THE PULSE-TO-CYCLE FRACTION AS A DETERMINANT OF CRITICAL FLICKER FUSION IN THE PIGEON

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Critical flicker fusion frequencies were determined as a function of pulse-to-cycle fraction for four white Carneaux pigeons. The Estes-Skinner conditioned-suppression paradigm was used to assess the thresholds. Five pulse-to-cycle fractions (.10, .25, .50, .75, .90) were studied at each of five stimulus intensities extending over a range of 6 log units (.0303 to .005 millilamberts). All animals showed a uniform relationship between the different pulse-to-cycle fractions. At high brightness levels, the shortest pulses produced the highest thresholds. As pulse-to-cycle fraction was increased at this intensity, critical frequencies were reduced almost linearly. When brightness was successively reduced the same relationship between PCF values was observed, but the differences became progressively smaller and disappeared entirely at the lowest brightness level investigated (.0303 millilamberts). Inter and intra-subject variability were well within the limits typically found in human psychophysical studies of flicker, attesting to the efficacy of the conditioned suppression paradigm as a procedure for threshold assessment.

Most of the recent studies of the relationship between pulse-to-cycle fraction (PCF) and CFF have been conducted by Bartley and Nelson (1960a; 1960b; 1961). Their findings and those of Lloyd and Landis (1960) have rather consistently shown that at low luminance levels (uncompensated) the highest CFF values occur when pulse length ($P_L$) is .5. At extreme $P_L$ values (.02, .10, .90, .98) fusion is achieved at significantly lower frequencies. The curve of CFF plotted against $P_L$ can generally be described as bowed at low luminance levels. As luminance is increased, highest CFF values are obtained when $P_L$ is small (.02-.10), and the curve progressively descends, reaching its lowest values when $P_L$ is large. When compensation is introduced, the effect is to produce curves which have their highest CFF values at.

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short pulse durations and descend gradually as pulse duration is increased. The rate of descent is more pronounced at high levels of luminance.

In recent years, psychophysical studies of CFF thresholds have relied mainly on human Ss. All of Bartley’s work has employed humans, as have the other studies previously mentioned which related to the influence of PCF upon CFF. The majority of behavioral studies in this area involving infrahuman species were conducted by Crozier and Wolf approximately 20 to 30 years ago. These authors employed a procedure based on the optokinetic effect.

Crozier and Wolf employed this procedure to assess the effects of different PCF’s upon CFF in a number of animal species. These included the sunfish (1938a); the anax larvea (1938b); the domestic sparrow (1944); the zebra finch (1941); and the turtle Pseudemys (1939). This work was remarkable in the consistency of its findings, which showed for all species except the zebra finch, approximately a straight line function with highest CFF at a PCF of 0.10 and lowest at 0.90. The curve for the finch is inverted upward with lowest CFF occurring at a PCF of 0.50, while the extreme ratios (0.10, 0.90) produce the highest CCF values.

There is some difference, then, between the most recent and reliable human psychophysical data, and the earlier, but highly consistent animal data of Crozier and Wolf, relative to the influence of PCF upon CFF.

In an effort to collect data relating to the differences between the Crozier and Wolf data and the more recent human psychophysical functions relating PCF to CFF, it seemed advisable that a technique be employed which exercises a high degree of control over the response being measured, and permits automation of this response. An experimental procedure permitting reliable cross-species comparisons was also preferred. The recent work of Hendricks (1966) seems to offer just such a technique. Employing the conditioned suppression paradigm originally developed by Estes and Skinner (1941), Hendricks investigated CFF thresholds in the pigeon at different intensities of light. She secured highly consistent results with a range of intra and inter-subject variability that falls well within the limits typically found with human Ss. Hendricks suggests a number of possible advantages for the conditioned suppression technique over other behavioral control techniques which have been employed in animal psychophysical problems. Chief among these is the establishment of differential responding in the presence of the experimental stimuli. Sidman (1960) has suggested that the most unequivocal demonstration of stimulus control over a particular form of behavior is the establishment of a baseline in which the behavior in question always occurs in the presence of the stimulus and rarely occurs in its absence.
CRITICAL FLICKER FUSION IN THE PIGEON

METHOD

Subjects

Four white Carneaux pigeons were used as Ss. The birds were maintained at approximately 80% of their free-feeding weight throughout the course of the experiment.

Apparatus

The experimental chamber was a Lehigh Valley pigeon box, Model 1519C, equipped with a translucent key. The stimulus light was displayed on the back of the key and provided the only illumination within the experimental chamber except for a dim light which accompanied each presentation of the grain hopper. All programming of experimental procedures was accomplished through a system of electrical switching circuits.

A diagram of the optical system is presented in Figure 1.

![Diagram of optical system]

Fig. 1. Diagram of the optical system: S₁, iodine lamp which provided the stimulus source; L₁, 250 ml flask which served as a heat absorbent and collimator lens; L₂, imaging lens; D, neutral density filter; S₂, exciter light; F₁, constant speed sectored disc; F₂, variable speed sectored disc which provided for intermittent photic stimulation; F, photo cell which provided for monitoring of the stimulus frequency; O, fiber-optic pipe; K, translucent pigeon key.

The visual stimulus was produced by a 620 watt iodine lamp operated on a highly filtered DC power supply to minimize AC ripple. This light was passed through a 250 ml flask filled with distilled water which helped to absorb the intense heat. This flask served also as a collimating lens. The light was imaged by a lens onto a fiber-optic pipe which transmitted the light to the back surface of the translucent key. This provided a stimulus spot approximately eight mm in diameter. A filter box was included in the optical system to permit changes in stimulus intensity. Just prior to entry into the fiber-optic pipe, the light was passed through either of two rotating discs from which sectors had been cut to provide the appropriate PCF. The standard stimulus had a frequency of 180 CPS, while the conditioning stimulus was changed through manipulations of a variable speed motor which drove the disc. Changeover from the standard to the condi-
tioning stimulus was accomplished through activation of a solenoid. In order to control for brightness differences, the PCF of both the standard and conditioning stimulus was always the same. The output from a photo-voltaic cell on one side of the variable disc was fed into a General Radio Corp. frequency meter. This permitted monitoring of the frequency of the conditioning stimulus at all times in the experiment.

Five different intensities of light were used covering a range of 6 log units from approximately 39,300 to 0.0003 millilamberts. There was a difference of 1.5 log units between each intensity which was accomplished through the insertion of a series of neutral density filters into the optical system. Stimulus intensity was measured by a Salford Electrical Instruments Exposure Photometer. Repeated measurements were made within the test chamber at an approximate distance of six inches from the response key. The means of the values obtained at the different intensities were taken as the stimulus values.

The aversive stimulus was an electric shock of 50 milliseconds duration provided by an AC shock source, which included 10,000 ohms resistance placed in series with the bird. The shock was delivered through internally implanted electrodes according to the technique developed by Azrin (1959).

A Gerbrands cumulative recorder provided continuous records of the animals’ responses during the experimental sessions. Responses made during presentation of the conditioning stimulus and during an equivalent period of time immediately prior to the onset of the CS were recorded separately on electrical impulse counters.

Procedure

Initial shaping of the birds’ key-pecking behavior was accomplished through the method of successive approximation. The birds were quickly advanced through successively extended schedules until a VI 2 min. schedule was reached, and this was used throughout the remainder of the study. Experimental sessions were programmed to last until five ascending series were completed.

During the early phases of the experiment, the key was lighted by the standard stimulus with a PCF of .5. The birds were given at least two sessions of experience at each of the five different levels of key illumination used in the experiment. When a stable baseline of responding was achieved on the VI-2 schedule, conditioned suppression training was inaugurated at the median intensity of light and with a PCF of .5. This consisted in the interruption of the 180 CPS light by 15 second intervals of 20 CPS light (the conditioning stimulus). A 50 millisecond shock was delivered to the bird simultaneously with the termination of the CS. Also, reinforcement was never delivered in the presence of the CS. Initial shock intensity was 40 volts, but this was varied as required in order to establish and maintain the suppression of key-pecking behavior.
The degree of suppression was measured by the ratio suggested by Hoffman, Fleshler, and Jenson (1963):

\[
\frac{\text{Pre-flicker Responses} - \text{Flicker Responses}}{\text{Pre-flicker Responses}}
\]

Complete suppression produces a ratio of 1.00 while no suppression results in a ratio of .00.

The criterion for the establishment of suppression was a ratio of .67 or more over 30 consecutive trials, which required that the animal make three times as many responses in the pre-flicker period as during the presentation of the CS. The training criterion was deliberately set higher than that to be observed in the threshold determinations in order to establish a high level of suppression initially.

When the criterion for suppression had been met, the ascending method of limits was employed to determine the CFF. An intermittent schedule of shock was employed at values near the threshold. When failure to suppress was obvious, the bird was not shocked. When suppression was clearly evident, the bird was shocked on approximately 60% of the trials. This precaution was taken to minimize the possibility of shocking the bird at frequencies above fusion, which could have resulted in a disruption of the animal's baseline.

One experimental session was run each day for each animal. Testing was done at only one intensity, and one PCF value per session, each of which included approximately 30 suppression trials. The normal duration of the experimental periods was 75 to 90 minutes. Four control trials were included in each experimental session. These were run at frequencies considerably above the measured thresholds, and were intended to assess the influence of the transient involved in the changeover from the constant to the variable stimulus.

The threshold for fusion was defined as that frequency of the stimulus which yields a suppression ratio below .50 on three or more trials, in a block of five presentations at the same frequency.

CPF thresholds were established for five PCF's, .10, .25, .50, .75, .90, at each of the five intensities of light. The full range of intensities was first covered for each PCF before a second PCF was investigated. Three threshold determinations were made at each of the 25 experimental values.

Results

Critical flicker fusion thresholds for each of the four Ss are plotted as a function of PCF in Figure 2.

It can readily be seen that small PCF's produce the highest thresholds when stimulus intensity is high, with successively lower thresholds being found as the fraction is enlarged. As intensity is reduced, the curves are observed to descend more gradually and they become
essentially flat at the lowest value (0.03 millilamberts) used in this study. This relationship is uniform for all subjects.

The range of threshold frequencies at all experimental parameters is given for each animal in Table 1. Three of the birds had maximum thresholds of approximately 145 CPS while the fourth (Pigeon 51) had a maximum of 110 CPS. The CFF values for this bird were consistently 25 to 30% lower than the other three at all stimulus intensities.

![Fig. 2. CFF’s as a Function of PCF for each Intensity for each Pigeon.](image)

Despite the large difference in terms of the absolute values of the thresholds, this animal still displayed the same relationship between PCF values as the other three birds. While such a degree of inter-
subject variability may appear striking, the same phenomenon has also been observed in human psychophysical studies of CFF. Data reported by Bartley (1960a) show differences of 30% in threshold frequencies of the two highest and two lowest Ss in a group of seven at a medium intensity of light (1164 c/lft²). Landis made the following statement regarding individual differences based on his review of the literature: “There exists a very wide inter-individual variability among

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observers and probably, if sufficient lapse of time occurs, considerable intra-individual variability.” (1954, p. 281.) The degree of inter-subject variability reported here, then, is not at all atypical.

Intra-subject variability is illustrated in Figure 3 which shows the mean of ranges and largest range for the three thresholds that were measured at each of the 25 experimental parameters. Each of the birds had a mean of approximately three CPS with the largest range being eight CPS. Of the 100 range values summarized in this figure, only 8 exceeded a range of four CPS.

DISCUSSION

The data obtained in this study show quite clearly that PCF is a very important determinant of critical flicker fusion in the pigeon. This is true, however, only in relationship to the intensity of the light. At the
lowest intensity used (.03 millilamberts), no difference was observed, but as stimulus intensity was increased, PCF was observed to produce an increasingly strong differential effect in terms of the CFF values obtained.

One of the major purposes of the present study was to collect systematic data relating to the apparent differences in results of earlier investigations of the influence of PCF upon CFF at various brightness levels. The present findings have elements of agreement with both the animal psychophysical data of Crozier and Wolf and the human data of Bartley and Nelson (1960a; 1960b; 1961) as well as that of Lloyd and Landis (1960). Because of differences in the characteristics of the light stimuli, it is perhaps best to compare these studies in terms of the flicker thresholds obtained. The feature common to all these studies is that small pulse to cycle fractions produce the highest threshold frequencies at the medium and high brightness levels used in these studies. In terms of threshold values, these were generally in the range of 50 CPS and above.

One of the most significant aspects of the current investigation was that it covered a higher range of brightness levels than has been reported in any other psychophysical study of CFF. As a consequence, it produced the highest flicker thresholds that have been observed in a behavioral investigation, for a lenseatic eye. The pigeon proved to be a fortunate choice as the experimental S, as it was able to work over extended periods of time at brightness levels that could be tolerated for only a few seconds by human observers, in whom enough of the cone pigment is apparently bleached in this time so that the observer is momentarily blinded.

In comparing the present results to the human psychophysical data of Bartley and Landis, several similarities can be observed, the most obvious being the flattening of the PCF curves as brightness is reduced. With human Ss also, flicker thresholds are successively reduced as the pulse-to-cycle fraction is extended at high brightness levels.

The greatest apparent difference between these two bodies of data is that human flicker thresholds start to decline as pulse length is reduced below .25 at medium and low brightness levels, whereas the PCF curves for the pigeon are either flat or slightly ascending in this range. Here we are speaking of CFF values in the range of 15-45 CPS. When the human data is compensated according to the Talbot-Plateau law, its similarity to the present uncompensated data is significantly increased. This indicates that the pigeon retina can temporally analyze brief PCF's in a range where the human retina requires a large boost in luminance to make a similar analysis. Nelson and Bartley (1965) have pointed out that latency is of primary importance when cycling makes pulse durations short, and it may be in this property that the two retinas differ. This might be a function of the much greater proportion of cones to rods in the pigeon retina as compared to the human
retina (Schultze, 1866). It must be recognized that there is some short pulse duration, below which the flicker thresholds of the pigeon must also begin to fall, if the Bunsen-Roscoe law is to be obeyed. A point will be reached when the pulse will be too short to produce a visual effect, no matter how high the intensity of the stimulus. Of course, the duration of a single pulse in the present case was determined by frequency as well as PCF, so the place where this break occurs should vary as a function of brightness level and a concomitant threshold value. The present data indicate that any decline in thresholds for the pigeon must commence with PCF's shorter than .10 in the range of brightness levels covered.

Nelson and Bartley (1965) have suggested that the mechanism by which variations in PCF manipulate flicker-fusion is to be understood on the same basis as that which produces flicker-fusion when rate of cycling is sufficiently increased. They state that when pulses are brief and the repetition rate is low, almost every channel discharges to every pulse. At this slow rate, the fact that channels vary in latency from one another is of little consequence. But these differences become increasingly important as the rate is increased as this reduces the proportion of channels in synchronous activity. When the rate of repetition separates successive inputs by amounts falling within the range of latencies, the period of no stimulation tends to be occupied by channel activity set in motion by the previous pulse. These two factors provide for fewer discharges every pulse and for distribution of the discharge density; hence fusion. Varying PCF is the same as varying pulse duration, while holding rate constant. It should be expected, therefore, that as PCF is increased, sensory effects will be observed to change in the same direction as those obtained from increasing rate. This is, in fact, what was observed to occur in the present study, a finding which seems to lend emphasis to Nelson and Bartley's contention that recovery is of primary importance when pulse durations are long.

These same authors had also made an earlier suggestion (Bartley & Nelson, 1961) that evocation of "off" responses in the visual system would tend to promote the perception of flicker, whereas inhibiton of these responses would produce fusion. Granit and Riddell (1934) and Granit and Therman (1935) had shown that an off-response is inhibited when followed after a brief interval by another photic pulse. This finding agrees with the behavioral observations in the present study, in that long pulses with short "off" periods result in much lower thresholds than do short pulses with long "off" periods.

The orderliness of the present results and their small degree of variability seem to attest further to the efficacy of the conditioned suppression technique in threshold determination. As Hendricks (1966) pointed out, this technique maintained stimulus control over the animal's behavior near threshold values and did not require frequent retraining throughout the experiment, as has been found with other threshold procedures.
REFERENCES


