

Technical Restrictions of Computer-Manipulated Visual Stimuli and Display Units for Studying Animal Behaviour

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Abstract

Computer-manipulated visual stimuli are a well-established tool to experimentally study animal behaviour. They provide the opportunity to manipulate single or combined visual stimuli selectively, while other potentially confounding variables remain constant. A wide array of different presentation methods of artificial stimuli has been used in recent research. Furthermore, a wide range of basic hardware and software has been used to conduct experiments. The outcomes of experimental trials using computer-manipulated visual stimuli differed among studies. Failing or contradictory results were mostly discussed in a behavioural and ecological context. However, the results sometimes may be basically flawed due to methodological traps in the experimental design. Based on characteristics and restrictions of technical standards, we discuss which kinds of computer stimuli and visual display units are available today and their suitability for experimental trials when studying animal behaviour. A computer-manipulated stimulus displayed by a certain visual display unit may be accurate to investigate behaviour in a specific species, if various preconditions are met. However, simply due to technical characteristics of the visual display unit, the set-up may be unsuitable for other test species. Thus, future research should critically apply the included technique, with respect to both the intended kind of stimulus and the species under investigation. If these preconditions are met, computer-manipulated stimuli provide a high degree of standardization and the potential to display visual signals without losing a crucial amount of information from the native data.

Introduction

Visual cues are very important as a signalling pathway in many species of the animal kingdom (Darwin 1871; Andersson 1994; Ladich et al. 2006). Behavioural research uses a variety of techniques to examine the role of visual signals, e.g. in social communication. Experimental methods include the presentation of live animals, mirrors, dummies, video recordings and computer animations (Rowland 1999).

Computer-manipulated visual stimuli feature many advantages and are increasingly used in recent research (Table 1). Computer-editing of visual signals provides the opportunity to manipulate single

or combined visual stimuli selectively, while other potentially confounding variables remain constant (e.g. Shashar et al. 2005). In addition, the use of live animals may be greatly reduced by presenting artificial stimuli with a high degree of authenticity. Furthermore, computer systems are easily available at relatively low costs.

Several alternative ways exist to produce and display artificial stimuli. In recent studies, various computer-aided methods were used to construct and present artificial stimuli, e.g. two-dimensional (2D) printouts, frame-by-frame manipulation of video signals and rendering of three-dimensional (3D) models (Table 1). Furthermore, the interface to the

Table 1: Overview of studies using artificial computer stimuli and visual display units as presentation form for non-human animals in alphabetical order grouped by taxon [excluding television as display unit and stimuli played from analogue video recorders, as they are discussed and reviewed by D'Eath (1998) and Rowland (1999)]

| Paper | Species | Context | Stimulus type | Type of display unit (refresh rate) | Discussion whether technical set-up is suitable | Miscellaneous |
|---|--|------------------------------------|---------------------------|-------------------------------------|---|------------------------------------|
| Birds | | | | | | |
| Blough & Blough (1997) and citations within | Pigeons (<i>Columba livia</i>) | Form perception – review | 2D monochrome | Not referenced | References to previous studies | |
| Cook & Katz (1999) | Pigeons (<i>C. livia</i>) | Object perception | 3D monochrome | CRT (not referenced) | References to previous studies | Training of test species |
| Cuthill et al. (2005) | Unspecific avian predators | Disruptive coloration | 2D colours and monochrome | Printout | Within study | Calibration |
| Ghosh et al. (2004) | Pigeons (<i>C. livia</i>) | Object perception | 2D colour images | CRT (not referenced) | No | Training of test species |
| Green et al. (1995) | Pigeons (<i>C. livia</i>) | Game theory | 2D colour still | Not referenced | No | Training of test species |
| Jansson & Enquist (2005) | Chicken (<i>Gallus gallus</i>) | Signal exaggeration | 2D colour | CRT (not referenced) | No | Training of test species |
| Lacourse & Blough (1998) | Pigeons (<i>C. livia</i>) | Prey recognition | 2D monochrome | CRT (not referenced) | No | Training of test species |
| Langley (1996) | Pigeons (<i>C. livia</i>) | Prey recognition | 2D colour images | CRT (not referenced) | Tests within study | Training of test species |
| Otorio et al. (1999) | Chicken (<i>G. gallus</i>) | Colour vision | 3D colour | Printout | Within study | Calibration of stimuli |
| Peissig et al. (2006) | Pigeons (<i>C. livia</i>) | Object perception | 2D monochrome | CRT (not referenced) | No | Training of test species |
| Smith et al. (2005) | European starling (<i>Sturnus vulgaris</i>) | Myoclonus induced by display units | 2D monochrome | CRT (100–150 Hz) vs. LCD | Within study, reference to previous studies | Calibration of stimuli (luminance) |
| Stevens et al. (2006) | Unspecific avian predators | Disruptive contrasts | 2D monochrome | Printout | Within study | Calibration |
| Fish | | | | | | |
| Watanabe & Troje (2006) | Pigeons (<i>C. livia</i>) | Discrimination of stimuli | 3D | Flat screen | Within study, pre-tests | Training of test species |
| Young et al. (1997, 2001) | Pigeons (<i>C. livia</i>) | Object perception | 2D monochrome | CRT (not referenced) | No | Training of test species |
| Bakker et al. (1999) | Three-spined stickleback (<i>Gasterosteus aculeatus</i>) | Sexual selection | 3D colour animation | CRT(120 Hz) | No | |
| Clotfelter et al. (2006) | Siamese fighting fish (<i>Betta splendens</i>) | Sexual selection | 3D colour animation | Flat screen | No | |
| Künzler & Bakker (1998, 2001) | Three-spined stickleback (<i>G. aculeatus</i>) | Sexual selection | 3D colour animation | CRT(120 Hz) | Within study, reference to previous study | |
| Mazzi et al. (2003, 2004) | Three-spined stickleback (<i>G. aculeatus</i>) | Sexual selection | 3D colour animation | CRT(120 Hz) | Within study, reference to previous study | |
| Wong & Rosenthal (2006) | Swordtail fish (<i>Xiphophorus birchmanni</i>) | Sexual selection | 2D monochrome | CRT (not referenced) | Reference to previous study | |
| Mammals | | | | | | |
| Zbinden et al. (2003, 2004) | Three-spined stickleback (<i>G. aculeatus</i>) | Sperm competition | 3D colour animation | CRT(120 Hz) | Reference to previous study | |
| Andrews (1994) | Bonnet macaques (<i>Macaca radiata</i>) | Object perception | 2D monochrome | CRT (not referenced) | Tests within study | Training of test species |
| Bussey et al. (2001) | Mice (transgenic) | Object perception | 2D monochrome | CRT (not referenced) | No | |
| Imura & Tomonaga (2003) | Chimpanzee (<i>Pan troglodytes</i>) | Object perception | 2D and 3D | Printout | No | |
| Langbein et al. (2007) | Dwarf goat (<i>Capra hircus</i>) | Visual discrimination | 2D monochrome | Flat screen | No | |

Table 1: Continued

| | Paper | Species | Context | Stimulus type | Type of display unit (refresh rate) | Discussion whether technical set-up is suitable | Miscellaneous |
|---------------|---------------------------|---|----------------------|---------------|-------------------------------------|---|---|
| Mammals | Leighty & Fragaszy (2003) | Capuchin monkeys (<i>Cebus apella</i>) | Joystick acquisition | 2D monochrome | CRT (not referenced) | No | |
| | Markham et al. (1996) | Rats (<i>Rattus norvegicus</i>) | Method establishment | 2D monochrome | Not referenced | No | Training of test species |
| | Prusky et al. (2000) | Mice and rats (laboratory) | Visual acuity | 2D colour | CRT (not referenced) | Pre-test | Training of test species |
| | Seymour & Juraska (1997) | Mice (laboratory) | Grating acuity | 2D monochrome | Printout | No | Training of test species |
| | Uller (2004) | Chimpanzee (<i>P. troglodytes</i>) | Goal detection | 2D | CRT (not referenced) | Pre-tests | |
| | Washburn & Astur (2003) | Rhesus monkey (<i>Macaca mulatta</i>) | Maze exploration | 3D animation | Not referenced | No | |
| | Witte et al. (1996) | Rhesus monkey (<i>M. mulatta</i>) | Visual orientation | 2D monochrome | CRT (not referenced) | No | Training of test species |
| | Wong & Brown (2005) | Mice (laboratory) | Visual detection | 2D | CRT (not referenced) | Reference to previous study | Training of test species |
| Invertebrates | Giurfa et al. (1997) | Honeybees (<i>Apis mellifera</i>) | Colour vision | 2D colours | Printout | Within study | Training of test species & calibration of stimuli |
| | Harland & Jackson (2002) | Spider (<i>Portia fimbriata</i>) | Prey recognition | 3D animation | Projector | No | Use of lenses and neutral-density filters |
| | Oliva et al. (2007) | Crab (<i>Chasmagnathus granulatus</i>) | Escape behaviour | 2D monochrome | Flat screen | Within study | |
| | Prete et al. (2002) | Praying mantis (<i>Sphodromantis lineola</i>) | Prey recognition | 2D monochrome | Not referenced | Reference to previous study | |
| Amphibia | Schülert & Dicke (2002) | Salamander (<i>Plethodon jordani</i>) | Prey recognition | 2D animation | Flat screen | Pre-tests | |

CRT, cathode-ray tube.

test subjects differed due to the experimental set-up and technical improvements, including paper, flat-screen [liquid crystal display/thin film transistor (LCD/TFT)] and cathode-ray-tube (CRT) televisions and monitors (Table 1).

In some cases, the use of computer-manipulated stimuli in investigating behaviour based on visual signals is limited. The technical design of computer systems is tailored to human vision and does not allow testing certain variables such as UV signals that are not emitted by visual display units (McFarland & Loew 1994; D'Eath 1998; Cuthill et al. 2000; Losey et al. 2000; Shashar et al. 2005; Rick et al. 2006). Other signal pathways such as olfactory or acoustic cues are initially not available, which may not be critical for animals relying entirely on visual cues. However, other species may rely on multimodal cues. In this case, other stimuli can be embedded into an experimental set-up in addition to the visual stimulus presentation (Künzler & Bakker 1998; Mehlis 2008).

In general, computer systems can provide a high degree of standardization and have the potential to display visual signals without losing information from the native data if the preconditions of accurate hardware and signal processing are met. However, many studies have not taken into account the technical limitations of their computer set-up, e.g. due to low awareness of technical problems, thus raising the probability of methodological flaws in the experimental design. Schlupp (2000) noted that the knowledge of technical details of a set-up is very important, but on the one hand basic information is lacking, and on the other hand studies rarely report the technical details of their equipment. While literature – particularly on visual psychophysics – has been dealing with equipment-specific limitations concerning experiments with humans for a long time, still little is known about problems that may occur, if non-human animals are under investigation.

We aim to show in the present paper how material for visual signal investigations must be handled due to the characteristics of data processing in computer systems. However, the vast quantity of different hardware and signal processing does not allow a discussion of every technical aspect. Below, we start by briefly describing the major types of computer-manipulated visual stimuli. The pros and cons of each stimulus type are pointed out, and notable sources of error are annotated. After giving hints how source data should be recorded, we discuss the suitability of different visual display units for experi-

ments based on technical restrictions of the hardware.

Types of Computer-Manipulated Stimuli

Still Photographs

Still photographs or their clippings can be edited using software packages and presented with a suitable visual display unit. They may show an original or manipulated version of the source image, depending on the intended investigation (Watanabe & Troje 2006). Furthermore, photographs can be a very important source of layer material for 2D or 3D animations, as well as a source for backgrounds in video presentations.

The question arises whether a non-moving still photograph is a suitable stimulus for behavioural experiments due to the lack of direct interaction between the test subject and the stimulus. However, a still-photograph presentation within a computer environment is a digital alternative to an analogous slide show, which was used for example in mimicry investigations with blue jays, *Cyanocitta cristata* (Pietrewicz & Kamil 1977; Bond & Kamil 2002). Furthermore, depending on the test species, interaction may be accomplished by installing additionally tools into the set-up, e.g. press buttons for tests with humans or measure specific behaviour, for example pecking in birds.

2D-Animation Sequences

2D animations are moving objects without offering depth cues. Stimuli may be build from clippings of digital photographs or constructed textures, with or without a background, and set in motion by software packages such as 'Adobe Photoshop', 'The GIMP', 'PowerPoint' or 'Paint Shop Pro' (Table 2). 2D animations are built in a relatively short amount of time at moderate costs, while reaching a comparatively high grade of authenticity of the visual signals or standardized manipulations.

Due to the nature of the stimulus, 2D animations are applicable for specific tasks, especially if depth cues are not needed. They can be used as a tool to study fixed body factors, such as preferences for colour signals and their extension, body size or forms. One could question whether a 2D artificial stimulus can be an appropriate experimental method, if the species under investigation is known to perceive stereoscopic visual cues. However, recent studies in humans successfully applied 2D artificial stimuli

Table 2: Web links to referenced software packages (alphabetical order)

| Software | Web link | Short information |
|------------------|---|---|
| 3D Studio Max | http://www.autodesk.com | Constructs and renders 3D objects and animations, commercial |
| Adobe Photoshop | http://www.adobe.com | Editor for images/textures, RGB and CMYK colour space, commercial |
| Blender | http://www.blender.org | Constructs and renders 3D objects and animations, free |
| Final Cut Studio | http://www.apple.com | Video-editing suite, commercial |
| Maya | http://www.autodesk.com | Constructs and renders 3D objects and animations, commercial |
| Paint Shop Pro | http://www.corel.com | Editor for images/textures, RGB colour space, commercial |
| Powerpoint | http://office.microsoft.com | Presentation program, commercial |
| Premiere | http://www.adobe.com | Video-editing suite, commercial |
| TheGIMP | http://www.gimp.org | Editor for images/textures, RGB colour space, free |
| Virtual Dub | http://www.virtualdub.org | Video-editing suite, free |
| VLC | http://www.videolan.org | Movie player with adjustable frame rate, free |

(Sherratt et al. 2004), although humans are able to perceive the third dimension – even from a 2D display – and there is no reason to assume that 2D stimuli cannot be applied in experiments with other animals. Furthermore, in many non-human species it is unknown, whether they have or use any stereoscopic visual cues at all (Zeil 2000).

Depending on the task and the test species, a disadvantage of 2D animations could be a missing interaction between the stimulus and the test subject. For example, while birds may be able to interact with a 2D display by pecking or monkeys by pressing buttons, an interaction between fish and a 2D stimulus may be harder to accomplish. However, for some species this problem may be overcome by training, e.g. three-spined sticklebacks (*Gasterosteus aculeatus*) can learn to bite a stick or swim through a hoop (Sevenster 1968).

Generally, when using 2D- or 3D-animation sequences, it may be necessary to install reference obstacles into the animation's background. For example, stimuli differing in body size may not be perceived as a small and a big stimulus as a consequence of body size – but instead as a result of greater distance (Zbinden et al. 2004). Furthermore, it is very important to consider the frame rate when using animated computer stimuli. Each second of an animation or video consists of a certain number of single frames. For human eyes approx. 15 frames/s are the threshold to perceive a motion picture without gaps in the sequence (judder). For example, many web video codecs use 15 frames/s to compromise about achieving a moving image and saving limited bandwidth, whereas cinematic motion pictures use 24 frames/s to ensure a judder-free sequence. However, the animal's perception may require much higher frame rates (Rowland 1999). The desired frame rate affects the distance in pixels

a 2D object shifts between two frames and must be recalculated, if the frame rate is altered due to missing response of the test subjects. If the chosen frame rate is higher than 24 frames/s, there may be playback-time problems due to the video-player software. Most player's software is programmed to play back 24 frames/s. If an animation of 1 h with 30 frames/s is build, but the software plays back 24 frames, there is a frame overrun of 6 frames \times 60 s \times 60 min = 21 600 frames (15 min at 24 frames). Thus, it is necessary to control the video-codec algorithm for frame adjustment, or use playback software that allows setting up the playback frame rate, for example 'VLC media player'. Instead of the frame rate, the refresh rate of a visual display unit may be more important for certain test species (D'Eath 1998), which will be discussed below.

Digital Video Sequences

Digital video provides all advantages of analogue video stimuli, which have been reviewed in detail by Rowland (1999) and Rosenthal (1999, 2000). An advantage of digital video compared to analogue video is a potentially lossless transfer of source data information into the computer system. The most common manipulation technique is a frame-by-frame alteration of the video by software packages that process digital graphics, e.g. 'Adobe Photoshop' or 'The GIMP' (Table 2). For example, a displaying behaviour can be recorded and the visual signal of interest can be manipulated over the playback time. Furthermore, video material can be used as a source for motion capture to transfer movements to a 3D animation.

Problems with digital video recordings may occur, if the illumination conditions of the source record strongly differ from the final experimental set-up,

thus creating an interfering milieu at the stimulus sides. However, milieu experiments may be the focus of an investigation. It is possible to record a video, cut the background in each frame and overlay the remaining stimulus on an artificial background. In this case, it must be considered that the contrast of the authentic stimulus compared to the backgrounds may be calibrated differently.

3D-Animation Sequences

3D animations are the most complex kind of artificial stimuli, providing the greatest experimental opportunities but at the same time the highest degree of possible errors. There are several software packages, such as 'Autodesk 3D Studio Max', 'Maya' or 'Blender' (Table 2), offering various options to construct 3D objects (Künzler & Bakker 1998; Hokkanen 1999; Shashar et al. 2005). Simulations of behavioural patterns can be created, thereby permitting the control of all parameters within an animation sequence. In addition to 2D animations, depth cues are added to the stimulus. However, the visual display unit (TFT, CRT) still is a 2D device. Thus, the perception of 3D depth cues may be accurate for experiments using humans. However, when studying animals, the use of 3D stimuli depends on how they perceive depth.

3D and 2D animations can be presented in two ways. First, they can be rendered (generate images from a model) and saved like a video sequence. Second, they can be rendered in real-time during the trial. Real-time rendering is the most striking advantage of animations, because it adds the opportunity of direct interaction between the test subject and the stimulus. The observer is able to control subsequent sequences presented to the test subject, depending on its reaction, but with a high risk of observer-biased results. Nonetheless, if 3D animations are rendered in real-time, expensive hardware is needed. Especially the type, amount and characteristics of processors, memory and the graphic board must be aligned to the task.

Recording Source Data

Before the manipulation of a stimulus can be achieved, source data have to be recorded and transferred into the computer system. This can be performed in two ways. First, source data can be achieved using analogue devices, i.e. an analogue photo- or video-camera. When transferred into the computer system, the analogue data are converted

into a digital data format, limited by the hardware. For example, a photograph has to be scanned into the computer. Even if the photograph was taken under standardized conditions, the scan result in the computer depends on the quality of the scanner's chip, which converts the reflection data into the RGB colour space, as well as on the quality of the light source, the optical resolution and the degree of artificial interpolation of pixels to achieve higher resolutions. This implies a loss of vital criteria of the original image, especially concerning colour information.

The capture of analogue video data is subject to similar problems. After recording, video images can be transferred to the computer system by TV-in adaptors and specialized software packages such as 'Adobe Premiere', 'Final Cut Studio' or 'Virtual Dub' (Table 2). The results of the hardware/software frame grabber, which works as an analogue-digital transducer, depends on the kind of playing device, the connection cable, the chip on the grabbing device and the compression format of the software. In summary, there exists no standardized method to transfer analogue data into a computer, which results in an unpredictable loss of the source-data authenticity. If there exist no alternative to source data from analogue devices, the stimuli must be (if possible) calibrated and intensely pre-tested with the species under investigation.

Second, original data can be taken by digital devices, i.e. digital photo- and video-cameras. The common standards are Charged-Coupled Device (CCD) Sensors to convert photons into an electric charge, which have quantum efficiency (sensitivity) up to 90% of the photons hitting the photoreactive surface. If the prerequisite of standardized conditions is met, the data can be transferred to the computer without the loss of information of the source image. However, there are premises the hardware needs to comply with.

The characteristics of a camera chip should be known. Currently, two major sensor types of CCD chips exist, differing in their absorption modes. In one-way CCD chips, every light-sensitive cell captures wavelengths for only one channel of red (R), green (G) or blue (B). The definite colour is interpolated with informations of the neighbour cells, thereby saving an approximated image instead of real colours. In three-way CCD chips, incoming light is broken by filters and sent to three separate chips, each responding to a particular colour of the RGB spectrum. Thus, the truest recording of RGB data from a location can be accomplished. However, both

sensor types reduce a continuous spectrum to three data points, R, G and B. The image quality, e.g. concerning coloration information, depends upon each individual sensor chip, varying from one production line to the next. If appropriate calibration data are collected, these RGB data can be used to reconstruct the true colour (Stevens et al. 2007), as perceived by humans or – under some assumptions – by some animals.

A digital camera should meet further prerequisites, for example concerning the data-saving format. Stevens et al. (2007) gave detailed information on essential features of digital cameras, for example, the necessity for manual white balancing, and how digital images should be taken and stored without compression losses. Concerning white balancing, it is necessary to understand from a technical point of view, why manual white balance is essential for digital photography in science as described in Stevens et al. (2007). The human brain is able to reference a white point in many illumination conditions due to chromatic adaptation. However, a digital camera's sensor chip needs to be balanced to a white point, thus adjusting the relative amount of every RGB channel within the spectrum of the current illumination condition. First, a digital camera may be white balanced manually by referring to a white area within the scene before taking pictures. Second, white reference standards, for example, a white piece of paper or a colour palette may be installed into a scene, and the white point can be referenced to it by the editing software. Third, if RAW images are taken, the white balancing can be accomplished during the import of the data to the computer system.

When editing or saving video data, it is necessary to avoid video-compression algorithms in which data are lost, so-called lossy compression. Most compression algorithms are designed to reduce the quantity of data of video images, which results in a loss of vital information from the source data. Some video-compression algorithms exist, such as 'H.264/MPEG-4 AVC' or 'Huffyuv', which perfectly match with the source data when the video is decompressed during playback.

The loss of source data authenticity while recording with RGB devices may be greatly reduced when taking into account the technical issues discussed above. However, the RGB colour space, which is optimized for the perception of the human cone classes, may not be accurate in all species (Cuthill et al. 2000; Fleishman & Endler 2000). The physiological attributes of an animal's eye may differ from

the human retina, i.e. due to a different number of cone receptors, or if the absorption maxima of the cones are shifted (Oliveira et al. 2000). Thus, in non-human species, the perception of coloration recorded with RGB devices may be different from the perception of the real object. In this case, the recording of source data needs to become more complex by embedding calibration techniques. Depending on the species characteristics and the task, a calibration of a recording RGB device could be carried out by utilizing optical filters and constant light sources, where each filter may represent the optimum perception range of a single cone class of a species (Parraga et al. 2002). The final picture is composed by a combination of the single photographs.

In general, when recording source data, it is necessary to standardize the parameters of the recording conditions. The illumination must be well considered to avoid the recording of wrong colour information. If in an experimental set-up the illumination strongly differs from the condition of the recording situation, a sufficient identification of the artificial stimulus may not be given due to wrong colours and contrasts. Furthermore, the background of a stimulus needs to satisfy various criteria depending on the task. It may be necessary to calibrate the background lighting to ensure an adequate figure-ground separation, for example, by calibrating the relative contrast between a stimulus and its background (e.g. Osorio et al. 1999; Rosenthal 2000; Cuthill et al. 2005; Stevens et al. 2006). Further distractions that are unrelated to the stimulus, for example, unintentionally recorded movements on video sequences, must be avoided.

Suitability of Visual Displays

Printouts

Digital photographs or single video frames may be printed out after manipulation and used as a stimulus during trials, i.e. as a still photograph or as skin patterns for dummies. Furthermore, Berggren & Merilä (2004) suggested that estimation of animal coloration can be accomplished with printouts from HTML colour charts. In contrast, Stevens & Cuthill (2005) measured different choice behaviour of individuals for the same RGB colours, and argued that RGB-based colour charts are not suitable for colour estimation due to differences in printer models and their quality/toner levels, as well as illumination dependencies.

Moreover, printouts are basically flawed due to different colour management of computer displays and printers. A computer display (CRT or flat screen) emits photons using the RGB colour space. The colour is an additive result of every single channel (red + green + blue). Thus, white will be perceived if all channels have the maximum value of 255, while black is a zero value of all channels. In contrast, printers do not use RGB cartridges to produce a specific colour. Instead, they use the CMYK colour space (cyan/magenta/yellow/key=black). Printers need to merge colours subtractive from white to produce a certain value. When pictures or charts are printed out, the software driver of the specific printer interprets the RGB values from the computer and translates them into CMYK space. Every printer manufacturer, even a different driver version of the same printer model, has its own translation of the RGB-to-CMYK colour space, resulting in great differences between printouts of the same picture.

Only few software packages exist, which allow previewing and editing in CMYK space, such as 'Adobe Photoshop'. However, the software must calculate the CMYK values from the original RGB space, which distorts the original colour informations of the recorded data. Besides the RGB-CMYK problem, another error source of original colour information is based on the print media. The reflectance of the same picture printed on photo paper or normal print paper is rather different. Thus, the kind of print media must be well considered depending on the experimental environment, for example, photo paper may be more conspicuous to predators due to its high reflectance, even at night.

In spite of all problems that printouts imply, they may be the best option to present artificial computer stimuli for certain research questions. Printouts are physical objects that provide the opportunity of shaping, e.g. into 3D objects, and of physical interaction between the stimulus and the test subject. Even in non-human species, this may offer advantages, for example in more rapid learning (Osorio et al. 1999, 2001). Furthermore, printouts reflect colorations under (natural) illumination conditions of the overall set-up, whereas self-illuminated visual display units may be a disturbing source of luminance within the set-up. In the field, it is often impossible to use visual display units that require electricity, thus making printouts the only alternative if computer-manipulated stimuli should be applied (Cuthill et al. 2005).

A mandatory precondition prior to the use of printouts is a proper calibration (1) of the input

device depending on the species under investigation, e.g. the digital camera (Stevens et al. 2007), and (2) between the RGB and CMYK colour spaces. One possibility to minimize the differences between the source data taken by an RGB device and the printout in CMYK colour space is the use of ICC profiles, which are standardized by the International Color Consortium (ICC 2004). To create an ICC profile, the reflectance values of source data must be measured by a spectrometer, and compared to the RGB or CMYK values generated or displayed by a hardware component (e.g. printer and flat-screen monitor, respectively). Thus, the differences between the RGB and CMYK devices can be linked and approximately regulated. Some manufacturers provide an ICC profile for their hardware component, but it may be necessary to control the manufacturer's measurements. Sharma (2006) gives an example, how the quality of an ICC profile can be measured. Additionally, stimuli should be checked via spectrophotometry by comparing the readings from nature and the stimulus, or comparing relative contrasts between stimuli (Cuthill et al. 2005; Stevens et al. 2006).

However, it is necessary to keep in mind that printouts, even when properly calibrated, do not precisely reproduce the natural coloration. Furthermore, the ICC profile just bridges differences between devices and colour spaces (RGB, CMYK), which are primarily designed for human perception. The visual perception of non-human animals may require other species-specific calibration methods, which have been discussed in recent research. (D'Eath 1998; Fleishman et al. 1998; Cuthill et al. 2000; Fleishman & Endler 2000).

Televisions

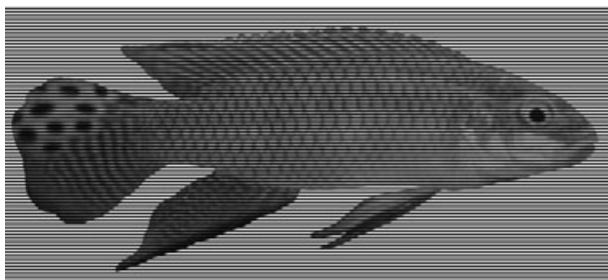
Televisions were intensely used as a visual display in association with video stimuli. One would suggest that colour television, for which the RGB colour space was initially invented, should smoothly guarantee the playback of RGB data. However, there is a strong difference between a computer and a television concerning the RGB-transmission signal.

While the computer RGB colour space is an addition of each channel, the television RGB signal transmits colour information as a subtraction from a black/white source image, due to compatibility issues to colourless TV and the saving of limited frequency bandwidth. While transferring manipulated data from a computer to a television playback device, the recorder modulates the additive RGB

colour to the subtractive signal, resulting in an error source of colour information and contrast. The loss of signal quality differs among the recording standards and the connection cable. Antennae cables transmit brightness and colour signals on a single high-frequency carrier, provoking the highest loss of signal quality. A Scart-connection is the best way to transmit television RGB signals, because it is designed with three wires destined for each colour channel. In general, it is unnecessary to re-record a computer-manipulated video to another device, because video can be played at a computer without losing signal information.

A general problem of television is the display of half-images, so-called interlacing. Single frames, e.g. each frame of 25 frames/s in a Phase Alternating Line (PAL) standard, are not written fully on the screen. Instead, 25 half-frames are displayed showing odd line numbers of an image alternating with 25 half-frames that consist of even lines (Fig. 1). The half-images delay for a certain time, thus creating the impression of a full-frame for the human eye, but the picture may be disturbing for non-human species. Flat-screen television supports the output of full-frames, so-called progressive pictures (Fig. 1). However, flat-screen televisions imply the same disadvantages as we will discuss for computer flat-screen monitors below.

Interlaced



Progressive



Fig. 1: A television display of a single frame of a fish (*Pelvicachromis taeniatus*), so-called interlaced picture, and the output of a full-frame of the same image, so-called progressive picture, e.g. by a flat screen.

Rowland (1999) discussed further disadvantages of the television in detail, and D'Eath (1998) referred to television standards, e.g. concerning National Television System Committee (American standard) and PAL (European standard), their frame rates and the CFF (critical flicker-fusion frequency).

Flat-Screen Monitors

Flat-screen monitors, i.e. LCD/TFT, organic light-emitting diodes (LED) or plasma displays are common today. In some studies, they were already used as visual display units during trials (Clotfelter et al. 2006; Swaddle et al. 2006). Like CRT monitors, they display colours in RGB mode. A striking advantage of flat-screen displays compared to CRTs is a flicker-free screen due to independency from refresh rates.

However, the assumed improvement comes along with a lot of technical disadvantages, especially if animated stimuli are presented. The most critical source of malfunction in experiments is the transition time of the light-emitting matrix. Each liquid crystal of the matrix needs a specific time frame to reach its initial point after being activated (transition time), thereby blurring moving objects on displays with high transition times. Until 2005, there was no official standard that bound manufacturers to measure the transition time of their displays. Thus, the technical features of flat-screen displays before 2005, i.e. transition time in milliseconds, are (1) not standardized, (2) not comparable among each other and (3) not comparable to recent standards.

Since May 2005 the Video Electronics Standards Association (VESA), an international non-profit corporation that sets industry-wide interface standards for the PC, standardized the measurements of a flat-screen display's transition time. It is quantified as time in milliseconds the display needs to change its brightness from 10% to 90% grey-to-grey (0% = black, 100% = white), excluding transition times concerning colours (VESA 2005). Modern displays take >1 ms within this grey-to-grey interval, while older display models take much longer time, including many displays with (not standardized) intervals >30 ms, which is the motion blur threshold for the human eye. However, until now the transition time from 0% (black) to 100% (white) has not been standardized, because it is not critical for the human eye. However, it may be critical in other species. This results in a still unknown time frame between full white and black. Usually, modern high-quality flat-screen displays are suitable for moving and non-moving computer-manipulated stimuli, if

humans are under investigation. However, the flat-screen display may become a severe problem for other test species if moving stimuli should be presented due to motion blur, or if the response of a test subject to luminance components of a stimulus should be investigated.

Another major problem is a test subject's perception of a colour when using a flat-screen display. The colour value varies depending on the viewing angle of the observer. No standard exists so far, which quantifies colour changes due to the viewing angle. A test subject may therefore view an artificial stimulus in a multitude of accidental colours, instead of the intended colorations. Some manufactures use foils to compensate problems with viewing angle and missing contrasts. However, these foils strongly alter the reflection of a display, thereby creating a mirror for the test subject. If humans are under investigation and a non-moving stimulus should be presented, the optimal viewing angle of a certain display model can be measured to standardize the distance and angle between the display and eyes in respect to body size. For non-human species, the standardization of the viewing angle of the same type of stimulus may be harder to accomplish. Some species could be trained to visit certain spots inside an arena that keep an optimal angle between the test subject and the display, such as it was performed with European starlings, *Sturnus vulgaris* (Smith et al. 2005). However, for other species such as fish, it may be impossible to standardize their distance and angle to the flat screen display within the set-up.

Cathode-Ray Tubes

CRT monitors have been used in many studies as visual interface for the test subjects (Künzler & Bakker 1998, 2001; Mazzi et al. 2003; Turnell et al. 2003; Zbinden et al. 2003; Wong & Rosenthal 2006). Like a flat-screen display, they are connected to a computer by a VGA (Video Graphics Array) cable, and colours are displayed in RGB mode. Additionally, the CRT monitor has the ability to compensate many disadvantages of flat-screen monitors. For each colour channel of the RGB spectrum, a fluorescence molecule (phosphor) is activated by an electron beam. In high-quality models, the inactive phosphors remain black, thereby offering full contrast between black and white. Furthermore, colours are not depending on the view angle of a test subject.

CRTs are criticized for their refresh rates, possibly resulting in a flickering image to the test subject (D'Eath 1998). The refresh rate is defined as the

time a CRT display needs to control its electron beam along a horizontal line (in Hertz). Flicker is perceived by the human eye, if the electron beam requires a too long time to pass the distance. Although human eyes already perceive non-flickering images at 72–80 Hz, recent CRT displays feature refresh rates of 140 Hz. For example, during a 3D computer animation with a frame rate of 20 single frames per second, each frame is refreshed approximately seven times by the CRT, before the next frame is displayed. Between each refresh interval of the frame, the phosphors do not emit photons.

Following the above example, a CRT needs approx. 3 ms to switch between a 100% black and photon radiation of the whole RGB colour spectrum, which is a predictable, much faster rate than the transition time of flat screens within their 10–90% grey-to-grey interval. Thus, even if flicker may be perceived by a species in spite of high refresh rates at 140 Hz, the pros may outweigh the cons.

However, there are some technical restrictions that must be considered when using CRT displays. The refresh rate of a CRT display decreases with a higher monitor resolution, because the horizontal space extends. For example, a CRT capable of 100 Hz maximum at 1024 horizontal pixels needs more time to refresh 1280 pixels. This implicates that the final resolution combined to the refresh rate in experiments must be considered. In addition, a higher resolution means more pixels at the same expanse of the monitor's projection area. Thus, a picture-clipping with a width of 100 pixels appears much shorter, if it is displayed in higher resolution. Especially, if the size of artificial stimuli is critical, for example, when testing size-assortative mating, the resolution of a display may be more important.

CRT displays use a magnetic field to control the electron beam. In species that perceive magnetic fields its use may be critical. Alternatively, depending on the stimulus and the test species, flat-screen monitors or video projectors complying with certain technical prerequisites can be used to avoid this problem. The limitation of the display size may also be compensated by projectors, if large species are the object of study.

Even if two monitors of the same model are connected to a graphic board with the same refresh rates and resolution, there may be a different display of colours, brightness and contrast. Each CRT display allows different settings in its set-up menu. It is necessary to match the settings of both displays equally.

Images that look excellent on visual display units to humans could be unrecognizable to non-human

animals due to different perception of colour, luminance or motion. Concerning the problem of colour reproduction for non-human animals on CRTs, it is possible to calibrate the phosphor intensities in a ratio as they would be perceived by the test species under natural conditions (Fleishman et al. 1998). This requires intense knowledge of the characteristics of both the test species and the display model (Fleishman & Endler 2000).

Video Projectors

Video projectors are capable of displaying visual data at large areas. Particularly with regard to larger species, or if a CRT's magnetic field could influence an experiment, they may be a suitable alternative to CRT monitors. Projectors strongly differ between models due to a variety of criteria. The most important difference is the projection method (CRT/LCD/LED/DLP). LCD- and LED-based models contain the same problems as flat-screen monitors, regarding motion blur and coloration errors. The most capable projectors are based on CRT and Digital Light Processing (DLP) technology, but there are some restrictions. The CRT projector is stationary because of its dimensions, thus making it difficult to be integrated in an experimental set-up. DLP technology appears in three versions, with one to three light valves, which strongly differ in the output quality of the projector. The most common problem of DLP projectors with one or two valves is a visible 'rainbow effect' of the colours, because the single chip must handle all channels of the RGB spectrum. Thus, visual signals are tampered. Projector models with three valves do not have this problem, because every valve is responsible for a single channel of the RGB spectrum. Furthermore, the background of the projection area must be premeditated, if video projectors are used. The quality and authenticity of the visual information differs depending on the colour, smoothness, reflectance and basic illumination of the background.

Conclusions

The number of different types of computer-manipulated stimuli, the vast quantity of hard- and software, and the number of species and their different physiologies do not allow to give clear recommendations, which technique should be used for which kind of task – and in which combination. However, there are basic steps, which future researchers should critically apply when using

computer-manipulated stimuli (Table 3). First, in many cases, the task limits the scope of available types of stimuli and their display method, e.g. working in the field with physical 3D objects would suggest (calibrated) printouts as display device. In a second step, the knowledge of a species' visual system and its physiology should be taken into account. This may offer valuable information which kind of equipment may be suitable for the experimental set-up. For example, bird species with a high visual time resolution may be critical when using a signal displayed by a CRT due to flicker, whereas fish may be disturbed by a flat screen due to unpredictable change of colours caused by non-standardized viewing angle. Third, if the physiology of vision in a species is known, the recording of source data, manipulation and presentation must be optimally calibrated. Methods of calibration may strongly differ depending on how species perceive visual cues. However, the physiology of a species' visual system may be unknown. In each case, it is necessary to pre-test the species with the intended set-up and its hard/software.

Generally, many questions arise when artificial stimuli are designed. How can original data be gained under standardized conditions? What are the technical restrictions of the record devices? How is the signal transferred to the computer and handled by the software? Which kind of visual interface is suitable in experiments? However, the most important concern in all processing steps should be what the test subject will finally perceive. The signal processing in the computer system must therefore be understood in order to avoid the loss of authentic data due to losses in the handling and technical set-up.

Regardless of the final method of presentation, computer-manipulated visual stimuli have one thing in common: as soon as their source data are transferred to the computer, they are displayed by an RGB device. Thus, the handling of visual signals in computer environments restricts the options, how a computer-manipulated stimulus must be recorded truly to the original, calibrated, manipulated and finally presented. In all steps, the hardware must be accurate, depending on the perception of the species under investigation, the task and the intended kind of artificial stimulus. Future technology may be able to solve some issues discussed in this paper, e.g. optimizing the viewing angle problems within flat-screen displays. However, future research must critically apply pros and cons of new technologies in experimental set-ups from a technical point of view

Table 3: Comparative overview of visual display units and their technical features

| | Flat screen | CRT | Projector | Television | Printout |
|--|--------------------|--------------------|--------------------|-------------------|-------------------|
| Electricity required | Yes | Yes | Yes | Yes | No |
| Stimuli as physical 3D objects | No | No | No | No | Yes |
| Environmental illumination | No | No | No | No | Yes |
| Unnatural light source | Yes | Yes | Yes | Yes | No |
| Display large objects | No | No | Yes | No | No |
| Flicker ¹ | No | Yes | No | Yes | No |
| Frame display ² | Progressive (full) | Progressive (full) | Progressive (full) | Interlaced (half) | Static |
| Viewing angle problems ³ | Yes | No | Yes ^{3a} | No | Yes ^{3b} |
| Blurred stimuli ⁴ | Yes | No | No ^{4a} | No | No |
| Reflectance/mirrors ⁵ | Yes ^{5a} | No | Yes ^{5b} | No | Yes ^{5c} |
| Magnetic fields ⁶ | No | Yes | No | Yes | No |
| Loss of signal quality ⁷ | No | No | No | Yes | – |
| Colour space ⁸ | RGB | RGB | RGB | Subtractive RGB | CMYK |
| Standardized black–white interval ⁹ | No | Yes | Yes ^{9a} | Yes | Yes |
| Rainbow effects ¹⁰ | No | No | Yes ^{10a} | No | No |

CRT, cathode-ray tube.

¹Flicker-free perception in humans at ~75 Hz and above, not critical in animal species with low critical flicker fusion, but some animals may require higher refresh rates (see D'Eath 1998), problematic in species with high critical flicker fusion (e.g. birds, honeybees).

²Not critical for the human eye, may be disturbing for animal species with high visual time resolution (e.g. birds).

³Critical in all species, can distort the perception of coloration and contrasts, especially if a standardized viewing angle is not applicable (^aprojectors: depending on the background; ^bprintouts: depending on the print media).

⁴Critical in all species (^aprojectors: blurring problematic with LCD/TFT models).

⁵Critical in all species (^aflat screen: depending on foils installed by the manufacturer; ^bprojectors: depending on the background; ^cprintouts: depending on the print media).

⁶Critical if magnetic fields are recognized by the test species (e.g. birds).

⁷Critical in all species, television signals lose quality strongly depending on their connection standard.

⁸Critical in all species, different colour spaces distort colour information.

⁹Critical in all species (^aprojectors: LCD/TFT models not standardized).

¹⁰Critical in all species (^aprojectors: in single valve DLP models only).

and their consequences for the perception in test species, especially non-human animals.

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Literature Cited

Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton.

Andrews, M. W. 1994: An automated identification system for use with computer-controlled tasks. *Behav. Res. Methods Instrum. Comput.* **26**, 32–34.

Bakker, T. C. M., Künzler, R. & Mazzi, D. 1999: Condition-related mate choice in sticklebacks. *Nature* **401**, 234.

Berggren, A. & Merilä, J. 2004: WWW design code – a new tool for colour estimation in animal studies. *Front. Zool.* **1**: 2.

Blough, D. S. & Blough, P. M. 1997: Form perception and attention in pigeons. *Animal Learning and Behaviour* **25**, 1–20.

Bond, A. B. & Kamil, A. C. 2002: Visual predators select for crypticity and polymorphism in virtual prey. *Nature* **415**, 609–613.

Bussey, T. J., Saksida, L. M. & Rothblat, L. A. 2001: Discrimination of computer-graphic stimuli by mice: a method for the behavioral characterization of transgenic and gene-knockout models. *Behav. Neurosci.* **115**, 957–960.

Clotfelter, E. D., Curren, L. J. & Murphy, C. E. 2006: Mate choice and spawning success in the fighting fish *Betta splendens*: the importance of body size, display behavior and nest size. *Ethology* **112**, 1170–1178.

Cook, R. G. & Katz, J. S. 1999: Dynamic object perception by pigeons. *J. Exp. Psychol. Anim. Behav. Process.* **25**, 194–210.

Cuthill, I. C., Hart, N. S., Partridge, J. C., Bennett, A. T. D., Hunt, S. & Church, S. C. 2000: Avian colour vision and avian video playback experiments. *Acta Ethol.* **3**, 29–37.

- Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, C. A. & Troscianko, T. S. 2005: Disruptive coloration and background pattern matching. *Nature* **434**, 72–74.
- D'Eath, R. B. 1998: Can video images imitate real stimuli in animal behaviour experiments? *Biol. Rev.* **73**, 267–292.
- Darwin, C. 1871: *On the Descent of Man and Selection in Relation to Sex*. John Murray, London.
- Fleishman, L. J. & Endler, J. A. 2000: Some comments on visual perception and the use of video playback in animal behavior studies. *Acta Ethol.* **3**, 15–27.
- Fleishman, L. J., McClintock, W. J., D'Eath, R. B., Brainard, D. H. & Endler, J. A. 1998: Colour perception and the use of video playback experiments in animal behaviour. *Anim. Behav.* **56**, 1035–1040.
- Ghosh, N., Lea, S. E. G. & Noury, M. 2004: Transfer to intermediate forms following concept discrimination by pigeons: chimeras and morphs. *J. Exp. Anal. Behav.* **82**, 125–141.
- Giurfa, M., Vorobyev, M., Brandt, R., Posner, B. & Menzel, R. 1997: Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **180**, 235–243.
- Green, L., Price, P. C. & Hamburger, M. E. 1995: Prisoners-dilemma and the pigeon - control by immediate consequences. *J. Exp. Anal. Behav.* **64**, 1–17.
- Harland, D. P. & Jackson, R. R. 2002: Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. *J. Exp. Biol.* **205**, 1861–1868.
- Hokkanen, J. E. I. 1999: Visual simulations, artificial animals and virtual ecosystems. *J. Exp. Biol.* **202**, 3477–3484.
- ICC. 2004: Specification ICC. Available at: <http://www.color.org>. Last accessed: 18th January 2008.
- Imura, T. & Tomonaga, M. 2003: Perception of depth from shading in infant chimpanzees (*Pan troglodytes*). *Anim. Cogn.* **6**, 253–258.
- Jansson, L. & Enquist, M. 2005: Testing the receiver bias hypothesis empirically with 'virtual evolution'. *Anim. Behav.* **70**, 865–875.
- Künzler, R. & Bakker, T. C. M. 1998: Computer animations as a tool in the study of mating preferences. *Behaviour* **135**, 1137–1159.
- Künzler, R. & Bakker, T. C. M. 2001: Female preference for single and combined traits in computer animated stickleback males. *Behav. Ecol.* **12**, 681–685.
- Lacourse, D. M. & Blough, D. S. 1998: Effects of discriminability, probability of reinforcement, and handling cost on visual search and prey choice. *Anim. Learn. Behav.* **26**, 290–298.
- Ladich, F., Collin, S. P., Moller, P. & Kapoor, B. G. (eds) 2006: *Communication in Fishes*. Science Publishers, Enfield, NH, USA.
- Langbein, J., Siebert, K., Nurnberg, G. & Manteuffel, G. 2007: Learning to learn during visual discrimination in group housed dwarf goats (*Capra hircus*). *J. Comp. Psychol.* **121**, 447–456.
- Langley, C. M. 1996: Search images: selective attention to specific visual features of prey. *J. Exp. Psychol. Anim. Behav. Process.* **22**, 152–163.
- Leighty, K. A. & Fragaszy, D. M. 2003: Joystick acquisition in tufted capuchins (*Cebus apella*). *Anim. Cogn.* **6**, 141–148.
- Losey, G. S., Nelson, P. A. & Zamzow, J. P. 2000: Ontogeny of spectral transmission in the eye of the tropical damselfish, *Dascyllus albisella* (Pomacentridae), and possible effects on UV vision. *Environ. Biol. Fishes* **59**, 21–28.
- Markham, M. R., Butt, A. E. & Dougher, M. J. 1996: A computer touch-screen apparatus for training visual discriminations in rats. *J. Exp. Anal. Behav.* **65**, 173–182.
- Mazzi, D., Künzler, R. & Bakker, T. C. M. 2003: Female preference for symmetry in computer-animated three-spined sticklebacks, *Gasterosteus aculeatus*. *Behav. Ecol. Sociobiol.* **54**, 156–161.
- Mazzi, D., Künzler, R., Largiadèr, C. R. & Bakker, T. C. M. 2004: Inbreeding affects female preference for symmetry in computer-animated sticklebacks. *Behav. Genet.* **34**, 417–424.
- McFarland, W. N. & Loew, E. R. 1994: Ultraviolet visual pigments in marine fishes of the family Pomacentridae. *Vision Res.* **34**, 1393–1396.
- Mehlis, M. 2007: Der einfluss von verwandtschaft auf das fortpflanzungsverhalten beim dreistachligen stichling (*Gasterosteus aculeatus*). MSc thesis, Univ. of Bonn, Germany, Bonn.
- Mehlis, M., Bakker, T. C. M. & Frommen, J. G. 2008: Smells like sib spirit: kin recognition in three-spined sticklebacks (*Gasterosteus aculeatus*) is mediated by olfactory cues. *Anim. Cogn.* [Doi 10.1007/s10071-008-0154-3](https://doi.org/10.1007/s10071-008-0154-3).
- Meier, M., Reinermann, R., Warlich, J. & Manteuffel, G. 1998: An automated training device for pattern discrimination learning of group-housed gerbils. *Physiol. Behav.* **63**, 497–498.
- Oliva, D., Medan, V. & Tomsic, D. 2007: Escape behaviour and neuronal responses to looming stimuli in the crab *Chasmagnathus granulatus* (Decapoda : Grapsidae). *Journal of Experimental Biology.* **210**, 865–880.
- Oliveira, R. F., Rosenthal, G. G., Schlupp, I., McGregor, P. K., Cuthill, I. C., Endler, J. A., Fleishman, L. J., Zeil, J., Barata, E., Burford, F., Gonçalves, D., Haley, M., Jakobsson, S., Jennions, M. D., Körner, K. E., Lindström, L., Peake, T., Pilastro, A., Pope, D. S., Roberts, S. G. B.,

- Rowe, C., Smith, J. & Waas, J. R. 2000: Considerations on the use of video playbacks as visual stimuli: the Lisbon workshop consensus. *Acta Ethol.* **3**, 61—65.
- Osorio, D., Vorobyev, M. & Jones, C. D. 1999: Color vision of domestic chicks. *J. Exp. Biol.* **202**, 2951—2959.
- Osorio, D., Miklósi, A. & Gonda, Z. 2001: Visual ecology and perception of coloration patterns by domestic chicks. *Evol. Ecol.* **13**, 673—689.
- Parraga, C. A., Troscianko, T. & Tolhurst, D. J. 2002: Spatiochromatic properties of natural images and human vision. *Curr. Biol.* **12**, 483—487.
- Peissig, J. J., Kirkpatrick, K., Young, M. E., Wasserman, E. A. & Biederman, I. 2006: Effects of varying stimulus size on object recognition in pigeons. *J. Exp. Psychol. Anim. Behav. Process.* **32**, 419—430.
- Pietrewicz, A. T. & Kamil, A. C. 1977: Visual detection of cryptic prey by Blue Jays (*Cyanocitta cristata*). *Science* **195**, 580—582.
- Prete, F. R., Hurd, L. E., Branstrator, D. & Johnson, A. 2002: Responses to computer-generated visual stimuli by the male praying mantis, *Sphodromantis lineola* (Burmeister). *Anim. Behav.* **63**, 503—510.
- Prusky, G. T., West, P. W. R. & Douglas, R. M. 2000: Behavioral assessment of visual acuity in mice and rats. *Vision Res.* **40**, 2201—2209.
- Rick, I. P., Modarressie, R. & Bakker, T. C. M. 2006: UV-wavelengths affect female mate choice in three-spined sticklebacks. *Anim. Behav.* **71**, 307—313.
- Rosenthal, G. G. 1999: Using video playback to study sexual communication. *Environ. Biol. Fishes* **56**, 307—316.
- Rosenthal, G. G. 2000: Design considerations and techniques for constructing video stimuli. *Acta Ethol.* **3**, 49—54.
- Rowland, W. J. 1999: Studying visual cues in fish behavior: a review of ethological techniques. *Environ. Biol. Fishes* **56**, 285—305.
- Schlupp, I. 2000: Are there lessons from negative results in studies using video playback? *Acta Ethol.* **3**, 9—13.
- Schülert, N. & Dicke, U. 2002: The effect of stimulus features on the visual orienting behaviour of the salamander *Plethodon jordani*. *J. Exp. Biol.* **205**, 241—251.
- Sevenster, P. 1968: Motivation and learning in sticklebacks. In: *The Central Nervous System and Fish Behavior* (Ingle, D., ed.). Univ. of Chicago Press, Chicago, pp. 233—245.
- Seymour, P. & Juraska, J. M. 1997: Vernier and grating acuity in adult hooded rats: the influence of sex. *Behav. Neurosci.* **111**, 792—800.
- Sharma, A. 2006: Methodology for evaluating the quality of ICC profiles - Scanner, monitor, and printer. *J. Imaging Sci. Technol.* **50**, 469—480.
- Shashar, N., Rosenthal, G. G., Caras, T., Manor, S. & Katzir, G. 2005: Species recognition in the blackbordered damselfish *Dascyllus marginatus* (Ruppell): an evaluation of computer-animated playback techniques. *J. Exp. Mar. Biol. Ecol.* **318**, 111—118.
- Sherratt, T. N., Rashed, A. & Beatty, C. D. 2004: The evolution of locomotory behavior in profitable and unprofitable simulated prey. *Oecologia* **138**, 143—150.
- Smith, E. L., Evans, J. E. & Parraga, C. A. 2005: Myoclonus induced by cathode ray tube screens and low-frequency lighting in the European starling (*Sturnus vulgaris*). *Vet. Rec.* **157**, 148—150.
- Stevens, M. & Cuthill, I. 2005: The unsuitability of html-based colour charts for estimating animal colours - a comment on Berggren and Merila (2004). *Front. Zool.* **2**: 14.
- Stevens, M., Cuthill, I. C., Windsor, A. M. M. & Walker, H. J. 2006: Disruptive contrast in animal camouflage. *Proc. R. Soc. Lond. B Biol. Sci.* **273**, 2433—2438.
- Stevens, M., Parraga, C. A., Cuthill, I. C., Partridge, J. C. & Troscianko, T. S. 2007: Using digital photography to study animal coloration. *Biol. J. Linn. Soc. Lond.* **90**, 211—237.
- Swaddle, J. P., McBride, L. & Malhotra, S. 2006: Female zebra finches prefer unfamiliar males but not when watching noninteractive video. *Anim. Behav.* **72**, 161—167.
- Turnell, E. R., Mann, K. D., Rosenthal, G. G. & Gerlach, G. 2003: Mate choice in zebrafish (*Danio rerio*) analyzed with video-stimulus techniques. *Biol. Bull.* **205**, 225—226.
- Uller, C. 2004: Disposition to recognize goals in infant chimpanzees. *Anim. Cogn.* **7**, 154—161.
- VESA. 2005: Flat Panel Display Measurements Standard. Available at: <http://www.vesa.org>. Last accessed 5th December 2007.
- Washburn, D. A. & Astur, R. S. 2003: Exploration of virtual mazes by rhesus monkeys (*Macaca mulatta*). *Anim. Cogn.* **6**, 161—168.
- Watanabe, S. & Troje, N. F. 2006: Towards a “virtual pigeon”: a new technique for investigating avian social perception. *Anim. Cogn.* **9**, 271—279.
- Witte, E. A., Villareal, M. & Marrocco, R. T. 1996: Visual orienting and altering in rhesus monkeys: Comparison with humans. *Behavioural Brain Research.* **82**, 103—112.
- Wong, A. A. & Brown, R. E. 2005: Visual detection, pattern discrimination and visual acuity in 14 strains of mice. *Genes Brain Behav.* **5**, 389—403.
- Wong, B. B. M. & Rosenthal, G. G. 2006: Female disdain for swords in a swordtail fish. *Am. Nat.* **167**, 136—140.
- Young, M. E., Wasserman, E. A. & Garner, K. L. 1997: Effects of number of items on the pigeon's discrimination of same from different visual displays. *J. Exp. Psychol. Anim. Behav. Process.* **23**, 491—501.
- Young, M. E., Peissig, J. J., Wasserman, E. A. & Biederman, I. 2001: Discrimination of geons by pigeons: the

- effects of variations in surface depiction. *Anim. Learn. Behav.* **29**, 97—106.
- Zbinden, M., Mazzi, D., Künzler, R., Largiadèr, C. R. & Bakker, T. C. M. 2003: Courting virtual rivals increase ejaculate size in sticklebacks (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.* **54**, 205—209.
- Zbinden, M., Largiadèr, C. R. & Bakker, T. C. M. 2004: Body size of virtual rivals affects ejaculate size in sticklebacks. *Behav. Ecol.* **15**, 137—140.
- Zeil, J. 2000: Depth cues, behavioural context, and natural illumination: some potential limitations of video playback techniques. *Acta Ethol.* **3**, 39—48.