TECHNICAL NOTE

ON THE PROPER CONTROL OF LUMINANCE CUES
IN PIGEON COLOR-VISION EXPERIMENTS

When an experimental design requires a differential response to two or more different stimuli that vary in spectral composition, it is usually necessary to equate the stimuli in luminance so that wavelength or spectral composition may remain as the sole controlling variable.¹ In the case of monochromatic lights, this may be done by setting

$$S_{\lambda} \times P_{\lambda} = \text{a constant}$$

where P_{λ} is the measured relative power of a monochromatic stimulus and S_{λ} is the psychophysical spectral sensitivity function operating with a given set of stimulus and adaptation parameters.

The success of this procedure depends, of course, on a careful specification of the function S . In most published experiments on pigeon color-vision, the investigators have used the pigeon photopic spectral sensitivity function reported by D. S. Blough (1957). This function was very carefully determined, and has been confirmed by other methods (P. M. Blough, Riggs, and Schafer, 1972; Graf, 1969). However, we have recently collected data that suggest that the D. S. Blough (1957) function is appropriate only for a restricted set of experimental conditions, and that serious luminance mismatches may have occurred in studies that used his function. Our experiments are reported in detail elsewhere (Romeskie and Yager, 1975); this brief summary suggests their implications for experiments with pigeons that use the wavelength continuum.

The experiment was conducted with White Carneaux pigeons in a standard operant-conditioning chamber, using a two-choice discrimination procedure. There were two circular stimulus patches, 4 mm in diameter and subtending about 6° visual angle at the pigeon's eye; they were separated by 19 mm (27° visual angle). The stimulus was presented for 3 sec, and between trials there was a 10-sec interval during which the pigeon was exposed to an adapting field at a level of 4 mL, with a color temperature of 5400°K. On each trial, one of the two stimulus patches was illuminated with monochromatic light from a Bausch and Lomb monochromator. The pigeon's task was to peck the illuminated patch, the location of which varied randomly from trial to trial. Relative radiance of different wavelengths required for 75% correct performance were determined.

¹In some circumstances, the experimenter may find it just as valid to employ a procedure in which the luminances of stimuli are permitted to vary in a fashion irrelevant to the required response.

The average spectral sensitivity function obtained from two subjects is shown in Figure 1. Spectral sensitivity is lowest in the long-wave region, rises to a peak near 600 nm, falls to a sharp minimum at about 460 nm, and rises again at the shortest wavelengths tested. Also shown in Figure 1 is D. S. Blough's (1957) average photopic function. The two curves are virtually identical from 620 to 700 nm, but both the peak and the minimum of the function from the present experiment occur at longer wavelengths than in Blough's curve. In addition, the present function shows a more rapid loss of sensitivity toward the middle of the spectrum, and a faster rise of sensitivity in the short-wave region.

Figure 1 also shows average spectral sensitivities of pigeon optic tectum units whose receptive fields lie in the "red" and "yellow" fields of the pigeon retina (King-Smith, unpublished observations, cited in Muntz, 1972). The "red" field, so-called because it contains a high proportion of cones with red oil droplets, occupies the upper temporal quadrant of the retina. The term "yellow" field refers to the remainder of the retina, which contains more cones with yellow and orange oil droplets. (See Muntz, 1972, for a general discussion of oil droplet transmission spectra.) Blough's spectral sensitivity curve is very similar to that obtained from the "yellow" field neurons, and the present curve is very similar to that of the "red" field neurons.

The discrepant psychophysical results may result from differences in procedure that affect the location of stimuli in the visual field of the pigeon. Figure 2 shows that the tip of the pigeon's beak projects onto the "red" field of the retina. In the present experiment, the pigeon pecked directly at a relatively small aperture, and thus the stimulus was probably restricted to the "red" field. In Blough's experiment (Figure 2), the pigeon pecked at keys *below* the stimulus, so the stimulus probably projected onto the "yellow" field. Since the bird's head was free to move in both experiments, the effective stimulus field cannot be certainly specified in either case. However, if, as appears likely, Blough's (1957) function is indeed determined by the "yellow" field, it is inappropriate for luminance matches when the pigeon pecks directly at a small stimulus. Mismatches will be produced for $\lambda < 600$ nm, with a relative error as large as about 0.5 log unit (Figure 1).

A number of investigators, including D. S. Blough (1961), P. M. Blough (1972), Schneider (1972), Wright (1972), and Wright and Cumming (1971), have used D. S. Blough's (1957) function for luminance computation, but in their studies the pigeon pecked directly at the stimuli, presumably viewing them primarily with

Fig. 1. Spectral sensitivity functions:

- This experiment
- Photopic curve (Blough, 1957)
- ×— Tectal units, red field (King-Smith, 1972)
- +-- Tectal units, yellow field (King-Smith, 1972)

The functions have been adjusted to coincide for $\lambda \geq 640$ nm.

the "red" field. (Due to head movement, and because the usual pigeon key subtends a large visual angle, the "yellow" field may have been involved in these studies

as well.) It may prove useful to examine some of these results for a possible influence of luminance variation.

We do not mean to imply that any *one* spectral sensitivity function should be used as a standard for luminance computations, because spectral sensitivity is affected by many variables (Graham, 1965); these include chromatic adaptation, adaptation level, stimulus size, and stimulus duration, as well as retinal locus. The only adequate method of specifying luminances in animal experiments, including pigeon studies, is to determine a spectral sensitivity curve in a given apparatus, with the same stimulus and adaptation parameters as used in the experiment.

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Fig. 2. View of the fundus of the pigeon eye, showing positions of the red and yellow fields. (Redrawn from Muntz, 1972) r: red field; y: yellow field; f: fovea. Also diagrammed are the stimulus arrangements for this experiment (S_2) and for D. S. Blough (1957) (S_1). In the present study, the bird pecked at the stimulus, and the stimulus projected to the red field; in Blough's experiment, the bird pecked either Key A or Key B, approximately 26° below the stimulus, and so the stimulus projected onto the yellow field.

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