



COMMENTARIES

Colour perception and the use of video playback experiments in animal behaviour

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Etologists have employed video and cine playback methods to study animal visual communication since the late 1960s, but in the last few years such methods have become extremely popular (reviewed in D'Eath, *in press*). However, there are some serious limitations to the use of video technology with animals that have not yet been adequately addressed. The distribution and spectral quality of light on a video screen and in the real world are different. Video systems rely on fundamental features of human visual processing to create a perceptual match between the video image and nature. This match will, in general, fail for nonhumans. In this paper we focus on issues related to perception of colour. Other potential shortcomings of video stimuli have been considered in detail elsewhere. These include the absence of depth cues, screen flicker, pixel size and visual acuity, the absence of interactiveness (D'Eath, *in press*) and the issue of correct viewing distance for the type of stimulus (Dawkins & Woodington 1997).

The Perception of Colour and Brightness

Light is detected by photoreceptor cells in animal retinas (rods and cones in vertebrates, reticular cells in invertebrates) that contain light-absorbing photopigments. Each photopigment absorbs photons maximally at a certain wavelength (called λ_{\max}), with decreasing probability of absorption at more distant wavelengths. The neural output from a single photoreceptor depends

on the intensity of stimulation (i.e. the rate of photon flux) and on the spectral distribution of the stimulus. Normal human colour vision is mediated by three classes of cones. Except for other Old World primates, the λ_{\max} values of the photoreceptors and the number of classes of photoreceptors present in the retina of nonhuman animals differs from that of humans (for reviews see Goldsmith 1990; D'Eath, *in press*).

The stimulation of animal photoreceptors can give rise to two distinct sensations: colour and brightness. The sensation of colour is a function of the ratio of neural outputs from the different classes of photoreceptors. Brightness (or perceived intensity) arises from the weighted sum of photoreceptor neural output from different classes of photoreceptors. The brightness of any image depends on its spectral composition, the spectral absorption function of the individual photoreceptors, and the weight given to the different photoreceptor types by the brain. The relationship between spectral composition of a stimulus and its brightness is known as an animal's spectral sensitivity.

How the Colour of Natural Images is Reproduced on a Video Monitor

Two different visual stimuli that elicit the same quantity and ratio of neural output from the different classes of photoreceptors must be perceived as identical. Since the neural output from each photoreceptor class depends both on stimulus intensity and spectral quality, one can stimulate the human visual system simultaneously with the sum of three spectral stimuli (typically referred to as a set of primaries) and, by independently manipulating the intensity of each, reproduce the pattern of photoreceptor

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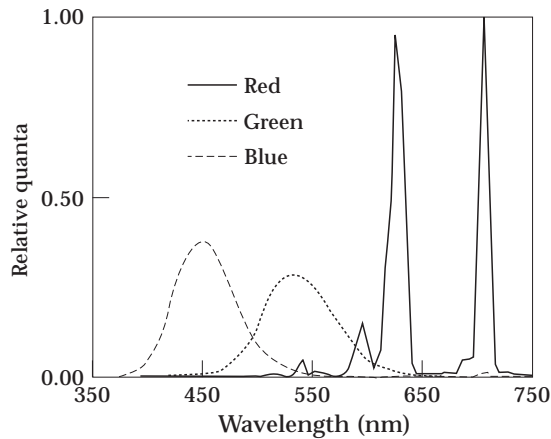


Figure 1. Typical phosphor spectra in relative quantal units measured from an Apple 20 inch monitor in author D.H.B.'s laboratory using a PhotoResearch PR-650 spectral radiometer. The phosphors are referred to as blue, green and red because of their appearance to a human observer.

neural output caused by almost any natural stimulus spectrum. The surface of a video monitor is covered with tiny pixels, each consisting of three types of phosphors (generally one red, one green, and one blue), each with a different spectrum (see Fig. 1). Each phosphor spectrum serves as a primary. The intensities of the phosphors are adjusted so that the resulting neural output from each cone class matches the ratio and total quantity of neural output stimulated by a natural colour. Some examples are shown in Fig. 2, and it can be seen that the spectra of the natural colour and its video rendering are quite different. They are, however, perceptually identical (colour and brightness) because they elicit the same quantity of neural output from each class of photoreceptors. In general, for a given set of primaries, only one combination of intensities will elicit the photoreceptor response that is identical to that produced by a given stimulus spectrum (Brainard 1995).

If a match to a natural colour is created on a video screen for one observer, and is then shown to a second observer who possesses one or more cone classes that differs slightly in λ_{\max} value, then the colour on the screen no longer appears correct. The relative intensities of the different phosphors have to be adjusted to reflect the change in stimulation ratio resulting from the repositioned photoreceptor absorption function. It has been shown empirically with humans that modest differences in photoreceptor λ_{\max} values lead to predictable changes in the phosphor ratios required to make a perceptual match of a given colour (Nietz et al. 1993; Brainard 1995; Nakano 1996). Using methods described below we have calculated that differences in λ_{\max} position of one photoreceptor of as little as 5 nm can cause easily detectable alterations in the perceived colour of a stimulus created by the sum of three primaries. In most animal visual systems the photoreceptor absorption functions are quite different from those of humans, and the colours on a video screen that appear correct to humans must appear incorrect to the animal viewer.

An additional limitation is that the range of spectral output of the video phosphors covers the range of human vision: ca. 400–710 nm. Many animals can perceive wavelengths shorter than 400 nm (ultraviolet, or UV, reviewed in Jacobs 1992; Tovee 1995) and some are sensitive to wavelengths longer than 710 nm (Provencio et al. 1992; Yokoyama & Yokoyama 1996). Ultraviolet sensitivity typically arises from a cone with peak sensitivity in the UV which contributes to the overall perceptual colour space of the animal (Bennett et al. 1994). Removal of the ultraviolet portion of a natural stimulus presumably alters the qualitative appearance of nearly all colours in a scene. This is analogous to removing blue from a scene viewed by humans: it not only eliminates blues, but changes other colours as well: for example, whites become yellow, purple becomes red. Bennett et al. (1996, 1997) have demonstrated that elimination of ultraviolet coloration significantly alters mate preference in starlings and finches.

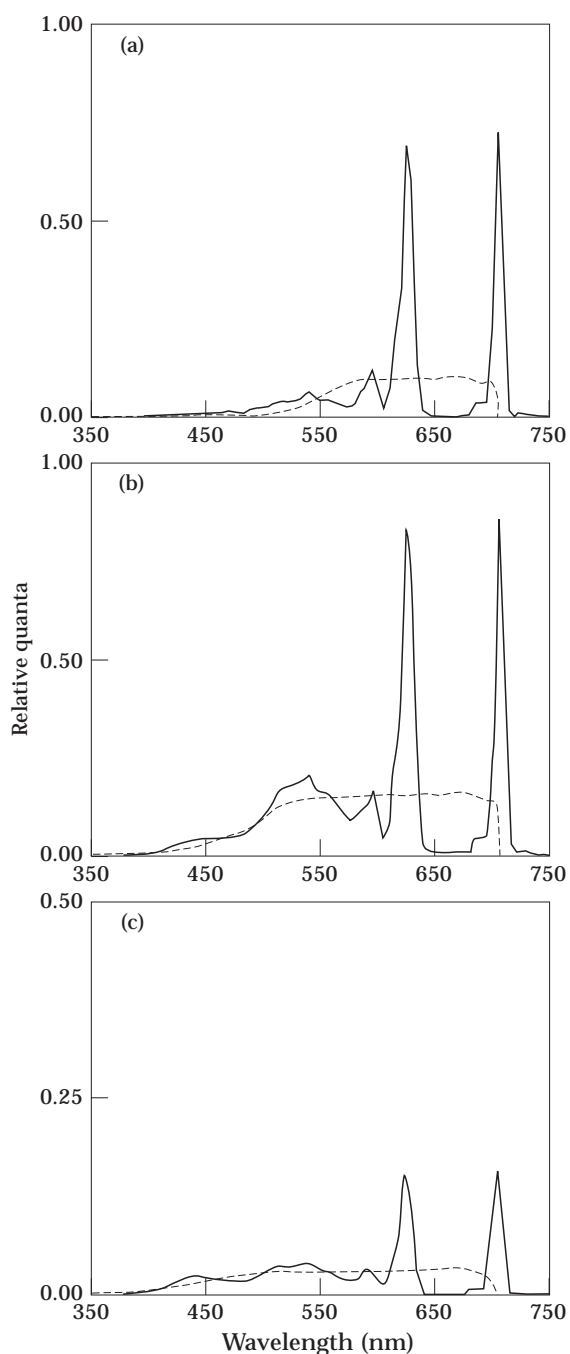
All video display devices (e.g. LCD screens, CRT monitors, projection systems) rely on the same basic principle: manipulation of the relative intensity of a set of three primaries. All print and photographic colour reproduction (including slides, prints and cine movies) relies on similar principles (Bennett et al. 1994). All should thus fail to reproduce accurately natural colours for most nonhuman observers.

Can the Problem be Corrected?

Under certain limited conditions it should be possible to calculate the necessary adjustment of the intensity of the phosphors on a video screen so that they create colours that are correct for nonhuman viewers. This will be possible if, and only if, the following conditions are met. (1) The spectral absorption functions of all classes of photoreceptors responsible for photopic vision for the viewing animal must be known (taking into account any natural filters in the eye). (2) No class of photoreceptors that is stimulated by the natural spectrum should absorb substantially at wavelengths outside the range of wavelengths produced by at least one of the videoscreen phosphors (e.g. no UV photoreceptor present). (3) The number of photoreceptor classes stimulated by the natural spectrum to be reproduced should be less than or equal to three. This condition exists because it has been shown mathematically and empirically that the number of primaries required to create a perceptual match of a natural colour must be equal to or greater than the number of photoreceptor classes stimulated by the natural colour (Brainard 1995). (4) The complete spectrum of each type of phosphor (or primary) in the particular display device being used must be known. (5) The complete spectrum (over the wavelength range to which the animal is sensitive) of every colour to be reproduced must be known.

The details of this calculation procedure appear in Brainard (1995), and are briefly illustrated here (Table 1, Figs 2, 3), for the guppy, *Poecilia reticulata*. Although the guppy possesses four cone classes, with one primarily sensitive in the ultraviolet, some of its body colours

reflect essentially no UV and do not stimulate this fourth, UV-sensitive, cone. It is thus possible to render some guppy body colours (those that reflect no UV) on a video screen so that they will appear correct to a guppy. To do this we started with the spectrum to be rendered, and computed how strongly each cone class responded by weighting the spectrum by the cone sensitivity and summing the result over wavelength. We then wished to find a linear combination of monitor phosphor spectra that produced the same total response in each cone class. From the cone sensitivities and monitor spectra, we computed how strongly each class of cones responded to each monitor spectrum. We found the correct weightings



for the three monitor spectra by solving a set of linear equations that expressed the constraint that the weighted sum of cone response to each monitor phosphor matched the cone responses to the spectrum to be rendered (see Brainard 1995 for details).

Table 1 gives the percentage change in intensity for each phosphor that was required to render each colour correctly for the guppy. It would be useful to be able to estimate how 'wrong' the human version of any colour appears to a guppy (or other animal), but we know too little about visual processing in the guppy brain to do so. We can do the reverse however, we can ask how wrong the colour appears to a human, when it is rendered correctly for the guppy. For this we used a metric from colour science, called the CIELUV ΔE^* error, which estimates numerically how different two colours appear to a human observer (Robertson 1977; Robertson & Fisher 1985; C.I.E. 1986; Brainard 1995). The values for the three guppy colour patterns are listed in Table 1. To gain a sense of what these values mean, two colours that have a difference of $\Delta E^*=3$ or greater are easily discernible by a human observer and differences of 3 or greater are considered unacceptable in industrial colour reproduction standards. A difference of $\Delta E^*=12$ is large enough for a colour to 'pop-out' in a visual search task (Carter & Carter 1981).

Although making colours on a video screen that appear correct for an animal is desirable, this procedure will be practical in only a very limited number of cases, because it is rare that all the conditions described above can be met. First, there are very few animals for which all photoreceptor classes contributing to colour perception are known. Second, many nonhuman animals possess UV-sensitive photoreceptors (Tovee 1995), and since UV wavelengths cannot be produced on the video screen, any natural spectrum that includes ultraviolet reflectance cannot be reproduced. In our example we could only reproduce those guppy colours that reflect no ultraviolet. Third, many species of birds (Bowmaker et al. 1997), reptiles (Fleishman et al. 1993), fish (Douglas & Hawryshyn 1990; Neumeyer 1992), and invertebrates (Goldsmith 1990; Cronin et al. 1996) possess more than three classes of photoreceptors, so only some colours (those whose spectrum covers the range of no more than three photoreceptor classes) can be reproduced. Finally, in order to carry out these calculations one must know the complete natural spectrum of every colour being

Figure 2. Plots of three guppy colour patterns (spectral radiance in units of relative quanta intensity) and perceptual matches for a normal human viewer as created on a video screen. Dotted lines are the actual spectra of the guppy colour patterns, solid lines are video monitor renderings. Colour patterns shown are (a) guppy orange-yellow spots, (b) guppy yellow spots, and (c) guppy body colours as measured by J. Endler in the field under natural sunlight. The video renderings of each colour are based on calculations described in Brainard (1995), although equivalent spectra can be achieved by videotaping the natural colour patterns. The spectra of the guppy colour patterns are plotted out to 700 nm only, but since both guppies and humans are very insensitive beyond 700 nm this has no impact on the calculations described.

Table 1. The percentage by which each of the three phosphors on a typical RGB (Apple 20 inch) monitor must be adjusted to render some natural guppy colour patterns on a video screen correctly for a guppy

Colour pattern†	Percentage change in phosphor intensity to render colour correctly for a guppy			CIELUV ΔE^* error‡
	Red	Green	Blue	
Orange-red	23	-114§	104	64
Yellow	16	-19	24	27
Body	44	-21	22	29

†The colour patterns are those shown with dotted lines in Fig. 2.

‡CIELUV ΔE^* is a metric designed to estimate numerically how different two spectra appear to a human observer: in this case the human rendering versus the guppy-correct rendering of each colour pattern. Values of greater than 3 are easily discernible by human observers. See text for details.

§Reducing intensity by more than 100% yields a small negative value. This result indicates that the proper rendering is slightly outside the gamut of this monitor.

reproduced over the range of visual sensitivity. Therefore, corrections must be made one colour at a time. Since each colour must be independently corrected (i.e. no global correction will be possible) this procedure will be applicable only to computer-generated stimuli in which phosphor intensities of each part of the image can be independently manipulated.

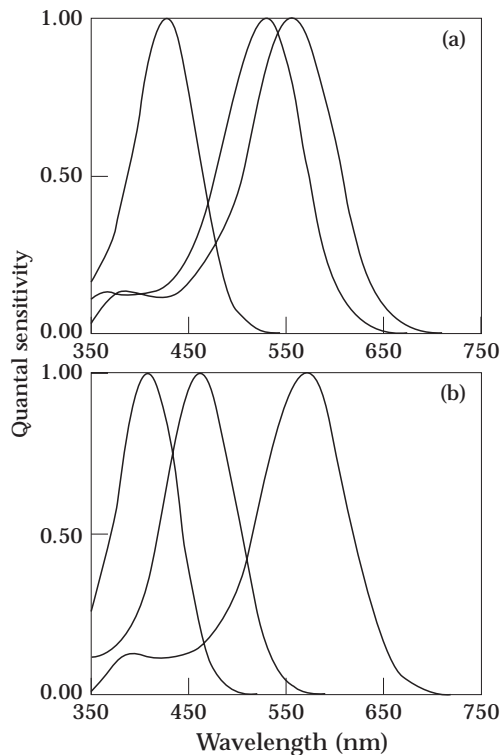


Figure 3. The estimated quantal spectral sensitivities of cones of (a) a normal human and (b) a typical guppy. These were obtained using a photopigment nomogram located at appropriate spectral peaks. Each cone type has been normalized to 1.0. Guppy cone peak sensitivities are based on Archer et al. (1987) while human peaks are based on Baylor et al. (1987) and Schnapf et al. (1988). Guppies also possess a fourth cone with peak sensitivity in the ultraviolet which we have not shown here.

Implications for Interpretation of Video Playback Studies

Unless the corrections described above can be carried out it is safe to assume that colours on a video screen that appear correct to a human will appear incorrect to the majority of other animal observers. One possible consequence is that the animal may simply fail to respond to the video image. Since failed experiments are rarely published (but see Pepperberg 1994; Ryan & Lea 1994; D'Eath & Dawkins 1996; Patterson-Kane et al. 1997) it is difficult to say how often this occurs, but three of us have had this experience in work with birds, fish and lizards, and we have spoken with a number of others for whom video playback experiments have failed.

There are, however, a number of studies in which animals responded to video playbacks with natural-appearing behaviours. This may be because noncolour cues such as shape or motion provided enough information to outweigh the incorrect colour information, and/or because the colour was not so incorrect in appearance that it eliminated response. Even where responses seem appropriate, however, the realization that colours are probably not accurately reproduced may give rise to reasonable alternative interpretations of results. For example Macedonia et al. (1994) used video playback to compare responses of *Anolis marcanoi* to visual displays of conspecifics and those of a sympatric congener, *Anolis cybotes*. *Anolis marcanoi* responded to the same extent to both images, although there were some subtle differences in the synchrony of display activity. In earlier experiments with live individuals of both species however, Losos (1985) observed much more dramatic differences in response to the two species. Macedonia et al. (1994) suggested that the discrepancy might be due to differences in the distance at which the stimuli were presented in the two studies. Another reasonable interpretation, however, is that lizards in the video experiment recognized video images of neither species as a conspecific, and the experiment was essentially comparing the response to two different heterospecific species. While the results of the study were certainly interesting, it

is not clear whether the responses of *A. marcanoi* to the video stimuli were indicative of how they would respond to live individuals of these species in nature. This illustrates a general problem: since the colour patterns of the video images do not match those of live individuals, it cannot be assumed that results of such studies are applicable to natural populations.

Since it is rarely possible to correct for the differences in colour vision between species, the most practical solution is to limit studies to those in which the colour of the animal is not critical for eliciting a response or an important variable in the experiment. However, given the potential for major uncontrolled differences in how an animal perceives the video image and the natural image, investigators should test for subtle differences between response to the video image and to the live image. Differences between the appearance of live and video animals may interact in complex ways with other variables being studied using video playback. For example, imagine an experiment in which one uses video playback to study the influence of male swimming velocity on mate choice in some species of fish. Suppose that the colours of the video males appear incorrect to the females, which makes the females regard the video males as abnormal or unhealthy individuals. The females might pay less attention to swimming velocity than they normally would because the males do not represent potential suitable mates, whereas swimming velocity might be a very important cue when females are choosing between males whose colours appear normal.

Colour and Brightness Confounds

Brightness contrast (i.e. differences in perceived intensity between objects and their backgrounds or between different objects) carries most of the information in a visual scene (Cornsweet 1970). Neurobiological and psychophysical studies have shown that some important visual tasks such as attention and motion detection rely primarily on brightness contrast (Lennie et al. 1990). Experiments with anoline lizards have shown brightness contrast to be the most important determinant of visibility in displays (Fleishman 1995), and Ellingson et al. (1995) showed that brightness was a critical component in female mate preference in a diurnal gecko. Since visual systems are differentially sensitive to different spectral stimuli, changes in colour generally result in simultaneous changes of the brightness of the stimulus. In a video playback study, regardless of whether the animal perceives colours to be correct (or regardless of whether this influences response), changes in colour will be accompanied by changes in brightness and brightness contrast between different parts of the scene.

Several video playback studies have attempted to study the role of colour change without correcting for the simultaneous change in brightness. In these studies colour was altered either with computer 'colour-morphing' programs (e.g. McKinnon 1995) or by adjusting the colour setting on a video monitor (e.g. Rowland et al. 1995a, b). Both of these procedures have been engineered so that constant brightness (perceived intensity) is

maintained for a human observer as colour is changed, by automatically correcting for human spectral sensitivity. For most nonhuman animal observers, however, whose spectral sensitivity does not match a human's, these manipulations lead to changes in the brightness contrast between the stimulus and its background, and/or among different colour patches on the stimulus animal. Changes of behaviour that are observed may be due either to the change in colour or the change in brightness, or both.

It is possible to correct for changes of brightness that co-occur with changes in spectral quality if one has an accurate estimate of spectral sensitivity for the test animal. Unfortunately spectral sensitivity functions in a given species may differ for different visual tasks (e.g. motion perception versus shape perception, Goldsmith 1990), making it difficult to obtain an accurate estimate for the particular experiment being carried out. The most practical solution is to design the experiment so that the differently coloured stimuli are presented at a wide range of different intensities (or contrasts with the background). If it can be shown that there is a consistent difference in response to two different colour patterns over a wide range of brightness conditions, it is reasonable to attribute the difference in response to differences in colour.

Conclusions

Video images differ from natural scenes in a number of ways, and any of these differences has the potential to complicate experimental results and interpretations. None the less many animals do respond to video. If an investigator can demonstrate quantitatively and unambiguously that an animal responds to a video image in the same manner that it responds to a live stimulus, then video playback may represent an effective means for studying noncolour phenomena such as motion or shape (see e.g. Clark & Uetz 1990; Evans & Marler 1991; Evans et al. 1993).

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