaging across adjacent intensities and adjacent RT bins. Note the leftward shift of the mode with increasing luminance over much of the range, followed by a rightward shift at high luminances.

luminance, increased variability progressively broadens the distribution and accounts for the increased mean median RT for the bird noted above (Bird 680, Figure 2). The other birds showed marked RT modes throughout the stimulus range at 525 nm; these modes also shifted somewhat to the left with increasing luminance.

At 625 nm, the picture is quite different. Here, a peak emerges with increasing luminance and moves leftward. There was no sign of short RT suppression, leading to a midrange inflection. This picture characterized the other birds also. The main differences among the birds were that, for Bird 487, the distribution tended to be bimodal and, for Bird 676, RTs were relatively long and the modes of the distributions relatively broad. Also, Bird 680 was unique in emitting some very short RTs that may have been responses to the ready signal; there seems no reason to believe that this affected the significant aspects of this bird's data.

DISCUSSION

Our data show that the reaction time of the pigeon's keypeck varies systematically and substantially with stimulus intensity under most conditions. This finding contrasts with previous data showing keypeck RT to be insensitive to stimulus parameters. Despite such results, it seems reasonable to expect RT to vary with luminance, because intensity-latency relationships are so common and are found even in the neural response to sensory stimulation (e.g., Samson & Young, 1973; Vaughan et al., 1966). Two of the earlier studies (D.S. Blough, 1978; Mulvanny, 1976) used a wavelength continuum in which luminance differences were minimized. Heinemann (1974) found invariant keypeck RTs in a study using a range of auditory intensities as discriminative stimuli, but several features of his method might account for his result. For example, his birds discriminated among intensities, and a choice procedure required them to respond to one of two keys following a peck-produced stimulus.

The studies cited above showed that frequency distributions of pigeon RTs were typically bi- or multimodal and that there were strong individual differences in this aspect of the data. For two of the

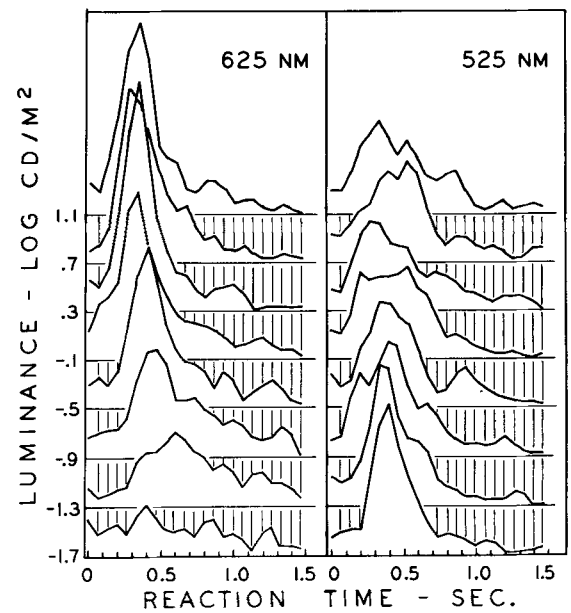

Figure 4. Frequency distributions of reaction times emitted by Bird 680 to the two monochromatic lights. Only data from alternate luminances are shown; the curves are smoothed by averaging adjacent RT bins, and RTs beyond 1.5 sec are omitted. Note that a sharp mode, absent at low luminances of 625 nm, gradually develops and moves leftward. In contrast, note the sharp low-luminance mode for 525 nm; this mode becomes broader and lower at higher luminances.

birds in the present study, the distribution showed a single pronounced mode whose height and position varied slightly but systematically with stimulus parameters. The third bird's data were similar except that its distributions often had two adjacent modes. Although these peaks disappeared at low luminance levels for the white and 625-nm conditions, they persisted in all the 525 data and were reflected in the flatter RT-luminance function at that wavelength. The clustering of keypeck RTs in one or several modes probably reflects the stereotyped response topographies. Sharply defined multiple modes are not as evident here as in the data of Heinemann (1974). As noted above, Heinemann used a choice method that might favor multiple modes; sharply defined modes would surely be favored by any method that, like his, measured RT from a previous peck, because the bird's initial head position is relatively constant in that case.

The present data cover a wide intensity range, and they probably reflect the functioning of both scotopic and photopic visual systems. The data in Figures 1 and 2 include evidence for separate rod and cone contributions. For example, the inflections in the functions in Figure 1 suggest separate processes at different luminance levels. Kohfield (1971) noted similar inflections in RT-intensity functions for human subjects and attributed them to a scotopic-photopic "break." However, his data did not suggest a rise in the function after the inflection, as in the present data, but simply a leveling off of RT in a midportion of the luminance range.

Figure 2 shows further evidence for separate scotopic and photopic influences. The 625-nm light, equal to the 525-nm light in terms of photopic threshold, should have a higher threshold at scotopic levels (D.S. Blough, 1956). Assuming an association between RT and sensitivity (Pollack, 1968), the high RT to low levels of 625-nm light may be attributed to the insensitivity of the rods at this wavelength. The continuity of the 625-nm curves in Figure 2, as well as the regularity of the mode shifts in Figure 4, suggest that the 625-nm data may be determined almost entirely by a single system, presumably the photopic. Other aspects of the picture shown in Figure 2 are more complex and suggest interacting effects of rods and cones. We turn to further consideration of this matter.

Other research has indicated that the scotopic and photopic systems interact, with some evidence indicating that cone activity may inhibit the response attributable to rods (D.S. Blough, 1958; Makous & Boothe, 1974; Wooten & Butler, 1976). D.S. Blough's data (1958) suggest that this interaction may be particularly prominent in the pigeon, which has many more cones in its peripheral retina than does the human. Such interaction may explain some of the peculiarities of the present data. For example, the increase in RT in an apparently mesopic luminance region (Figure 1; Figure 2, Bird 487) could occur because cone activity was sufficient to diminish the input from rod activity although insufficient to be the sole determiner of the response. A similar account could apply to the plateau in Kohfield's 1971 RT-intensity data, although such a plateau could also result from an asymptote in scotopic input.

Cone-rod interaction could also account for the fact that RTs to 525 nm were longer than they were to 625 nm at higher luminances for two of the birds. An explanation in terms of such interaction would have to assume that the interaction took place over a fairly wide luminance range in these birds. Such effects, since they would compete with the usual RT-intensity relation, would account for the flatness of the 525-nm function. It would place the region of interaction at a lower luminance level for Bird 487. There are, of course, several alternatives to such an account. The wavelengths might not have been well matched for luminance; there is some uncertainty about pigeon spectral sensitivity (P.M. Blough, 1978; Romeskie & Yager, 1976), and individual birds probably differ in relative sensitivity. Still another account could appeal to specific wavelength effects of RT, although it is unclear whether such effects exist (see review by Uttal, 1973). The present data do not clearly discriminate among these alternatives.

All of the white-light data and some of the monochromatic data showed an RT increase in the higher luminance regions, sometimes a very large one. In a study with humans, Steinman (1944) found a similar upturn, but his experiment investigated RT to luminance increments superimposed on varying background levels. Thus, his account of the increased RTs in terms of poor light adaptation probably does not apply to the present findings. Other data, however, suggest related effects. D.S. Blough (1959) found that pigeons "prefer" (peck faster to) moderate luminances (about 0.4 to 1.4 log cd/m^2) over high luminances. Hodos (1976) found that pigeon visual acuity, while improving with luminance over a wide range, deteriorated when the test field was very bright (3 log cd/m^2). Possibly, intense lights are aversive to pigeons or elicit startle responses that compete with keypecks and yield longer RTs.

One purpose of the present study was to determine whether or not keypeck reaction time might be a useful measure in stimulus intensity scaling procedures. Stebbins (1966), for example, used RTs to generate equal-loudness contours in the rat. Two difficulties appear to confront such usage in the pigeon, at least for the visual modality. First, as we have noted, the paradoxical increases in the luminance-RT function, particularly that at high luminances, may be due to some non-sensory process that makes it questionable

to equate "equal RTs" with "equal brightnesses." Second, the marked shift in overall RT level that was seen in some of the replications (Figure 1) could pose a serious variability problem in a long-term study. Perhaps the use of "deadlines" that shorten RTs and confine them to a narrower range (Mulvanny, 1976) would reduce some of this variability.

To summarize, we have found that, over much of the range studied, the RT-luminance relation in the pigeon is basically the decreasing one known in humans and some other species. The relation is complicated by a number of factors, however. These appear to include the separate contributions of rod and cone systems and perhaps the interaction of these systems. They also include unknown factors that slow down the keypeck to very bright lights. The factors just mentioned, as well as considerable variability, indicate that the RT-luminance relationship has poor potential for sensory scaling in the pigeon. On the other hand, it appears very promising as a psychophysical index of other features of sensory function.

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