

# Considerations in video playback design: Using optic flow analysis to examine motion characteristics of live and computer-generated animation sequences

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## Abstract

The increasing use of the video playback technique in behavioural ecology reveals a growing need to ensure better control of the visual stimuli that focal animals experience. Technological advances now allow researchers to develop computer-generated animations instead of using video sequences of live-acting demonstrators. However, care must be taken to match the motion characteristics (speed and velocity) of the animation to the original video source. Here, we presented a tool based on the use of an optic flow analysis program to measure the resemblance of motion characteristics of computer-generated animations compared to videos of live-acting animals. We examined three distinct displays (tail-flick (TF), push-up body rock (PUBR), and slow arm wave (SAW)) exhibited by animations of Jacky dragons (*Amphibolurus muricatus*) that were compared to the original video sequences of live lizards. We found no significant differences between the motion characteristics of videos and animations across all three displays. Our results showed that our animations are similar the speed and velocity features of each display. Researchers need to ensure that similar motion characteristics in animation and video stimuli are represented, and this feature is a critical component in the future success of the video playback technique.

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**Keywords:** Computer-generated animations; Jacky dragon (*Amphibolurus muricatus*); Motion characteristics; Optic flow analysis; Video playback

## 1. Introduction

The increasing use of the video playback technique in behavioural ecology reveals a growing need to insure precise control of the visual stimuli that focal animals experience. Early successful experiments in mate choice (Clark and Uetz, 1990, 1992; McDonald et al., 1995; Rosenthal et al., 1996; Ikebuchi and Okanoya, 1999), conspecific (Adret, 1997) and predator recognition (Evans and Marler, 1991; Evans et al., 1993), intraspecific aggression (Rowland, 1995; McKinnon and McPhail, 1996), and social learning (McQuoid and Galef, 1993, 1994) have demonstrated that video playback is a powerful tool in behavioural research.

Technological advances in video editing and broadcasting software now allow researchers to develop computer-generated

animations of demonstrators to be used in video playback experiments instead of video sequences of live-acting individuals. Animation sequences can be edited in order to produce a large range of behaviours, but then the question arises about the realism of these created stimuli compared to natural ones. Numerous studies have highlighted some technical considerations when developing computer-generated models, in particular about luminosity (D'Eath, 1998; Fleishman and Endler, 2000), colour (Fleishman et al., 1998), and depth perception (Zeil, 2000) of video-based stimuli.

However, if strong efforts have been employed to increase the resemblance of computer-generated animations to real animals, the success of the digital animation approach requires that they exhibit realistic motion patterns. The success of animations to reproduce realistic motion patterns is validated only by the consistency of the qualitative behavioural responses that are exhibited by focal individuals when in presence of either live or animated demonstrators. Our aim is to present an alternative means to control for an accurate use of animations in video

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playback experiments by measuring the resemblance of motion characteristics exhibited by computer-generated animations to videos of live-acting animals.

Video playback design involves the presentation of video sequences of live-acting animals filmed in the wild or in the laboratory. However, computer-generated animations necessitate that developers reproduce motion patterns based from observation of natural behaviours exhibited by live individuals. Motion patterns are critical features in behavioural ecology and researchers have long championed the ability of some particular visual displays to elicit specific behavioural responses. These behavioural responses often require that motion patterns exhibited by demonstrators conserve strict characteristics in terms of speed (i.e., distance over time), frequency (i.e., number of occurrences) or velocity (i.e., change of position over time). Nicoletto and Kodric-Brown (1999) found that female guppies (*Poecilia reticulata*) preferentially choose males who exhibit courtship behaviour of rigorous lateral movement of the body and tail with a higher rate and duration. Courtship rates may indeed indicate the quality of potential males; for example, in the damselfish (*Stegastes partitus*) the courtship rate is highly correlated with the egg survival, a measurement of male investment in parental care, therefore indicating greater fitness (Knapp and Kovach, 1991). As suggested by Rosenthal et al. (1996), the motion characteristics of the courtship displays are expected to trigger inherent preferences from females. Thus, variations in the speed and velocity of motions may stimulate receiver sensory biases for preferential selection of mates (Fleishman, 1992; Fleishman et al., 1998).

The ability to discriminate moving objects and their motion pathways (i.e., the change in speed over time) is a particular primary advantage of the visual system (Clifford and Ibbotson, 2002). Although there are many alternative optic flow techniques to specifically look at motion perception (Barron et al., 1994), we elected to base our approach on the use of a program called Analysis of Image Motion (AIM) to measure the changes in perceived movement characteristics within the visual field (Peters et al., 2002). Optic flow analysis measures the velocity of an object moving through a spatial field environment that is calculated by an observer. Movement analysis and visual detection mechanisms rely on the organism's ability to receive velocity characteristics from apparent motion cues (Srinivasan et al., 1996; Zeil and Zanker, 1997). In using this tool, we can compare the differences between videos of live-acting animals and the animation sequences based on the changes in their motion characteristics.

Here, we illustrate the use of the optic flow analysis in a study where motion characteristics of displays exhibited by computer-generated animations of Jacky dragons (*Amphibolurus muricatus*) were compared to videos of live displays. The Jacky dragon is an Australian agamid lizard found in visually complex habitats, such as sclerophyll forests and coastal heathland. Jacky dragon's signalling repertoire is characterized by highly stereotyped visual displays used in social interactions, such as territorial disputes or courtship (Ord et al., 2002; Van Dyk and Evans, 2007). These displays constitute an assertive tail-flick (TF) (Peters and Evans, 2003a), an aggressive push-up

body rock (PUBR) (Ord and Evans, 2003), and a submissive slow arm wave (SAW) (Ord and Evans, 2002). Jacky dragons are sensitive to high-speed motion critical in resolving social displays used in communication, but are particularly poor at perceiving movement patterns that exploit the lower threshold (Woo et al., in preparation). The perception of motion is critical for resolving signals displayed across noisy habitats, such as windblown vegetation (Peters and Evans, 2003b); however, Jacky lizards are sensitive to changes to the speed of environmental noise in local habitats due to windblown vegetation (Peters et al., 2007).

We present a means to ensure similarities the design of animation stimuli that are extracted from the original video. Initially, we tested for differences between signal orientations (i.e., frontal and orthogonal) for an appeasement display to see if motion patterns varied based on display angle. We subsequently compared video to animation sequences. If our computer-generated animations match the motion characteristics of the three natural displays, we could expect, when using an optic flow analysis, to find no significant differences in speed and velocity and to conserve the distinct speed rate characterising the function of each display.

## 2. Materials and methods

### 2.1. Subjects

Lizards were initially collected from Lane Cove, La Perouse, and Royal National Parks in New South Wales, Australia. They were held in enclosures measuring 64 cm × 75 cm × 120 cm surrounded by white panels and a front panel of clear Perspex® (supplied by All Plastics, Chatswood, Sydney, Australia). Each enclosure had wooden branches for basking and shelter, Sydney sand substrate, and native leaf foliage. Lizards were fed live crickets (*Acheta domesticus*) and mealworms (*Tenebrio molitor*) twice a week (supplied by Pisces Enterprises, Brisbane, Queensland, Australia). Invertebrates were dusted with vitamin supplements (Herptivite with beta carotene, calcium, and vitamin D<sub>3</sub>—Rep-Cal Research Labs, Los Gatos, California, USA). Water was provided *ad libitum* in small plastic bowls. Lizards were maintained on a 14:10 h L/D cycle with additional heat lamps (125 W Spotone, Phillips, NSW, Australia) for 10 h per day. Ultraviolet (UV) lamps (300 W Ultra-Vitalux, Osram, NSW, Australia) were illuminated for half-an-hour in the morning (07:30) to prevent vitamin deficiency. Animals remained in captivity for a period of 3 years, after which they were released at their original site of capture. Animals were maintained in accordance with the guidelines established by the NSW National Parks and Wildlife Services (License No. S11024) and the Macquarie University Animal Ethics Committee (Research Protocol No. 2003/014).

### 2.2. Stimulus acquisition

Staged live interactions transpired in order to acquire archival video footage of lizard displays (see Ord and Evans, 2002; Ord et al., 2002; Van Dyk and Evans, 2007). In these studies, the archival video was used to elicit aggressive social responses:

tail-flicks and push-up body rocks. All aggressive social displays were recorded on miniDV. The recorded sequences were played on a Sony MiniDV (Model No. GV-D300E, Sony Corporation, Japan) digital videocassette recorder and presented the displays to the subjects on a Sony Trinitron (Model No. PVM-14M2A, Sony Corporation) colour monitor situated one meter from the enclosure, which was also the distance at which subjects were recorded. Responses were recorded using a Canon (Model No. MV650i, Canon Inc., Japan) digital camcorder with 22× optical zoom. This system was later used to elicit and record appeasement displays (slow arm wave) (Woo, in review). All stimuli were recorded in an interlaced PAL-DV standard (5:1 compression; horizontal resolution 575 lines; 25 frames s<sup>-1</sup>).

### 2.3. Animation

We used a taxidermic model lizard to acquire tridimensional scan of an object used for our animation. The model was scanned using a Konica Minolta VI-9i (Konica Minolta Holdings, Inc., Japan) by New Dawn<sup>®</sup> (Bexley North, NSW Australia) and the shape consisted of approximately 50,000 polygons. The data was collected with Raindrop Geomagic<sup>®</sup> (Raindrop Geomagic, Inc., Research Triangle Park, North Carolina, USA) software that collated scanned surfaces of the object into a single polygon mesh.

We used Lightwave<sup>®</sup> 3D v8 (NewTek Inc., San Antonio, TX, USA) as the animation program to reconstruct a realistic model. In the Lightwave<sup>®</sup> 3D Modeler program, we created bones inside the model that acted as the basic skeletal structure. Bones were closely matched to the number of actual bones of a real Jacky lizard, which provided the basic components that allowed changes in posture and position. We then added a weight shade to regional body parts to balance the overall movement of the model. We acquired digital photographs using a 12.8 megapixel Canon EOS 5D camera (Canon Inc., Tokyo, Japan) from a live lizard in three positions (dorsal, orthogonal, and ventral) and three angles (anterior, central, and posterior) to capture realistic texture. We used Adobe<sup>®</sup> Photoshop<sup>®</sup> Elements v3.0 (Adobe Systems Incorporated) to extract the texture from the photographs while maintaining the silhouette of the animal. In Lightwave<sup>®</sup> 3D Modeler, an atlas UV map was created. This procedure separates polygons into UV coordinates that are used to match areas of texture onto the model. A UV map is a textural blueprint of the UV coordinates that correspond to the model. We then extracted corresponding texture regions on a layer that matched UV coordinates, and placed them onto the UV map (Woo, 2007).

We selected six video exemplar sequences for three social displays with different functions: assertive tail-flick, aggressive push-up body rock, and appeasement slow arm wave. The animation sequences were replicated from these exemplars. Each clip was exported as an image sequence into individual consecutive JPEG files using Apple Quicktime<sup>™</sup> v7.0 (Apple Computer Inc.).

We imported our model and designed our sequences in Lightwave<sup>®</sup> 3D Layout by creating scenes that matched video stimuli. We matched the animation stimuli to video sequences

using a process called rotoscoping (Gatesy et al., 1999). Individual images from the image sequence, starting with the first JPEG, were imported into the background of the sequence. We then manipulated bones within the animation to match the object to the postural position of the digital photograph in the background. When the animation was manipulated to match the background image, the frame was keyframed to maintain the positional displacement of the object. The background was then removed, and replaced with the next image in the sequence. The animation was then matched to the next position and keyframed. We repeated this procedure in a frame-by-frame process until the display was complete. The background sequence was replaced with a photograph of a fabricated wooden perch to add a consistent background to each sequence.

All sequences were rendered using Render Farm Commander V2.9.9 (Bruce Rayne<sup>®</sup>, Lalor Park, NSW, Australia), which allows for all computers connected to a network to increase the efficiency of mass rendering for large sequences. Animation sequences were rendered initially as JPEG still frames in an image sequence. We imported the image sequence into Apple Quicktime<sup>™</sup>, and exported the combined sequence as a single movie file (MOV). All animations were created for PAL-DV standard. A detailed description of stimulus design is described in Woo (2007).

### 2.4. Analysis of Image Motion

We analysed our video and animation sequences using AIM v2.0 (Peters et al., 2002; available for download by RAP at <http://richard.eriophora.com.au/aim/aim.html>), a MATLAB v7.1 (The MathWorks, Inc., Natick, MA) based program running on Microsoft Windows XP Professional that was installed on a Xenon<sup>®</sup> Nitro Series (Xenon<sup>®</sup> Systems Pty. Ltd., Clayton South, Victoria, Australia) PC compatible processor (Xeon<sup>™</sup> Intel<sup>®</sup> CPU 3.00 GHz and 3.00 GB of RAM), to examine the changes of speed (pixels per frame) and velocity (across frames). AIM uses a gradient motion detection algorithm because of its robust ability to estimate the velocity of both realistic and synthetic video (Barron et al., 1994). This optic flow algorithm generates arithmetic and geometric means of movement rate based on changes in pixels per frame. In this calculation, the arithmetic mean is as the overall average change in pixels per frame. In contrast, the geometric mean incorporates the relative change in pixels per frames. AIM also calculates the changes from the spatial structure of a motion component across *X* and *Y* coordinates. Data can be represented as standard ellipses, tridimensional representations of continuous change in *X* and *Y* coordinates over time (frames), and velocity signatures, an alternative method to summarise motion where *X* and *Y* plane identifies the direction of motion and the distance from the original coordinates is the velocity magnitude. In order to account for textural contrasts, AIM filters temporal and spatial derivative of the image intensity, and thus transforms all colour video into a grey-scale format. In this smoothing function, AIM calculates differences in image velocity to constrain the effects of image noise produced at neighbouring locations, and accounts for a spatial weighting average across varying velocity fields.

## 2.5. Procedure

For both experiments, we measured the arithmetic and geometric mean changes in speed–time profiles of video and animation sequences (pixels per frame).

### 2.5.1. Experiment 1—frontal versus orthogonal slow arm wave design

To test for differences between display orientation, we compared the presentation of a slow arm wave in two positions: frontal and orthogonal. These two angles provide us with a biologically meaningful sample of natural orientation. In an examination of active space, Peters and Evans (2007) found no significant difference in lizard orientation when synthetic animations displayed each of the three social displays at 0°, 45°, or 90°. In addition, Woo (in review) found no significant side bias in slow arm wave display, despite the onset of a display with the arm away from a conspecific in an orthogonal position that would obstruct the majority of the sweep area.

Slow arm waves were elicited by video playback of aggressive displays and were then recorded in a similar fashion as archival previous stimulus acquisition (see Ord and Evans, 2002; Ord et al., 2002; Van Dyk and Evans, 2007), but at a later date (Woo, in review). In particular, for each slow arm wave, a camera was mounted in the front of a glass enclosure (30 cm × 30 cm × 60 cm) and an additional camera was placed adjacent to the enclosure to record orthogonal video of the same exact display. The viewing distance from the lizard was scaled for 1 m.

We examined 24 live SAW clips comprised of frontal (12 clips) and orthogonal (12 clips) angles. We examined the differences in signal velocities for live footage. Within-group and between-group analysis should produce no significant differences between motor pattern structures to ensure similar movement characteristics to live footage.

### 2.5.2. Experiment 2—live versus animation consistency of display characteristics

We compared the representative video sequences to the animation stimuli. Live TF, PUBR, and SAW clips were compared within-group and then between-group with the animated counterparts for consistency in animation design. Here, we analysed sequences according to type of media (video or animation) and display (TF, PUBR, and SAW). Peters and Evans (2007) have shown that lizard animations elicit orientation responses towards an animated stimulus. No differences between groups should be expected since movement characteristics are expected to mimic natural movements in display rate, duration, and amplitude.

## 2.6. Statistical analysis

We compared statistical differences for arithmetic and geometric means and their standard deviations. For Experiment 1, we used a paired samples *t*-test to compare the pixels per frame changes between frontal and orthogonal positions. For Experiment 2, we used a general linear model univariate ANOVA to

compare the interaction between type of media (two factors: video and animation) and display (three factors: tail-flick, push-up body rock, and slow arm wave) as well as the main effect for each factor. We used Tukey post hoc tests to compare between media type for each display. All values are reported to the nearest significance threshold with a minimum alpha value of 0.05. SPSS® 11 for Mac OS X (SPSS Inc., Chicago, Illinois, USA) was used to perform all statistical comparisons.

## 3. Results

### 3.1. Experiment 1—frontal versus orthogonal slow arm wave design

We found no significant difference in speed using arithmetic means between frontal and orthogonal slow arm wave displacement [ $t(2105) = 1.05, p = 0.30$ ] suggesting no biases in signalling orientation (Fig. 1a). Speed did not differ between in signalling orientation using geometric means [ $t(2105) = -1.17, p = 0.24$ ;

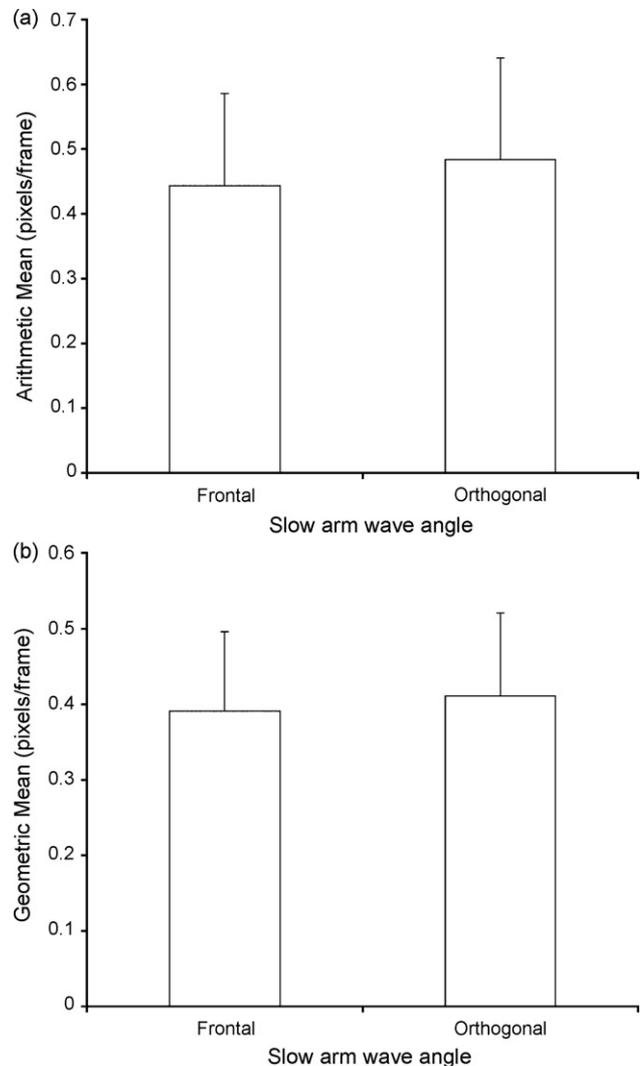


Fig. 1. No difference in response orientation is found between frontal and orthogonal slow arm wave displays in average and relative pixel change: (a) arithmetic mean (+S.D.) and (b) geometric mean (+S.D.).

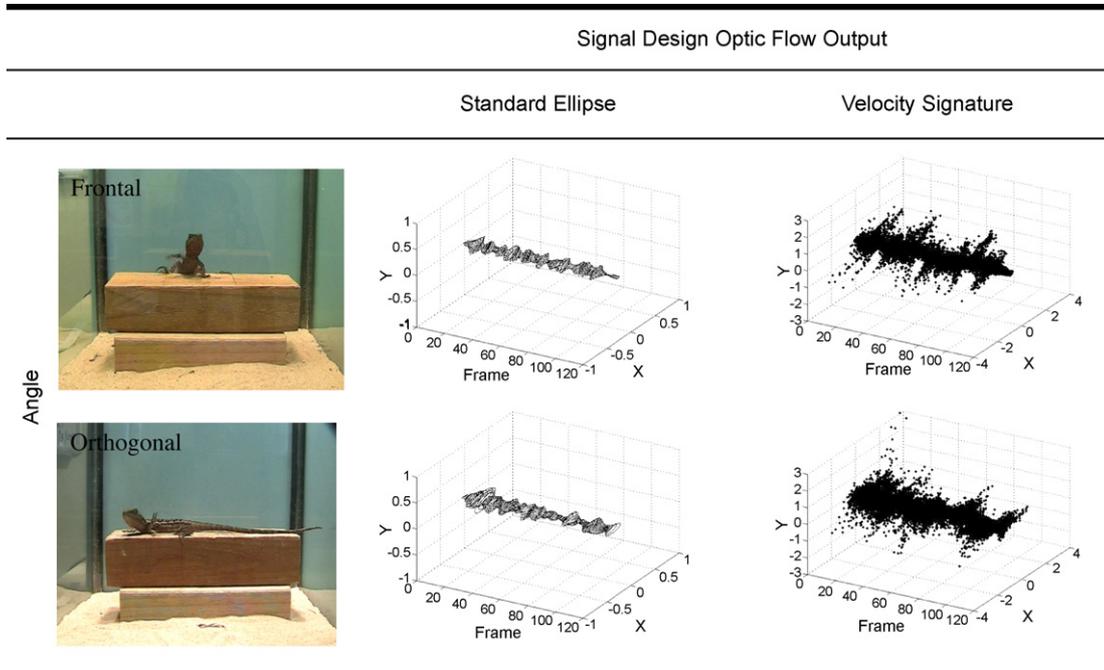


Fig. 2. Representative standard ellipse and velocity signature of slow arm wave design for frontal and orthogonal positions.

Fig. 1b]. Fig. 2 also shows little differentiation between angular orientation of display when comparing typical standard ellipses and velocity signatures.

### 3.2. Experiment 2—live versus animation consistency of display characteristics

In examining the arithmetic mean, we detected a significant interaction between the type of media and the display component ( $F_{5,3502} = 5.17, p < 0.05$ ; Fig. 3a). However, there was no effect for media ( $F_{1,3506} = 1.23, p = 0.27$ ) suggesting that the type of media (animation versus video) for display is not differentially represented. The type of display showed a strong effect ( $F_{2,3505} = 364.86, p < 0.05$ ). Tukey post hoc tests for the arithmetic means revealed that there was no difference between the type of display media for tail-flicks, push-up body rocks, and slow arm waves ( $p > 0.05$ ); however, when the display type was examined across the same media, all comparison were significant ( $p < 0.05$ ).

Further examination of the geometric mean also revealed a significant interaction between the type of media and display component ( $F_{5,3502} = 5.28, p < 0.05$ ; Fig. 3b), with a significant effect of display ( $F_{2,3505} = 267.91, p < 0.05$ ) and no main effect of media ( $F_{1,3506} = 1.73, p = 0.20$ ). Similar to post hoc analysis for arithmetic means, Tukey post hoc tests for geometric means showed no difference between the type of display media for tail-flicks, push-up body rocks, and slow arm waves ( $p > 0.05$ ). We found that when the display type was examined across the same media for geometric means, all comparison were significant ( $p < 0.05$ ).

Fig. 4 shows representative standard ellipses and velocity signatures of signal design characteristics for each display component. Both standard ellipses and velocity signatures between

representative video and animation sequences for each display show similar displacement characteristics across time (frames), suggesting little difference in the speed characteristics between the two types of media.

## 4. Discussion

We presented a means to compare the motion characteristics (in speed and velocity) of videos of live-acting animals to animations for playback experiments using optic flow analysis. This tool provides an element of control for researchers who want to develop efficient computer-generated animations to ensure that the design features will elicit similar response patterns. Movement-based signal perception is functionally important because this ability is a main component involved in communication (Peters et al., 2002). Reproducing similar motion characteristics in animated stimuli is thus a critical component in the future success of the video playback technique.

We illustrated the use of the optic flow analysis in comparing the display characteristics exhibited by computer-generated animations of Jacky dragons to videos of live displays. We first did not detect significant differences between the motion characteristics of video and animation sequences across the slow arm wave angle comparisons. Secondly, results revealed no significant differences between media type for all three displays. The absence of any difference demonstrates that the animations matched the speed and velocity features of the live video sequences. Similarly matched signal designs suggest that there is no expected perceptual difference between using a video of a live lizard or computer-animated sequence.

Our results also showed a significant effect of display. The high-speed signals used for social communication are displayed at different speed rates, and the sensitivity to these signals

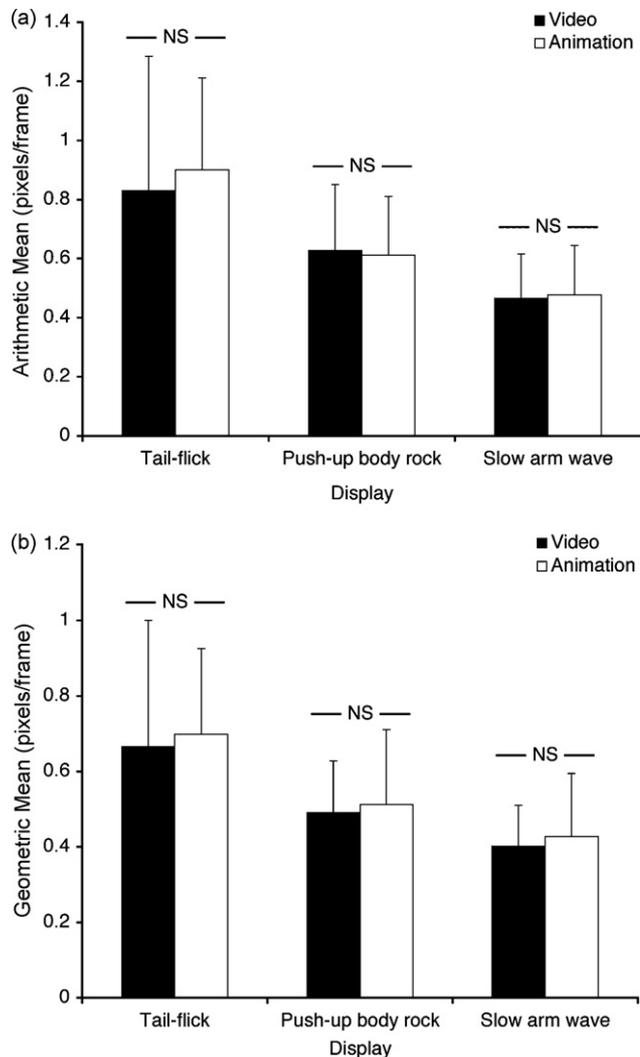


Fig. 3. Animation models designed from video sequences do not show a significant difference in motion characteristics across three social displays, tail-flick, push-up body rock, and slow arm wave: (a) arithmetic mean (+S.D.) and (b) geometric mean (+S.D.).

matches their analogous function. Consequently, conservation of speed rate realism of the behavioural displays exhibited by digital animations appears to be critical. For example, the tail-flick functions as a broadcast signal and alerting component, suggesting that speed of the signal is critical in recruiting attention from potential receivers (Peters and Evans, 2003a). The push-up body rock is an aggressive signal used in territorial disputes as well as courtship (Ord and Evans, 2003). This signal is energetically demanding, and speed of the display may not be as critical during mid-range or close interactions as opposed to broadcast signalling (Peters and Evans, 2007). In contrast, submissive signalling is not energetically demanding or executed rapidly for two possible reasons (Barlow, 1970): (1) costly submissive signals reduce the probability of reserving enough energy for an escape (Haller and Wittenberger, 1988) and (2) faster signals may elicit aggressive signals by attempting to match the speed characteristics of opponent displays (Van Dyk and Evans, 2007; Ord and Evans, 2003).

Previous steps have insured that video stimuli do not elicit differential responses from live individuals. As shown in Ord et al. (2002), the presentation of actual live and video-recorded Jacky dragons did not elicit different responses during playback. However, there are two directions in which using computer-generated animations, along with measuring its motion characteristics, may be used to examine alternative questions as well as improve upon this technique. First, information from optic flow measurements may not be limited to the visual system, but links to multimodal signalling may also facilitate how individuals respond to changes in their environment (Partan and Marler, 1999). For instance, in a playback experiment with the túngara frog (*Physalaemus pustulosus*), the call of a male was coupled with the inflation of the vocal sack, and it was found that females preferred males where both auditory and visual signals were present (Rosenthal et al., 2004). Secondly, although using an optic flow algorithm to understand the characteristics of motion provides us with an insight of how individuals may perceive environmental changes from the receiver's visual perspective, we would still ultimately need to test for the responses to video and animation stimuli, and then compare whether there are any significant differences in the response pattern between the sequences (Clark and Stephenson, 1999).

We limited our analysis strictly to examine the similarities between the speed and velocity attributes of focal individual video and animation sequences. In the study by Clark and Stephenson (1999), they compared the behavioural response behaviour of (*Puntius tetrazona*) schooling groups to live, video, and animated schools. Clark and Stephenson (1999) had manufactured both video and animation stimulus sequences to match the live groups, and found no differences in their schooling behaviour to all types of media. However, in our study, we presented a way to compare the individual motion characteristics between media types to ensure that the design features will elicit similar response patterns.

Recommendations directed at enhancing the video playback technique typically advocate that the first step to any experiments is to evaluate the behavioural responses of focal animals to the video stimuli that are broadcasted (Clark and Uetz, 1992; Evans and Marler, 1991). We suggest that our approach can be used initially for any video playback experiments with computer-generated animations in order to reduce uncertainties associated with stimulus development, especially when such stimuli involved dynamic visual signals.

To further refine this technique would be to incorporate two more rigorously empirical tests. First, the use of the video sampling method for rotoscoping has been restricted to NTSC (29.97 frames  $s^{-1}$ ) and PAL (25 frames  $s^{-1}$ ) standards. These sampling methods may neglect high-frequency components necessary for high-speed motion cues. To address the possibility of missing aspects of high-speed motion, one could use a high-speed camera video to record social displays and then downsample the rate to 25 frames  $s^{-1}$ . Both the raw and downsampled video could be analysed with AIM to compare the differences between the speed and velocity rates of these two treatments. Secondly, like most vertebrates, motion features stimulate the visual grasp reflex, where the position of the eye

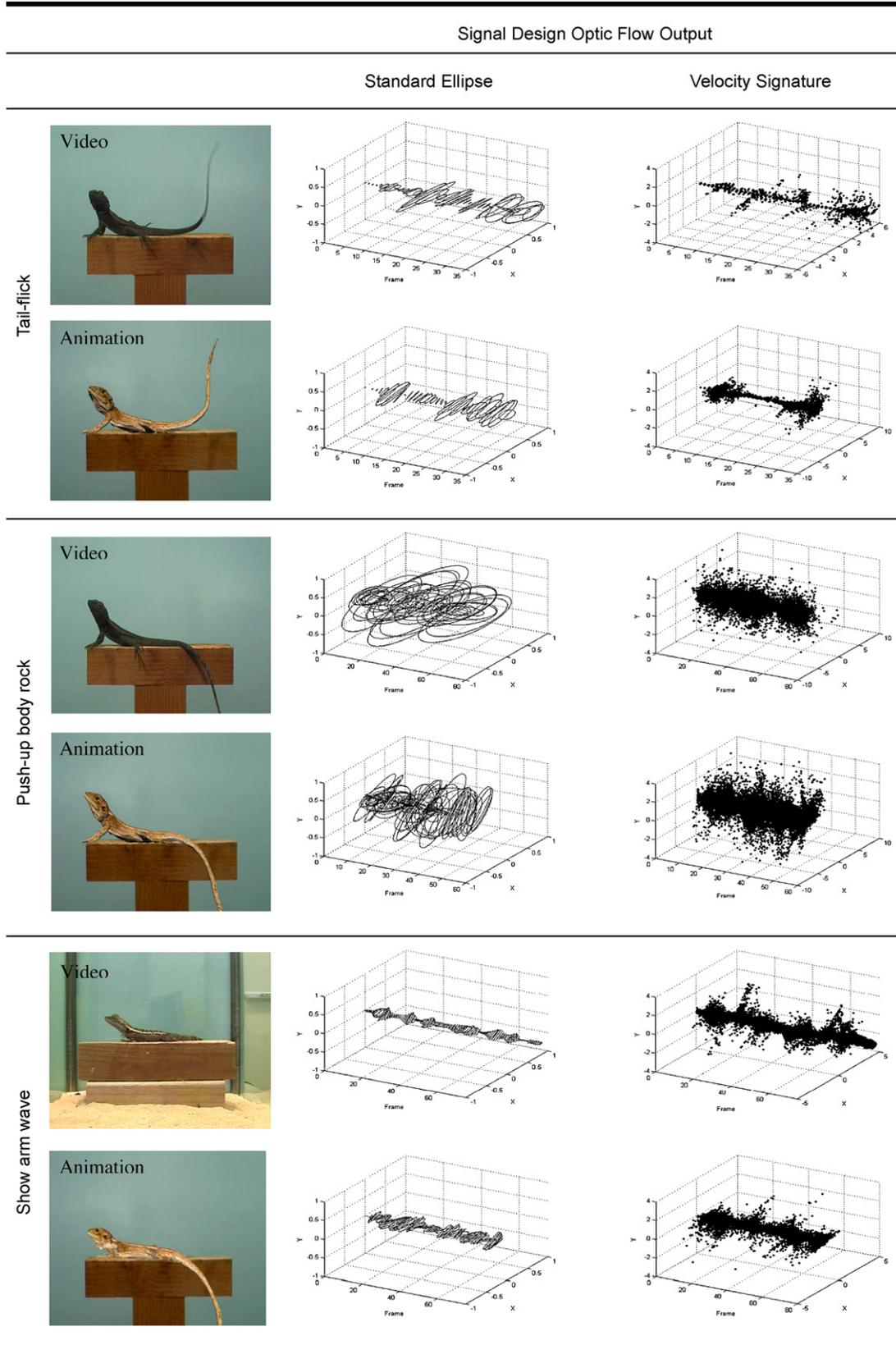


Fig. 4. Representative standard ellipses and velocity signatures of motor patterns for video and animation sequences show little variation in design.

shifts to place the image of importance on the central fovea (Fleishman, 1992). Moving images that are closer to an individual may be perceived as accelerating faster than objects in the distance, despite equal speeds of the two objects in motion. Thus, proximal objects may be more salient than distal objects. In particular, Jacky lizards are capable of gauging changes to environment noise caused by windblown vegetation in local habitats (Peters et al., 2007). However, signalling across distances means that Jacky dragons would be required to gauge the distance of local and distal (i.e., neighbouring opponents) stimuli amongst changes in complex environmental noise (Peters, 2008). It would be beneficial to further examine other visual components that may be necessary using a detailed Fourier analysis. Similar to the noise gating method of acoustic signals, a Fourier analysis could be used to extract motion amplitudes from other aspects of visual noise (as detailed in Fleishman, 1986; Fleishman, 1988). We can then compare the perceived motion of the two types of media in various complex habitats and different distances to provide a more exhaustive sample of simulated ecological conditions.

The use of animation stimuli has provided researchers with a tool for greater control over the behaviours of interest during social interactions. Furthermore, to insure consistency with live animals and video sequences, care must be taken to match the motion characteristics of the animation to the original source. In this study, we have presented a method to compare video and animation based sequences while taking into account motion as a critical parameter for successful stimulus design. Further refinements to this technique may be employed so that important visual motion is not neglected.

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## References

- Adret, P., 1997. Discrimination of video images by zebra finches (*Taeniopygia guttata*): direct evidence from song performance. *J. Comp. Psychol.* 111, 115–125.
- Barlow, G.W., 1970. A test of appeasement and arousal hypothesis of courtship behavior in a cichlid fish, *Etroplus maculatus*. *Z. Tierpsychol.* 27, 779–806.
- Barron, J.L., Fleet, D.J., Beauchemin, S.S., 1994. Performance of optical flow techniques. *Int. J. Comput. Vis.* 12, 43–77.
- Clark, D.L., Stephenson, K.R., 1999. Response to video and computer-animated images by the tiger barb, *Puntius tetrazona*. *Environ. Biol. Fish.* 56, 317–324.
- Clark, D.L., Uetz, G.W., 1990. Video image recognition by the jumping spider, *Maevia inclemens* (Araneae: Salticidae). *Anim. Behav.* 40, 884–890.
- Clark, D.L., Uetz, G.W., 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Anim. Behav.* 43, 247–254.
- Clifford, C.W.G., Ibbotson, M.R., 2002. Fundamental mechanisms of visual motion detection: models, cells, and functions. *Progr. Neurobiol.* 68, 409–437.
- D'Eath, R.B., 1998. Can video images imitate real stimuli in animal behaviour experiments? *Biol. Rev.* 73, 267–292.
- Evans, C.S., Macedonia, J.M., Marler, P., 1993. Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. *Anim. Behav.* 46, 1–11.
- Evans, C.S., Marler, P., 1991. Of the use of video images as social stimuli in birds: audience effects on alarm calling. *Anim. Behav.* 41, 17–26.
- Fleishman, L.J., 1986. Motion detection in the presence and absence of background motion in an *Anolis* lizard. *J. Comp. Physiol. A* 159, 711–720.
- Fleishman, L.J., 1988. Sensory influences on physical design of a visual display. *Anim. Behav.* 36, 1420–1424.
- Fleishman, L.J., 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* 139, S36–S61.
- 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., Brainards, D.H., Endler, J.A., 1998. Colour perception and the use of video playback experiments in animal behaviour. *Anim. Behav.* 56, 1035–1040.
- Gatesy, S.M., Middleton, K.M., Jenkins, F.A., Shubin, N.H., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature* 399, 141–144.
- Haller, J., Wittenberger, C., 1988. Biochemical energetics of hierarchy formation in *Betta splendens*. *Physiol. Behav.* 43, 447–450.
- Ikebuchi, M., Okanoya, K., 1999. Male zebra finches and Bengalese finches emit directed songs to the video images of conspecific females projected onto a TFT display. *Zool. Sci.* 16, 63–70.
- Knapp, R.A., Kovach, J.T., 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. *Behav. Ecol.* 2, 295–300.
- McDonald, C.G., Reimchen, T.E., Hawryshyn, C.W., 1995. Nuptial colour loss and signal masking in *Gasterosteus*: an analysis using video imaging. *Behaviour* 132, 965–977.
- McKinnon, J.S., McPhail, J.D., 1996. Male aggression and colour in divergent populations of the threespine stickleback: experiment with animations. *Can. J. Zool.* 74, 1727–1733.
- McQuoid, L.M., Galef, B.G., 1993. Social stimuli influencing feeding behaviour of Burmese fowl: a video analysis. *Anim. Behav.* 46, 13–22.
- McQuoid, L.M., Galef, B.G., 1994. Effects of access to food during training on social learning by Burmese red junglefowl. *Anim. Behav.* 48, 737–739.
- Nicoletto, P.F., Kodric-Brown, A., 1999. The use of digitally-modified videos to study the function of ornamentation and courtship in the guppy, *Poecilia reticulata*. *Environ. Biol. Fish.* 56, 333–341.
- Ord, T.J., Evans, C.S., 2002. Interactive playback and opponent assessment in lizards. *Behav. Process.* 59, 55–65.
- Ord, T.J., Evans, C.S., 2003. Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): an experimental analysis. *Behaviour* 140, 1495–1508.
- Ord, T.J., Peters, R.A., Evans, C.S., Taylor, A.J., 2002. Digital video playback and visual communication in lizards. *Anim. Behav.* 63, 879–890.
- Partan, S.J., Marler, P., 1999. Communication goes multimodal. *Science* 283, 1272–1273.
- Peters, R.A., 2008. Environmental motion delays the detection of movement-based signals. *Biol. Lett.* 4, 2–5.
- Peters, R.A., Clifford, C.W.G., Evans, C.S., 2002. Measuring the structure of dynamic visual signals. *Anim. Behav.* 64, 131–146.
- Peters, R.A., Evans, C.S., 2003a. Introductory tail-flick of the Jacky dragon visual display: signal efficacy depends upon duration. *J. Exp. Biol.* 206, 4293–4307.

- Peters, R.A., Evans, C.S., 2003b. Design of the Jacky dragon visual display: signal and noise characteristics in a complex moving environment. *J. Comp. Physiol. A* 189, 447–459.
- Peters, R.A., Evans, C.S., 2007. Active space of a movement-based signal: response to the Jacky dragon (*Amphibolurus muricatus*) display is sensitive to distance, but independent of orientation. *J. Exp. Biol.* 210, 395–402.
- Peters, R.A., Hemmi, J.M., Zeil, J., 2007. Signaling against the wind: modifying motion-signal structure in response to increased noise. *Curr. Biol.* 17, 630–636.
- Rosenthal, G.G., Evans, C.S., Miller, W.L., 1996. Female preference for dynamic traits in the green swordtail, *Xiphophorus helleri*. *Anim. Behav.* 51, 811–820.
- Rosenthal, G.G., Rand, A.S., Ryan, M.J., 2004. The vocal sac as a visual cue in anuran communication: an experimental analysis using video playback. *Anim. Behav.* 68, 55–58.
- Rowland, W.J., 1995. Do female stickleback care about male courtship vigour? Manipulation of display tempo using video playback. *Behaviour* 132, 951–961.
- Srinivasan, M.V., Zhang, S., Lehrer, M., Collett, T.S., 1996. Honeybee navigation en route to the goal: visual flight control and odometry. *J. Exp. Biol.* 199, 237–244.
- Van Dyk, D.A., Evans, C.S., 2007. Familiar-unfamiliar discrimination based on visual cues in the Jacky dragon, *Amphibolurus muricatus*. *Anim. Behav.* 73, 33–44.
- Woo, K.L., 2007. Computer-generated animal model stimuli. *J. Vis. Exp.* 6, <http://www.jove.com/Details.htm?ID=243&VID235>.
- Zeil, J., 2000. Depth cues, behavioural context, and natural illumination: some potential limitations of video playback techniques. *Acta Ethol.* 3, 39–48.
- Zeil, J., Zanker, J.M., 1997. A glimpse into crabworld. *Vis. Res.* 37, 3417–3426.