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SHORT COMMUNICATION

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Considerations on the use of video playbacks as visual stimuli: the Lisbon workshop consensus

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Abstract This paper is the consensus of a workshop that critically evaluated the utility and problems of video playbacks as stimuli in studies of visual behavior. We suggest that video playback is probably suitable for studying motion, shape, texture, size, and brightness. Studying color is problematic because video systems are specifically designed for humans. Any difference in color perception must lead to a different color sensation in most animals. Another potentially problematic limitation of video images is that they lack depth cues derived from stereopsis, accommodation, and motion parallax. Nonetheless, when used appropriately, video playback allows an unprecedented range of questions in visual communication to be addressed. It is important to note that most of the potential limitations of video playback are not unique to this technique but are relevant to all studies of visual signaling in animals.

Key words Visual communication · Experimental design · Vision · Motion · Color

Video playback allows the presentation to animals of image sequences retaining much of the complexity of natural visual scenes, yet containing controlled characteristics determined by the experimenter. The approach allows the manipulation of a vast array of stimulus parameters within and outside ranges of natural variation, independently of one another, and with substantial precision. A number of recent studies have used video playback to address problems in visual communication that would have proven difficult or impossible to approach using other techniques (see D'Eath 1998 and Fleishman et al. 1998, for examples).

Two recent reviews (D'Eath 1998; Fleishman et al. 1998) have raised serious concerns about the external validity of some aspects of video playback experiments. The concerns have centered primarily on the physical mismatch between video systems, which are designed to represent moving color images adequately for humans, and the natural stimuli they attempt to mimic in the video playback paradigm. The debate over video playbacks also resembles the controversy, in the late 1980s, over the issue of pseudoreplication in acoustic playback studies, in that it has begun to polarize practitioners and critics of the approach. A workshop among the protagonists of the acoustic-playback debate resulted in a consensus paper (McGregor et al. 1992) that addressed many of the key points of contention. This helped to defuse some of the more acrimonious disputes in the acoustic-playback field.

We were participants in a similar workshop held at the Instituto Superior de Psicologia Aplicada in Lisbon, Portugal, in July 1999. The workshop was designed to bring together researchers spanning the spectrum of the video-playback debate and those considering the methodology for their work. A major aim of the workshop was to pre-empt counterproductive debates in the literature by forming a consensus on methodological issues. The present article briefly addresses several important considerations in the use of video playbacks as visual stimuli. It is important to emphasize two points: first, that we make no claim to address exhaustively all the issues in the perception of video playbacks. Visual stimuli are ex-

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Table 1 Overview of the utility of video playback

Feature	Appropriate for video playback?	Reference
Brightness	Yes	Fleishman and Endler 2000
Size	Yes (if not confounded with distance)	Zeil 2000
Texture	Yes (within the resolution of the monitor and viewer)	Bando 1991, Fleishman and Endler 2000
Shape	Yes	Rosenthal 2000
Motion	Yes (object motion in screen plane)	Zeil 2000, Fleishman and Endler 2000
Color	No (except in special cases)	Cuthill et al. 2000, Fleishman and Endler 2000
Depth	No (except in special cases)	Zeil 2000

traordinarily complex, and even a gathering of researchers with a broad range of expertise will fail to consider all the important aspects of video playback. Second, we do not claim to speak for the many scientists interested in video playback who did not attend the workshop. Nevertheless, we are encouraged by the degree of consensus that was reached by workers with widely different backgrounds and from opposite ends of the video-playback debate.

A salutary consequence of the use of video playbacks is that it has forced serious discussion of the physical and biological nature of visual stimuli and visual systems *in general*. We present an open-ended set of considerations for the use of video playbacks, focusing on what we believe are the key issues determining the external validity of the approach. Many of the concerns we raise are applicable to all studies of visual communication. We hope that this article will encourage methodological rigor in both video playback and other studies.

Much of the controversy over video methods has resulted from the perspective that researchers are striving to create stimuli perceptually indistinguishable from their natural counterparts. We believe this goal to be unattainable for most animals; we think, rather, that video can be tremendously valuable as an analytical tool, where the experimenter presents an animal with selected, controlled stimulus features. In this article we attempt to identify which natural features can be recreated well enough by video for one to be confident that the animal perceives the altered image in a predictable, quantifiable way. We encourage authors to report their methods in great detail to make this approach maximally feasible [see article in this issue by Schlupp (2000)]; this includes quantifying the physical characteristics of the video output as much as possible [see article in this issue by Fleishman and Endler (2000)]. We also encourage comparisons of responses to video across studies using different technologies or model organisms. One helpful approach to doing this is to calibrate monitors to PAL or NTSC standards.

Broadly, video playback is appropriate for most studies addressing object motion in the plane of the monitor, shape, texture, and size (Table 1). Video playbacks generally do not yield interpretable results for studies of color unless specific conditions are met. These general recommendations are detailed below.

A more general problem must also be kept in mind. Because conversion to video will alter the perceived appearance of an image to an animal from its natural counterpart – often in ways that the experimenter cannot control for or may not even be aware of – the experimenter must be alert to the possibility that the responses of the animal to changes in the video images may not be the same as responses to comparable changes in a live stimulus.

Temporal resolution

The screen refresh rate for video monitors is 50 or 60 Hz depending on the video standard (PAL and NTSC, respectively) and 50–95 Hz for computer monitors[1]. This is just above the critical flicker fusion frequency (CFF) for humans under bright light conditions. CFF is higher in some animals (D’Eath 1998). A criticism of video playback is that animals with a CFF higher than the screen refresh rate [the frequency with which half-frames are renewed on the screen (D’Eath 1998)] may not perceive apparent motion on video as continuous. While a high CFF may cause perception of flicker, the illusion of continuous motion depends not on CFF but on the degree of movement and displacement between successive images. As long as displacements between successive fields are relatively small, and images are presented at the highest possible frame rate, temporal resolution does not present a serious limitation for video playback, except perhaps to diurnal birds and flying insects whose visual systems have a much higher temporal resolution than humans’. Nonetheless, flicker may be aversive or distracting for the test animal (Fleishman and Endler 2000).

Spatial resolution

Video and computer monitors come in various sizes and with various numbers of rows and columns of picture elements (pixels). Most current video monitors are matrices of roughly 700 horizontal by 500 vertical picture elements, or pixels. If an animal is close enough to a monitor, and has a high enough spatial resolution, then it will perceive the image as a mosaic of dots rather than a con-

[1] Recent advances in technology are pushing these limits to higher rates, up to 200 Hz for some video monitors

tinuous image and may not recognize the image as anything other than a noisy background. It is essential to choose a monitor or LCD screen with the smallest pixel spacing. Smaller monitors may or may not have closer pixel spacing; it is essential to choose these on the basis of technical specifications. Monochrome monitors have higher resolution (closer pixel spacing) than color monitors because in color monitors, each pixel consists of a triplet of three pixels (red, green, and blue channels). Consequently, the observable dot spacing of a color monitor is two to three times larger than monochrome monitors. To determine if the pixel spacing is close enough not to be resolved by the viewing animal at the viewing distance in the experiment, a simple approximation can be calculated. It basically says that the angular separation of two neighboring pixels as seen from distance *D* should be very much smaller than the smallest angle the animal can resolve.

A rule of thumb is to make sure that

$$\alpha = \arctan(p/D) << \Delta\phi$$

where α is the angular separation of neighboring pixels [$\tan(\alpha) = p/D$], *p* is the pixel spacing in cm, *D* is the minimum viewing distance in cm, and $\Delta\phi$ is the minimum separable (smallest resolvable angle) for the animal in question (Fleishman and Endler 2000).

Depth perception

A unique limitation of video images is the absence of many depth cues. It is important to realize that for an animal with depth vision, a video image is nothing but a plane, a two-dimensional surface with (moving) texture, not a window into a three-dimensional scene. Depth cues derived from focusing, from distance-dependent apparent motion (motion parallax), and from binocular disparity inform an animal attending to these cues that all the contours in a video image lie in one depth plane. It is hard to say when these limitations of video become a concern, but they are likely to play an important role whenever the absolute size of animals (or their signals) and the spatial context in which interactions take place determine the responsiveness of animals. To reduce complicating factors in video-playback experiments introduced by depth perception through focusing, motion parallax, and binocular stereopsis, we suggest two rules:

1. Animals as seen on the video image should be life size, because smaller images of them seen at the distance of the video screen will indicate a small absolute size.
2. Textured backgrounds should be avoided. They are always seen at the same depth plane as the object of interest and therefore do not offer differential depth cues for object–background segmentation.

This is not to say that other cues to depth cannot be simulated in video images. Change in the angular size of a stimulus object, for instance, is a potent cue to a change in distance of the object. Also, at least in human observers, occlusions and texture gradients produce powerful illusions of depth in two-dimensional images. The relevance of these cues for interacting animals needs to be tested, however, especially in those cases where responses to video images differ significantly from behavior in the natural context [see article in this issue by Zeil (2000)].

Color perception

A serious concern about video images is the mismatch between the color output of video screens and the natural stimuli they are attempting to represent. Video gives humans the illusion of rendering a broad range of colors, by using red, green, and blue phosphors that are tuned to the absorption spectra of the corresponding human photoreceptors, and that may be varied independently to stimulate the three cones in all possible natural combinations [see articles in this issue by Cuthill et al. (2000) and Fleishman and Endler (2000)]. There are three main problems with applying video playback to non-human animals. First, photoreceptor absorption spectra vary widely across species, within species, and even on a seasonal basis within individuals (Cronly-Dillon and Sharma 1968). Human-tuned phosphors thus fail to represent the appropriate colors in most cases. Second, many animals have four or more classes of photoreceptors, each with its own distinct absorption spectrum. Three phosphors are generally inadequate for simulating colors in these cases, since they will often stimulate different photoreceptor classes non-independently. Finally, video monitors do not emit the directed ultraviolet light that many animals can detect (Fleishman and Endler 2000, Fig. 1). Color balance will also be altered at different stages in the production process and with different playback devices. Photographic and cine images use an analogous process to render color and are subject to the same problems.

Many studies using live animals, dummies, or video playback do not adequately reproduce natural light conditions. Standard fluorescent lights have an output limited to a relatively narrow range of the visual spectrum. Moreover, the output contains several discrete peaks. Most light sources do not produce levels of ultraviolet light encountered in nature. Glass or acrylic barriers used in live-animal experiments appear transparent to humans but often filter out critical parts of the spectrum (Hunt et al. 1997; Fleishman et al. 1998; Cuthill et al. 2000; Fleishman and Endler 2000). Live-animal experiments on color are also uniquely compromised by the fact that animals often do not express natural color patterns in an artificial environment, whether due to differences in the light environment, diet, or social cues. While many of these problems can be remedied technically, it is possible that color expressed in the laboratory will differ in salient aspects from what an animal might observe in the field.

When using any experimental presentation technique, one should approximate as closely as possible the spectral characteristics of the stimulus encountered in nature, both during stimulus acquisition and playback. This is particularly critical if questions about color are part of the research program. Video playback is appropriate for such questions only for certain species, like some non-human primates, with photoreceptor absorption spectra similar to humans', or in cases in which video output can be corrected using physiological information about the study species (Fleishman et al. 1998). If color is not being addressed, the use of monochrome monitors, which contain a single class of phosphor, is preferred, even though the output may appear chromatic to an animal observer. It should be noted that simply turning down the color setting on a color monitor may not be sufficient; the "gray" perceived by humans is still produced by distinct red, blue, and green phosphors. Phosphors stimulating human cones at relative rates of 1:1:1 (perceived as white) will almost certainly not stimulate animal cones at the same relative rates, particularly if animals have more than three cone classes (Cuthill et al. 2000; Fleishman and Endler 2000). A few studies (see Przyrembel et al., 1995, for an example) have used computer playback with color quite effectively. In these cases the screen was effectively used as a light source: using a controlled array of blue, green, and red phosphors (whose intensity and position in space could be carefully controlled), Przyrembel et al. (1995) studied the color vision of salamanders viewing moving objects. The screen was used to create small squares of known color viewed against known backgrounds, but neither the squares nor the background stimuli bore any relationship to any natural stimulus that the salamanders evolved to perceive and act upon.

Background and contrast

Vision depends critically on resolving differences between an object and its background, and on internal contrast within objects. It is impossible to isolate the detection of an object from its background context. In this sense it differs from other sensory modalities, such as hearing. In acoustic playback, playing a stimulus against a silent background represents a standard, optimal condition for signal detection. There is no meaningful analogy to silence in a visual background: a black object will be invisible against a black background, but quite conspicuous against a white one, and vice versa. It is difficult to determine a priori what the optimal background for a particular visual cue might be, and such an effort could lead to misleading results if the background is outside the range of what an animal might encounter in nature. Studies that address stimuli based on internal contrast, like patches or stripes on the body, generally place them in the appropriate context – the background body pattern of the animal. Many video and other studies addressing ornaments, shape, or other cues dependent on external contrast, however, do so without reference to the appropriate background, which can often lead to misleading results (Endler 1978; Rosenthal 1999). Experimental presentations, whether of video stimuli, models, or live animals, should use a background informed by the context in which the stimulus is encountered in nature. Ideally, the same background should be used in portions of the testing environment outside the video screens. This is straightforward for animals that communicate against a homogeneous background, such as many aquatic taxa. For animals typically viewed against spatio-temporally complex backgrounds (e.g. Fleishman 1992), experimenters must balance the need for an appropriate background against potential artifacts introduced by misleading depth cues (see above). All studies should strive to maintain the ratio of stimulus to background contrast encountered in nature. Contrast perception also depends on adaptation to the ambient light conditions of the moment. The appropriate light intensity and adaptation should be approximated when setting an acclimatization time prior to and during stimulus presentation (Fleishman and Endler 2000).

Illumination

In general, the illumination used during stimulus construction [see article in this issue by Rosenthal (2000)], monitor output, and ambient illumination during playback should approach natural light conditions as much as possible (Endler 1993). The direction of incident light can have a pronounced effect on the appearance of a stimulus (Endler 1978; Lythgoe 1988; Rosenthal 1999), and stimuli should be filmed in a natural setting from an appropriate viewing angle, and constructed with reference to natural light conditions. When possible, the radiance of the stimulus and the background should approximate that of its natural equivalent. To minimize artifacts caused by adaptation to abnormal light conditions, both the spectrum and intensity of ambient light in the testing environment should also approximate light conditions in nature. In particular, one should avoid a strong mismatch between the screen and adjacent areas of the testing environment. Finally, since prolonged exposure to restricted or artificial light conditions can affect visual perception (Kröger et al. 1999), experimenters should try to use wild-caught animals or animals reared under natural-light conditions. Fluorescent light sources not only produce highly unnatural spectra but also flicker, depending on the current used. This may lead to interference with the flicker rate of the playback monitors. Again, these concerns are by no means unique to video experiments; studies using live animals and dummies also should consider these same issues.

As a group composed mainly of ethologists and behavioral ecologists, we have taken as our general approach to emphasize an understanding of the ways in which stimuli are perceived under natural conditions. Implicitly or explicitly, video-playback studies in animal behavior are designed to address communication and perception in nature. As such, their external validity depends critically on the extent to which they can reproduce the salient aspects of visual stimuli in a meaningful way. We have emphasized the psychophysical aspects of video stimuli, particularly those that are poorly represented by video equipment. Just as important, for both video and other studies, is that the phenotype of animals used as stimulus can be adequately represented. Both the morphology and behavior of animals can vary dramatically between field and laboratory conditions. A unique property of video methods is that phenotypes sampled in the wild can be presented in a laboratory setting as long as they can be adequately represented by a video system for the visual system of the animal in question. An understanding of an animal's natural context is a critical part of any behavioral research program and is an integral part of designing a video-playback experiment.

Data on an animal's behavior and environment are of course extremely valuable in their own right. A major benefit of the advent of video playbacks, in addition to their power as research tools, is the extent to which they have stimulated an examination of the structure of visual stimuli. Traditional studies of behavioral responses to morphological and behavioral characteristics have often neglected to consider these in terms of visual communication. The very limitations of video equipment force us to consider the nature of how the animal perceives the stimulus in these studies, which will also have the highly desirable result of stimulating more research that bridges the gap between behavior and sensory physiology.

We hope that researchers considering video playback will not take our discussion of methodology as either an exhaustive list of the concerns that need to be addressed, or as a statement of absolute requirements that must be satisfied to obtain interpretable results. Most video-playback experiments, and indeed virtually all studies of visual communication, will likely fall short in some important aspects. Researchers are constrained by the practical limitations of their study systems, which will often preclude a thorough understanding of natural light regimes, visual physiology, and other factors. This does not mean that studies of visual communication for these systems are off limits, but rather that one should take these factors into consideration when interpreting the results [see article in this issue by McGregor (2000)]. Video manipulations represent an increasingly important approach to the study of visual stimuli. If designed with the biology of the organism in mind, video playbacks can be used to address an almost limitless range of questions in animal communication.

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