Introductory tail-flick of the Jacky dragon visual display: signal efficacy depends upon duration

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Summary

Many animal signals have introductory components that alert receivers. Examples from the acoustic and visual domains show that this effect is often achieved with high intensity, a simple structure and a short duration. Quantitative analyses of the Jacky dragon *Amphibolurus muricatus* visual display reveal a different design: the introductory tail-flick has a lower velocity than subsequent components of the signal, but a longer duration. Here, using a series of video playback experiments with a digitally animated tail, we identify the properties responsible for signal efficacy. We began by validating the use of the computer-generated tail, comparing the responses to digital video footage of a lizard tail-flick with those to a precisely matched 3-D animation (Experiment 1). We then examined the effects of variation in stimulus speed, acceleration, duration and period by expanding and compressing the time scale of the sequence (Experiment 2). The results identified several variables that might mediate recognition. Two follow-up studies assessed the importance of tail-flick amplitude (Experiment 3), movement speed and signal duration (Experiment 4). Lizard responses to this array of stimuli reveal that duration is the most important characteristic of the tail-flick, and that intermittent signalling has the same effect as continuous movement. We suggest that signal design may reflect a trade-off between efficacy and cost.

Movies available on-line

Key words: Jacky dragon, *Amphibolurus muricatus*, signal design, visual ecology, movement-based signals, tail-flick.

Introduction

Most theories of animal communication emphasise the importance of conspicuousness in signal design. Effective long-range signals stimulate the sense organs of intended receivers (Capranica, 1965), and degrade slowly and predictably (Morton, 1982) as they propagate through the environment (Whitehead, 1987). The likelihood of detection can also be enhanced by choosing to signal when the receivers' sensory systems are most sensitive (Aho et al., 1988), when environmental conditions are favourable (Endler, 1991), or when the signals of other species are absent (Greenfield, 1988). In the visual domain, effective signals are likely to be those that contrast with the background against which they are typically seen (Endler, 1992; Fleishman, 1992; Macedonia et al., 2002). The structural correlates of conspicuousness in static visual signals have been studied extensively in recent years (Bernard and Remington, 1991; Endler, 1991; Fleishman et al., 1993; LeBas and Marshall, 2000; Marshall, 2000; Macedonia et al., 2002; Heiling et al., 2003). In contrast, much less is known about movement-based signals, although work by Fleishman (1988a) demonstrates that these, too, are most effective when they stimulate the visual system at frequencies that are absent in the background.

Structural differences between the signal and background noise are not always sufficient for reliable detection. Many animal signals also have introductory components, which are designed to alert intended receivers to the elements that follow (Wiley and Richards, 1982; Fleishman, 1992). In songs and calls, the attention of conspecifics is typically engaged by high intensity sounds with simple structure and short duration (Wiley and Richards, 1982). The initial portions of some movement-based visual signals have similar properties (Fleishman, 1988b). Lizards (*Anolis auratus*) increase the amplitude of push-ups in the first part of their display when the intended receiver is distant and may not be oriented toward them ('assertion displays'). These initial push-ups have greater velocity and acceleration, but shorter duration, than those that follow and are not accompanied by dewlap extension and contraction. When the receiver is close and detection is straightforward, there is little variation in push-up structure over the course of the display ('challenge displays'), and the amplitude of these movements is lower than that in assertion displays (Fleishman, 1988b).

High amplitude push-ups are required to generate the velocity and acceleration characteristics necessary to engage a visual grasp reflex (Fleishman, 1992). In a series of experiments using artificial lures, Fleishman (1986) showed

that responses were sensitive to movement amplitude and that abrupt changes in position (square waveform) were more effective than smooth sinusoidal waveforms. When velocity and acceleration were continuously varied, response probability was greatest to the stimulus that had large values for both of these parameters. The sensory properties of *A. auratus* lizards are thus well matched to display structure, and have likely influenced the design of this signal.

Quantitative analysis of the movement-based visual display of another lizard, the Jacky dragon *Amphibolurus muricatus*, suggests an alternative strategy for attracting the attention of receivers (Peters and Evans, 2003). Displays consist of five distinct motor patterns, which are produced in an obligatory sequence (Peters and Ord, in press). The initial component is always a tail-flick. This achieves lower velocity and acceleration values than the other components, but sweeps a large region of the visual field and has much greater duration than the motor patterns that follow it (Peters and Evans, 2003). Short displays may be ineffective for attracting the attention of receivers in this system, regardless of intensity. Introductory motor patterns with long duration confer the obvious benefit of increasing the time period available for signal detection. The tail-flick of the Jacky dragon display, and the assertion display of *A. auratus*, may hence be different design solutions to the same functional problem.

Both of these signals are highly conspicuous against their respective backgrounds of wind-blown vegetation (*A. auratus*: Fleishman, 1988a; Jacky dragon: Peters and Evans, 2003); however, almost all of the motor patterns in the visual display of the Jacky dragon have velocity characteristics distinct from those of background plant movement (Peters and Evans, 2003), so conspicuousness alone is not sufficient to explain why the tail-flick is invariably used as the introductory component. In the present study, we explore the efficacy of Jacky dragon tail-flicks in order to identify the additional factors that must be invoked fully to account for signal design.

To assess signal processing by receivers we used digital video playback, which has previously been shown to be highly effective in this system (Ord et al., 2002b). Increased control over stimulus parameters was achieved by using a digitally animated tail. This approach allows precise mathematical definition of movement and hence is becoming increasingly popular for work on movement-based signals (Clark and Uetz, 1993; Evans et al., 1993; Rosenthal and Evans, 1998; Clark and Stephenson, 1999; Nicoletto and Kodric-Brown, 1999; Morris et al., 2003). We began by validating the use of the computer-generated tail, comparing responses to digital video footage of a lizard tail-flick with those of a precisely matched 3-D animation (Experiment 1). We then examined the effects of variation in stimulus speed, acceleration, duration and period by expanding and compressing the time scale of the sequence (Experiment 2). The results of this experiment identified several variables that might mediate recognition. These were varied systematically in two follow-up playback studies that assessed the importance of tail-flick amplitude (Experiment 3) together with movement speed and signal duration (Experiment 4).

Materials and methods

Subjects

Subjects were sexually mature male Jacky dragons *Amphibolurus muricatus* White, ex Shaw 1970 (>72 mm snout–vent length; Harlow and Taylor, 2000), wild-caught from Botany Bay National Park, south of Sydney, Australia. Each lizard was wormed on arrival and held in a glass aquarium (36 cm × 92 cm × 38 cm high). Cardboard screens between adjacent tanks ensured that animals could not see their neighbours. After approximately 4 weeks, lizards were transferred into larger pens (64 cm × 75 cm × 120 cm high). These had aluminium frames, sides of rigid opaque white plastic sheeting, and a clear Perspex front. Pens were arranged so as to maintain visual isolation from other lizards. Both aquaria and pens contained sand substrates, with branches suitable for basking and vegetation for cover. Lizards were maintained on a 14 h:10 h light:dark cycle, corresponding to midsummer. Heat lamps (125 W, 240 V Philips Spotone) and UV lamps (300 W Osram Ultra-Vitalux) were suspended above the aquaria. Room temperature was maintained at approximately 26°C. Lizards were fed crickets dusted with vitamin supplements (RepCal, Los Gatos, CA, USA), and mealworms. Water was available in small bowls, and pens were sprayed daily to provide additional moisture.

All experiments were carried out between July 2002 and January 2003. Twenty lizards were used in each of the four experiments, although any individual animal was used in no more than two. Subjects will eventually be released at the site of capture. Housing and experimental procedures were approved by the Macquarie University Animal Care and Ethics Committee (Protocol No. 2001/014) and the NSW National Parks and Wildlife Service (License No. B2125).

Design

Our general approach was based upon a long tradition of successful playback experiments in bioacoustics (reviewed by Gerhardt and Huber, 2002). To obtain sufficient control over the tail-flick motor pattern, it was necessary to use a completely synthetic stimulus in which all of the aspects of morphology and movement could be defined precisely. First, we tested the effectiveness of this computer-generated animation against that of the representative digital video sequence upon which it was modelled (Experiment 1). Note that this comparison does not involve pseudoreplication (Kroodsma, 1989), in the sense of using a sample size inappropriate to the hypothesis being tested (McGregor et al., 1992), because our question was precisely framed: we wished to determine whether a particular animation was matched in effectiveness to a natural exemplar, rather than to establish that all stimuli drawn from these two populations would evoke indistinguishable responses. In this case, adding exemplars would actually have degraded the experimental design by increasing the probability of Type II error (i.e. we

Table 1. *Manipulation of motion variables in the four experiments*

| Experiment | Manipulation | Stimulus parameters | | | | | | |
		Duration	Speed	Acceleration	Amplitude	Reversals	Period	Duty cycle
1	Calibration	–	–	–	–	–	–	–
2	Time scale	+	+	+	–	–	+	–
3	Amplitude	–	+	–	+	+	+	–
4	Speed and duration	+	+	+	–	+	+	+

–, Fixed parameter; +, variable parameter.

would have been more likely to fail to detect a subtle deficiency in the animation). This initial 'calibration' test was followed by a series of three further playback experiments (2–4), all using synthetic sequences only. The issue of pseudoreplication does not arise in these experiments because the populations of interest are each fully characterised by the single stimulus used to represent them (i.e. there was zero variance in parameters other than those manipulated).

We varied tail-flick duration, speed, amplitude, number of direction changes (reversals), period (time elapsed between the beginning of successive flicks) and duty cycle (proportion of the stimulus containing movement). Changes in tail-flick speed for stimuli of equal duration necessarily produced corresponding changes in acceleration. The tail-flick is a complex movement, and several properties are highly correlated in natural sequences. Our strategy was hence to manipulate a different subset of motion variables in each experiment (Table 1), so as to isolate the feature(s) responsible for evoking an orienting response.

The simplest description of tail-flick structure is obtained by tracking the position of the tail tip in each frame, and then calculating the Euclidean distance between these coordinates and the corresponding values in the first frame of the sequence. These data define a display action pattern (DAP; Fig. 1A), which has traditionally been used to depict display structure (Carpenter et al., 1970). The number of reversals is reflected in the number of peaks in the DAP, while the duty cycle describes the proportion of frames containing motion.

Playback procedure

Our test setup was based upon one used in a recent video playback study (for a detailed description, see Ord et al., 2002b). All stimuli were presented on a Sony PVM-14M2A colour monitor (resolution >600 lines; screen size 34 cm measured diagonally). In Experiment 1, sequences were stored on an Apple PowerBook G3 running Final Cut Pro 2 (Apple Computer Inc.). Video was streamed as a digital signal to a Sony GV-D300E mini-DV deck, using an IEEE 1394 Firewire interface. The S-video analog output from the deck was then connected to the Sony monitor. The digital video sequences for Experiments 2, 3 and 4 were too large to store on the computer, so these were played from digital videotape (Sony DVM60EX2) using the same deck as in Experiment 1. In both of these techniques, stimulus resolution was limited only
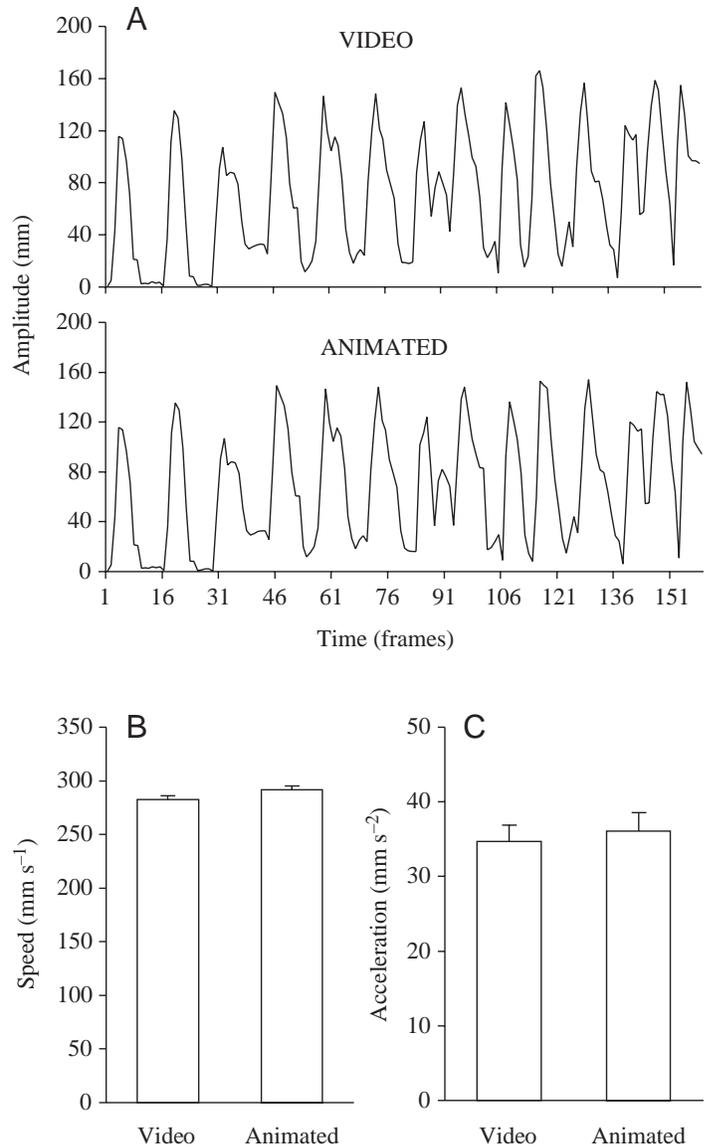

Fig. 1. Structure of the VIDEO and ANIMATED tail-flick sequences. (A) Plots of the Euclidean distance (mm) between the tip of the tail in each frame (PAL standard: 40 ms), and its position in the first frame of the sequence. (B) Speed and (C) acceleration for each sequence. Values are means + S.E.M. (N=162 frames).

by the PAL DV standard (5:1 compression; horizontal resolution 550 lines; 25 frames s^{-1}).

Lizard responses were recorded using a Panasonic WV-CP240 CCTV camera with a WV-LZ62/2 lens, connected to a VHS video deck. All stimuli were presented with the soundtrack muted, but a marker tone (inaudible to the subject lizard) was dubbed directly to the VHS deck so that responses could later be scored relative to stimulus onset. We conducted all playback tests between 08:00 h and 12:00 h, which corresponds to the period of peak activity in our captive population (Ord, 2001). Presentation time was standardised within each lizard, so that the inter-playback interval was always approximately 24 h.

The movie sequences are available in the Supplementary material to this paper and also at: http://galliform.bhs.mq.edu.au/lizard/supplement.html.

Statistical analysis

Our dependent measure was the orienting response, which we operationally defined as an observable movement of the head toward the monitor. For each stimulus presentation, we scored whether or not an orienting response occurred and latency to the nearest frame (temporal resolution 40 ms). Lizards that failed to respond to any of the stimuli in an experiment were excluded from analyses.

We used Friedman's analyses of variance (ANOVAs) to assess variation in the probability of response over all stimuli, followed by Wilcoxon signed-ranks tests for pairwise comparisons between conditions. Formal analyses of response latencies could only be conducted for Experiments 1 and 3. The stimuli used in Experiments 2 and 4 varied in duration, and this would have introduced a systematic bias in response latencies if we had considered the whole stimulus presentation. To overcome this, we windowed responses, and considered only those that occurred within a period equivalent to the duration of the shortest sequence (42 frames in both experiments). In addition, only lizards that responded to all stimuli in our repeated measures design could be included in standard statistical models. With both of these constraints in place, our effective sample size for latency analysis was reduced to two animals in Experiment 2 and zero in Experiment 4.

Results
Experiment 1

Systematic manipulation of tail-flick structure requires the unique level of control afforded by high-resolution computer animations. In a recent study, we showed that digital video recordings of a displaying male evoke aggressive responses just as effectively as the same animal presented live (Ord et al., 2002b). In this experiment, we conducted an analogous comparison between a computer-generated tail-flick and digital video footage of a real lizard tail-flick.

Stimulus sequences
Videorecorded tail-flick

We randomly selected a digital video sequence from an archival collection that depicted a Jacky dragon tail-flicking on a wooden perch (Fig. 2). Full details of recording procedure are presented in Ord et al. (2002b). Footage was edited, using Final Cut Pro 2 software on a Macintosh G4/500 computer (Apple Computer Inc.), to isolate the tail-flick motor pattern. We added fade transitions before and after the tail-flick to avoid spurious orienting responses that might be caused by an abrupt change in the displayed image. The final stimulus (LIVE) consisted of 10 s of an empty perch before the lizard's tail faded into view (1 s), and then remained stationary for a further 1 s before a single bout of continuous flicking (162 frames, 6.5 s). The tail then faded away (1 s), and an empty perch was presented

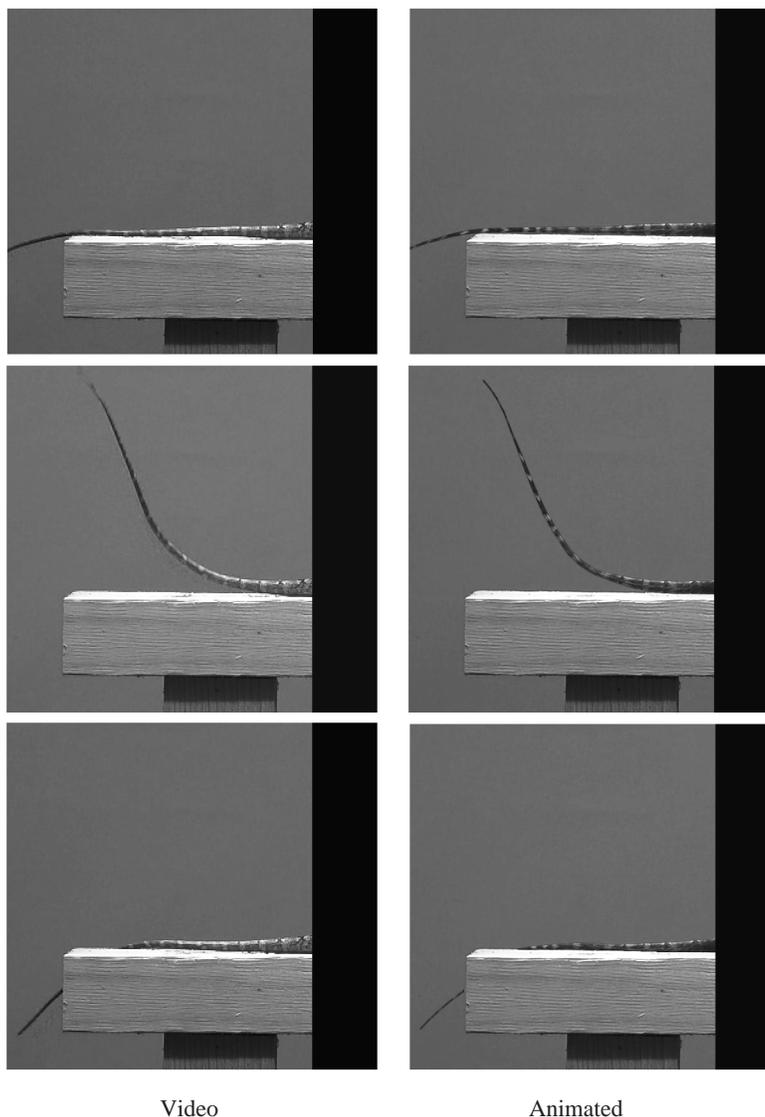|	
Video	Animated

Fig. 2. Representative frames from the VIDEO (left) and ANIMATED (right) sequences. The black mask on the right side of each frame has been cropped.

for a further 10 s. A black mask was added to the right side of each video frame to conceal the lizard's body (Fig. 2).

Animated tail-flick

Construction of the 3-D computer-generated tail-flick sequence (ANIMATED) involved the following steps: (1) building a model with appropriate shape and surface markings, (2) manipulating the model to match the live sequence, (3) adjustments to lighting to match the natural exemplar, followed by sequence rendering and (4) final editing to overlay the synthetic tail on the same digital video background as in the LIVE tail-flick sequence, and also to add identical fades and mask. The following description provides a brief overview of procedure; recent reviews provide additional background on the use of computer animation to create visual stimuli (Kunzler and Bakker, 1998; Clark and Stephenson, 1999; Nicoletto and Kodric-Brown, 1999; Rosenthal, 1999).

Model construction. Measurements of tail morphology from the time of recording were not available, so current measurements were used as an approximation (other physical data showed only moderate growth: 3 mm increase in snout–vent length and 3 g mass increase). We measured overall tail length, as well as diameter at equally spaced points along the tail. Digital photographs of the tail were taken from above and from the sides, using a Panasonic NV-DS15 digital video camcorder, and then transferred to computer for editing.

We used the modeller module of LightWave 3D v6 (NewTek Inc. 2001, San Antonio, TX, USA) to construct the synthetic tail. Briefly, we began with a cylindrical object scaled to match the length of the real tail, and then modified this using shaping functions to match the circumference at each point. We then used the digital photographs of real tail skin to create a texture map of the tail in Adobe Photoshop v6 (Adobe Systems Inc.), which was overlaid onto the 3-D wire-frame model. This process produced a tail structure with shape and surface characteristics that closely resembled those of the original.

Animating the 3-D model. We used the animation module of LightWave to define changes in position over time, so that the movement of the synthetic tail matched precisely that of the original. To assist in this process, we added a skeleton, made up of 24 artificial 'bones'. These are invisible elements that facilitate adjustment of a model in which there is both global displacement and local movement of some sectors, relative to others. To animate the tail, we used a technique known as 'rotoscoping' (Gatesy et al., 1999). This involved superimposing the computer-generated model over sequential frames from the original sequence, and then adjusting the model to match each one.

The LIVE sequence was exported as a series of still images using MovieShop v 5.2 software, on a DraCo nonlinear video editing workstation (MS MacroSystem Computer GmbH). The first frame was then used to determine the appropriate position of the animation 'camera' in three-dimensional space, so that the artificial tail would be rendered from the same perspective as the real one. LightWave allows manipulation of the spatial location of each bone in three planes (x, y and z), as well as orientation and range of movement. To achieve a match, it was necessary to utilise this level of control, making judgements about how the tail would move that took into account both the shape required in future frames and the mechanical constraints of the bones. Once the model matched the background image, a 'key-frame' was used to save the location of all bones. We then advanced to the next animation frame, imported the next image in the video tail sequence, and repeated the process for the whole sequence. Although LightWave has powerful interpolation algorithms, manual definition of tail location in each of 162 frames ensured the closest possible match between the VIDEO and ANIMATED tail-flicks.

Lighting and sequence export. The last stage in the animation process was to add 'lights' to the scene in locations that matched those used in the original videorecording setup. We selected a random frame in the original sequence and measured Red, Green and Blue values at three different points on the tail using Photoshop. We then adjusted light specifications (angle, intensity and hue), rendered a single frame to compare model and original values, and iterated this process. The animated tail was then exported as a digital video (DV) stream with a homogenous black background.

Final editing. The DV stream was imported into Final Cut Pro 2 and then combined with background video footage from the original lizard filming setup, so that the only difference between the two finished sequences was that the tail was recorded in one case and animated in the other. We used a chroma-key effect to make the black region of each frame transparent and then combined these with video recordings of the empty perch, so that the animated tail was superimposed on the same structure and background as the video exemplar (Fig. 2). A black mask was then added to the right-hand side of each frame.

Quantitative comparison of movement

In a recent paper (Peters et al., 2002), we describe our strategy for exploring the design of dynamic visual signals and show that local changes in image intensity can be used to measure the direction and speed of motion (see also Zeil and Zanker, 1997). A summary estimate for speed over time can be calculated by averaging velocity magnitude (i.e. vector length) over the whole sequence (Peters et al., 2002; Peters and Evans, 2003). We compared movement in the two sequences using DAP profiles (Fig. 1A), and average speed and acceleration (Fig. 1B,C). These complementary analyses reveal that the video and animated sequences were closely matched on all parameters. Full details of analysis procedures can be found elsewhere (Peters et al., 2002; Peters and Evans, 2003).

Playback

We presented tail-flick sequences twice each to 20 lizards, over 4 successive days. The first frame of the stimulus depicted an empty perch in both cases; this appeared on the monitor from the start of the session. We waited until the
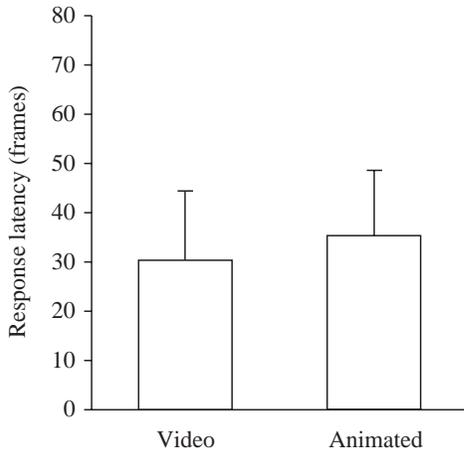
Fig. 3. Response latencies for the VIDEO tail-flick and the ANIMATED replica. Values are means + S.E.M. (N=18).

lizard was oriented away from the front before cueing the stimulus (mean 255±75 s, mean ± S.D.). We used a randomised block design in which half of the lizards were shown the stimuli in the order VIDEO–ANIMATION and the other half ANIMATION–VIDEO. Each group was then re-tested with the reverse sequence. Order effects were thus controlled both by random assignment at the group level and by counter-balancing within individual. Two lizards were excluded from the analysis because they did not respond to any of the stimuli.

Results

Both stimuli were highly effective; 68 of the 72 presentations evoked an orienting response. There was no difference between VIDEO and ANIMATED in the proportion of sequences that evoked a response (Friedman's χ^2=2.000; d.f.=3; P=0.572). The mean latency to respond was also very similar (Fig. 3), and did not differ between the two stimulus types (t=0.66, d.f.=17, P=0.515). We used power analysis (Power & Effect 2.0.3) to assess the probability of Type II error; this revealed a very small estimated effect size (η^2=0.016).

Experiment 2

Experiment 1 showed that computer-generated and video tail-flicks are equally effective in eliciting orienting responses. This finding validated the use of animated stimuli for the remaining experiments of this series, each of which required a highly controlled manipulation of movement characteristics (see Introduction). In Experiment 2, we manipulated the duration of the ANIMATED tail-flick used in Experiment 1. This produced sequences in which the tail moved through a nearly identical series of x, y, z coordinates, but over varying time periods (Fig. 4), with concomitant differences in speed and acceleration.
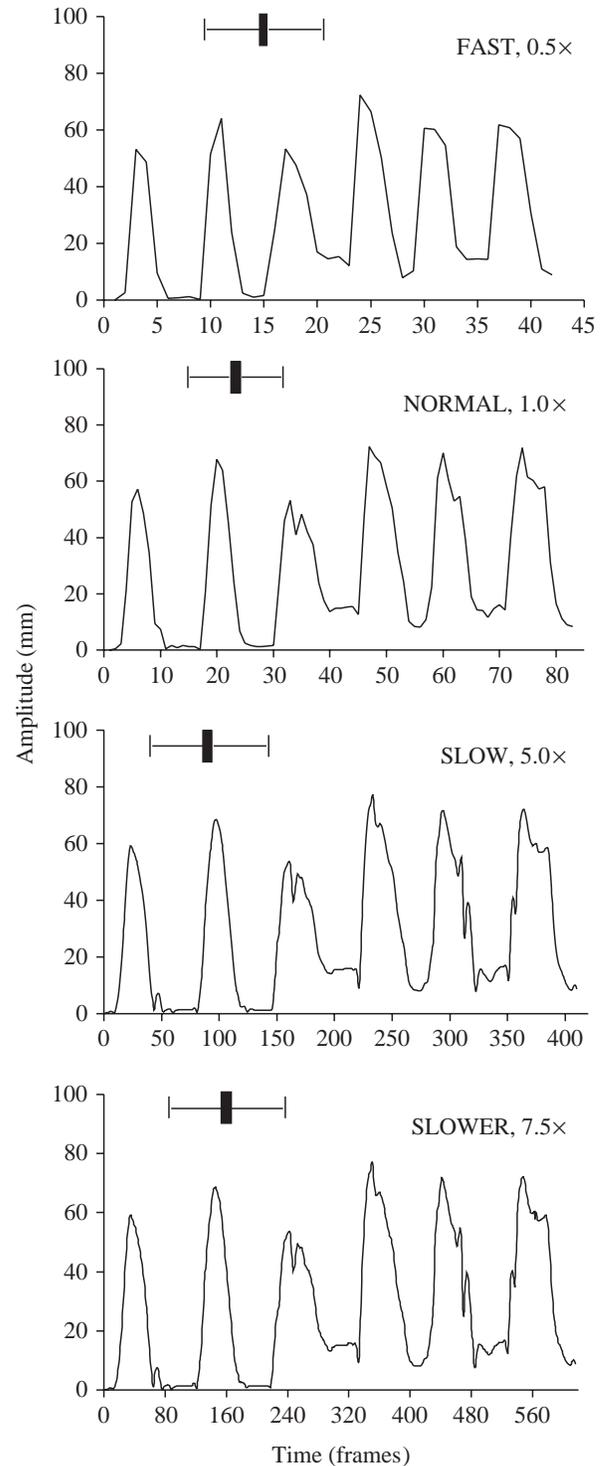

Fig. 4. Display action patterns for the four stimulus sequences used in Experiment 2. Lines represent the Euclidean distance (mm) between the tip of the tail in each frame, and its position in the first frame of the sequence. Plots are shown from the shortest sequence (FAST; top) to the longest sequence (SLOWER; bottom). Note that the time base varies to accommodate changes in stimulus duration. Sequence length relative to NORMAL is indicated in each panel. Horizontal bars represent the response latency (mean ± 1 S.D.).

The response latencies for the ANIMATED tail-flick used in Experiment 1 indicated that when orienting responses were evoked, these occurred well before the end of the sequence. To avoid a ceiling effect, we only used the first half of the original sequence (82 of 161 frames), and scaled the tail to half its original size. This represents an apparent distance of 1.50 m from the observer. The time scale was then systematically varied using LightWave, without changing other parameters that define movement, such as amplitude and plane of motion (Fig. 4). Increased duration was achieved by interpolating between the key-frames defined in the original sequence. This technique ensures smooth slow motion and produces much better results than the algorithms available in video-editing software, which simply repeat frames, producing discontinuous motion.

The time base was expanded to create sequences that were longer than the original, and compressed to produce shorter ones. We selected three stimuli that sampled the natural range observed in our captive population. In addition to the original sequence (NORMAL), we used sequences that were 0.5× (FAST) and 5.0× (SLOW) the duration of NORMAL. We also included a sequence 7.5× the original duration (SLOWER), which is probably outside the natural range. This design allowed us to test whether lizard responses are approximately matched to the distribution of conspecific tail-flick durations, and also to evaluate the alternative possibility that exceptionally long signals might prove more effective (i.e. supernormal; Tinbergen, 1951).

In Experiment 1, we used a homogenous background to maximise stimulus conspicuousness. However, Jacky dragon displays will usually be seen against wind-blown vegetation (Peters and Evans, 2003), which acts as background noise. We reasoned that lizards are likely to habituate to the movement of wind-blown plants (Fleishman, 1992) and that signal efficacy would therefore best be assessed in terms of ability to engage visual processing after a period spent viewing irrelevant background motion. This general approach of using background footage videorecorded in the animal's natural habitat has recently been advocated by Rosenthal (1999).

Tail-flick animations were overlaid onto footage of wind-blown plants (Fig. 5), recorded at the site where the subject lizards had been caught. A continuous 15 min plant sequence was used, during which wind speed had varied between 0.7 and 2.2 m s^{-1}. Recording procedure and vegetation movement characteristics have recently been described (Peters and Evans, 2003). The animations and vegetation sequences were combined using a chroma-key effect in Final Cut Pro, in the same way as the model tail-flick and background in Experiment 1. The tail appeared at the twelfth and fourteenth minute of each sequence, and commenced flicking immediately. To assess whether there was an effect of the tail structure appearing, independent of movement, we added a control sequence that depicted a stationary tail of the same duration as the original stimulus (82 frames).

The five stimuli were presented to 20 lizards on successive days. We used the stationary tail stimulus to obtain a baseline score on the first day. Each lizard was then shown the four animated tail-flick stimuli in a unique random sequence.

Results

There was significant variation in the probability of an orienting response to the first trial in each sequence (Fig. 6; Friedman's χ^2=35.415; d.f.=4; P=0.000). To ensure that this was not simply attributable to a difference between the four moving stimuli and the non-moving control sequence, we repeated the analysis with data from the stationary condition excluded. This revealed that response probability varied significantly as the time base for the tail-flick was expanded and compressed (Friedman's χ^2=12.636; d.f.=3; P=0.005). Pairwise comparisons indicate that the FAST sequence was significantly less effective than each of the other sequences (NORMAL: Z=–1.667, P=0.048; SLOW: Z=–2.828, P=0.0025; SLOWER: Z=–2.449, P=0.007). Responses to NORMAL were also significantly different from those to the SLOW stimulus (Z=–1.732, P=0.0415). None of the other comparisons was significant.

Formal analysis of response latencies was not possible (see Materials and methods). However, examination of the distribution of latencies, relative to tail position, in plots of amplitude over time reveals a marked correspondence between mean response time and the DAP profile (Fig. 4).

Fig. 5. Representative frame showing the vegetation used as the background in Experiments 2–4 (left), and an enlarged view of the tail against the background (right).

Experiment 3

It has been shown previously that lizard responses to moving stimuli are sensitive to amplitude (Fleishman, 1986). Experiment 3 was designed to test this idea. We systematically varied tail-flick amplitude, while controlling stimulus duration. Speed, acceleration, total sweep area and number of reversals also varied systematically across the stimulus set. Response to these parameters was assessed by planned comparisons across the amplitude series, and also by including an additional control sequence.

Stimulus sequences

The modelling process for Experiment 1 produced an animation precisely matched to a real tail-flick, and Experiment 2 stimuli were created by expanding and compressing the time scale of this sequence. In this experiment, it was necessary to manipulate tail-flick parameters in a way that would have been impractical with the original complex movement, as this included excursion into the z (depth) plane. Instead, we created a simplified tail-flick, which was constrained to the x–y plane (i.e. all movement was orthogonal to the camera). The modelling process used bones as invisible elements that controlled the configuration of the tail model as before (see methods for Experiment 1), but took advantage of the structural relationship between these components to better define movement. Each bone was connected to the next in the series and was set up to have a restricted range of motion and relative stiffness; bones further from the base of the tail had a greater range of motion and were lower in stiffness. The last bone in the series was linked to an invisible target, which allowed us to manipulate the entire chain by setting a single coordinate location. LightWave's powerful inverse kinematics algorithms (NewTek), which take into account each bone's range of motion and stiffness, then calculated the shape of the tail in each frame, producing realistic flicking movements (Fig. 7).
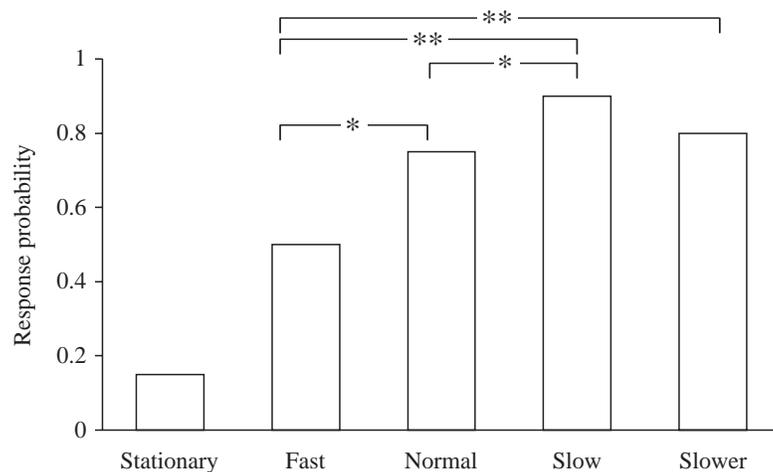

Fig. 6. Probability of an orienting response to Experiment 2 sequences, in which the tail-flick time-scale was manipulated (*P<0.05; **P<0.01). For details, see text.

Stimulus sequences depicted elevation of the tail from its resting position to one of three maximum amplitudes (measured from the tip of the tail): SMALL, MEDIUM and LARGE, followed by return along the same path (Fig. 7). The motor pattern was then repeated, such that each tail-flick animation swept across the same number of total pixels (distinct from the number of unique pixels swept, which covaried with amplitude). Animation DAPs are presented in Fig. 7. To assess whether there was an effect of variation in the number of direction changes across the sequences (24 SMALL to 6 LARGE), we constructed a fourth tail-flick sequence (CONTROL) that had the same number of reversals as the MEDIUM sequence (12), but the same amplitude as the LARGE sequence. Velocity estimates (Peters et al., 2002) were calculated for each of the tail-flick animations. Mean acceleration did not differ across the stimuli. The SMALL and MEDIUM animations were matched for speed, but were faster than the LARGE sequence. The CONTROL sequence matched the LARGE sequence for average speed.

The tail-flick animations were overlaid onto footage of wind-blown plants, as in Experiment 2. A fifth sequence (BLANK), which depicted the background only, was added to examine spontaneous response to wind-blown vegetation. Stimuli were presented on five successive days. The order of presentation of SMALL, MEDIUM and LARGE tail-flick sequences was randomised across lizards; these stimuli were presented on the first, third and fifth days. The CONTROL and BLANK sequences were then randomly allocated to either the second or fourth day of testing.

Results

No spontaneous orienting responses occurred during the BLANK stimulus sequence, so we excluded data for this treatment from the analysis (Fig. 8A). In this experiment, in which stimuli were matched in duration, differences in tail-flick amplitude did not affect the probability of an orienting response (Fig. 8A; Friedman's χ^2=1.077; d.f.=2; P=0.584), or the latency to respond (Fig. 8B; $F_{2,12}$=1.234; P=0.326). Sequences matched for the number of reversals, but differing in amplitude, also did not differ in response probability (MEDIUM vs. CONTROL: Z=–0.333, P=0.739), or latency (t=–0.801; d.f.=8; P=0.446). Similarly, increasing the number of reversals, while maintaining the same amplitude, did not affect response probability (LARGE vs CONTROL: Z=–1.134, P=0.257), or latency to respond (t=0.361; d.f.=9; P=0.726).

Experiment 4

In this final experiment, we considered the interaction between duration and speed in a 2×2 Latin Square design. Amplitude was held constant. Based on the results of Experiment 2, together with previous work on movement-based signals (Fleishman, 1992), we predicted that longer signals

would be more effective than short ones, and that the most effective signal would be a long duration tail-flick at fast speed. We also wished to establish whether continuous movement was necessary for optimal tail-flick efficacy. Natural tail-flicks typically have pauses after each sweep, so we added a fifth stimulus designed to test whether such discontinuous motion has a cost in terms of reduced receiver response.

Stimulus sequences

Sequences were constructed using the same procedure as in Experiment 3. The LARGE amplitude tail-flick formed the basis for five new stimuli that varied in speed of movement and sequence duration. Display action patterns for these stimuli are presented in Fig. 9A. We began with a tail-flick that had slow speed and short duration (SLOW,SHORT), and then increased speed fourfold, while keeping duration constant (FAST,SHORT); this change produced a corresponding increase in the number of reversals. To assess whether any change in response was caused by the number of reversals, rather than speed, we created a longer version of the SLOW,SHORT stimulus (SLOW,LONG) with a matched number of reversals. To test the combined effect of speed and duration, we created a stimulus (FAST,LONG) which matched the duration of SLOW,LONG, but had a fourfold increase in both speed and number of reversals.

A fifth stimulus (INTERMITTENT) tested the effect of naturalistic motion, while controlling duration, matched to that of the two long stimuli, speed, matched to the two fast stimuli, and number of reversals, which matched FAST,SHORT and SLOW,LONG (Fig. 9B). This was achieved by removing flicks from the FAST,LONG sequence and spacing the four remaining movements at equal intervals so that the stimulus began and ended with movement like the others (Fig. 9B). The five tail-flick animations were then overlaid onto footage of wind-blown plants, in the same way as in the previous experiments.

Stimuli were presented on successive days using the same test procedure as Experiments 2 and 3. Each lizard was assigned a unique random sequence of the five stimuli.
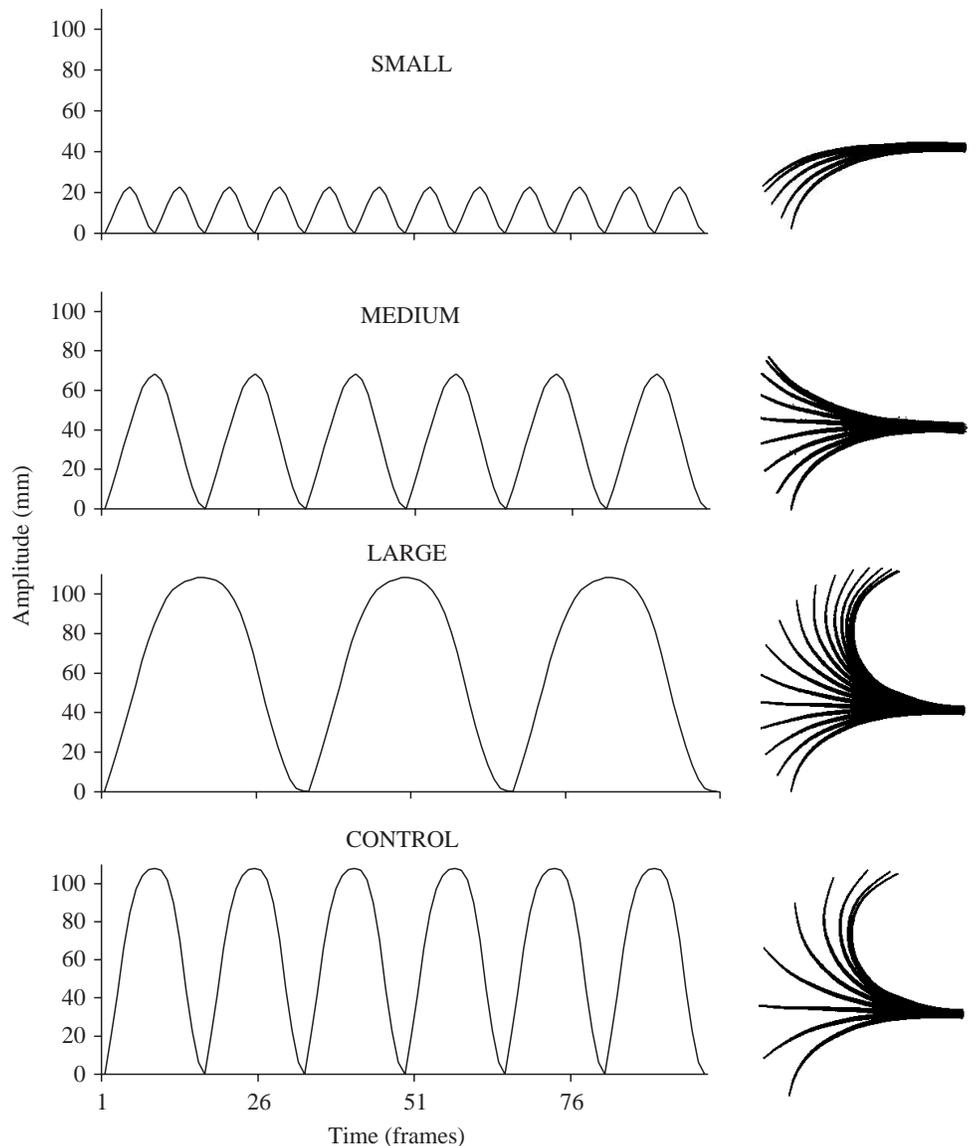

Fig. 7. Tail-flick sequences used in Experiment 3. All stimuli had the same duration, but they varied systematically in tail-flick amplitude and number of reversals. The tail position in each frame of the upward sweep of the tail-flick is shown together with display action patterns.

Statistical analysis

We compared the frequency of response in several ways. First, we determined if there was a main effect for either speed or duration using Wilcoxon signed-ranks tests on the pooled data from pairs of stimuli differing on these parameters. Next we performed an overall Friedman's test of the four speed/duration sequences (Fig. 9A), and conducted planned pairwise comparisons. We asked if increased signal duration affected responses within a speed class (SLOW,SHORT *vs* SLOW,LONG; FAST,SHORT *vs* FAST,LONG). These sequences also differed in number of reversals, so we compared the SLOW,LONG and FAST,SHORT sequences, which were matched on this parameter. We then compared responses to the FAST,LONG sequence with those to the two

slow sequences. Finally, we compared responses to the INTERMITTENT stimulus with those to the other long duration sequences, and with the FAST,SHORT sequence. The latter comparison tests for a difference between stimuli with an equal number of reversals, as a consequence of adding pauses to increase duration.

Results

Consistent with results of Experiment 2, response probability increased with stimulus duration (Fig. 10). The largest values were obtained with the INTERMITTENT stimulus. Faster signals did not improve response probability (Z=–0.943, P=0.346), but longer duration signals were more effective than short ones (Z=–2.556, P=0.011).

An overall Friedman's test revealed sufficient variation in response to the four continuous sequences (Fig. 9A; Friedman's χ^2=9.778, d.f.=3, P=0.021). Comparisons between short and long durations within each speed class suggest that the duration main effect above was largely due to differences

in response to the two fast signals (Z=–2.530, P=0.011); differences in duration between the slow signals did not affect orienting probabilities (Z=–1.414, P=0.147). The comparison between the FAST,SHORT and SLOW,LONG sequences revealed that the increased effectiveness of long signals is unlikely to be a consequence of correlated increase in number of reversals (Z=–1.265, P=0.206). The FAST,LONG stimulus evoked more orienting responses than SLOW,SHORT (Z=–2.53, P=0.011), but was comparable in effectiveness to the SLOW,LONG sequence (Z=–1.414, P=0.147). The INTERMITTENT stimulus was as effective as the FAST,LONG sequence (Z=–0.378, P=0.705), but significantly more effective than the other three sequences (SLOW,SHORT: Z=–3.00, P=0.003; FAST,SHORT: Z=–3.00, P=0.003; SLOW,LONG: Z=–1.890, P=0.059).

Discussion

Previous work has shown that digital video playback is a suitable approach for measuring social responses to movement-based signals in Jacky dragons (Ord et al., 2002b). The present series of experiments replicates and extends this finding by demonstrating that a computer-generated tail-flick can be used to explore the effects of variation in signal structure. As several recent papers have argued (Clark and Uetz, 1993; Evans et al., 1993; Rosenthal and Evans, 1998; Clark and Stephenson, 1999; Nicoletto and Kodric-Brown, 1999; Rosenthal, 1999; Morris et al., 2003), high resolution animations modelled on real structures (Fig. 2) provide unique flexibility for the examination of visual perceptual processes that have, until recently, been inaccessible to experimental analysis.

In Experiment 2, we performed straightforward manipulations of the time scale of a tail-flick sequence, keeping the motor pattern otherwise unchanged. The appearance of a stationary tail was relatively ineffective (Fig. 6), which emphasises the importance of movement for reliable signal detection. Response probabilities also suggested that longer duration tail-flicks were more likely to evoke an orienting response than shorter ones (Fig. 6), even though speed was progressively reduced.

In Experiment 3, we manipulated maximum flick amplitude, while keeping sequence duration constant and controlling other parameters (speed, acceleration and total sweep area). Amplitude increases did not increase response probability or reduce latency under our testing conditions. Clearly, all tail-flicks used in this experiment exceeded the amplitude threshold required for detection. It is, however, likely that amplitude interacts with distance, such that an efficacy benefit of higher amplitudes might only be apparent at longer range. If so, the principal advantage gained from having large amplitude motor patterns would be increased signal active space (i.e. visibility to more distant opponents; Fleishman, 1988b). Additional playback experiments are planned to test for this predicted effect.

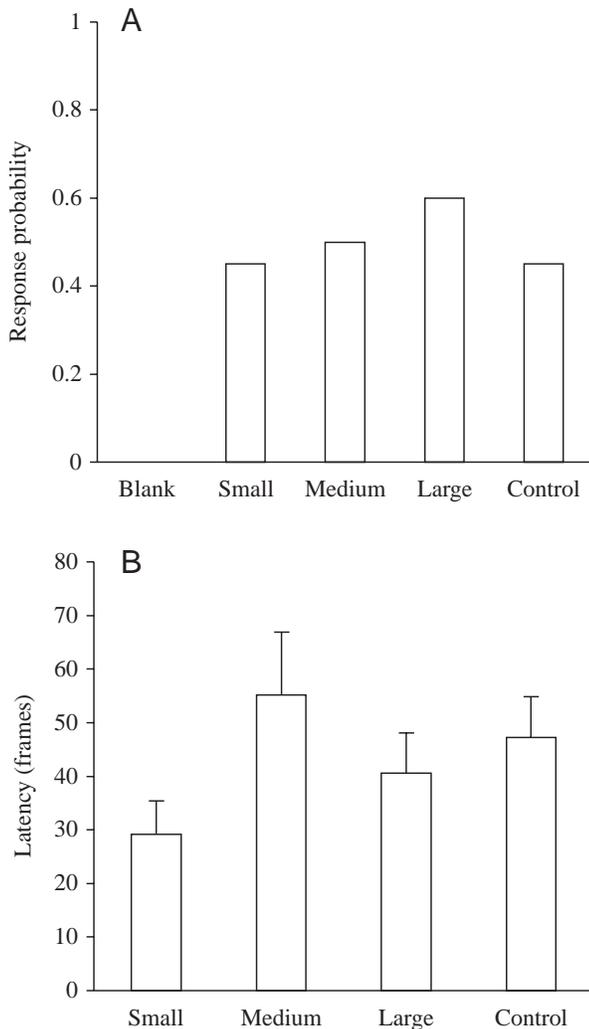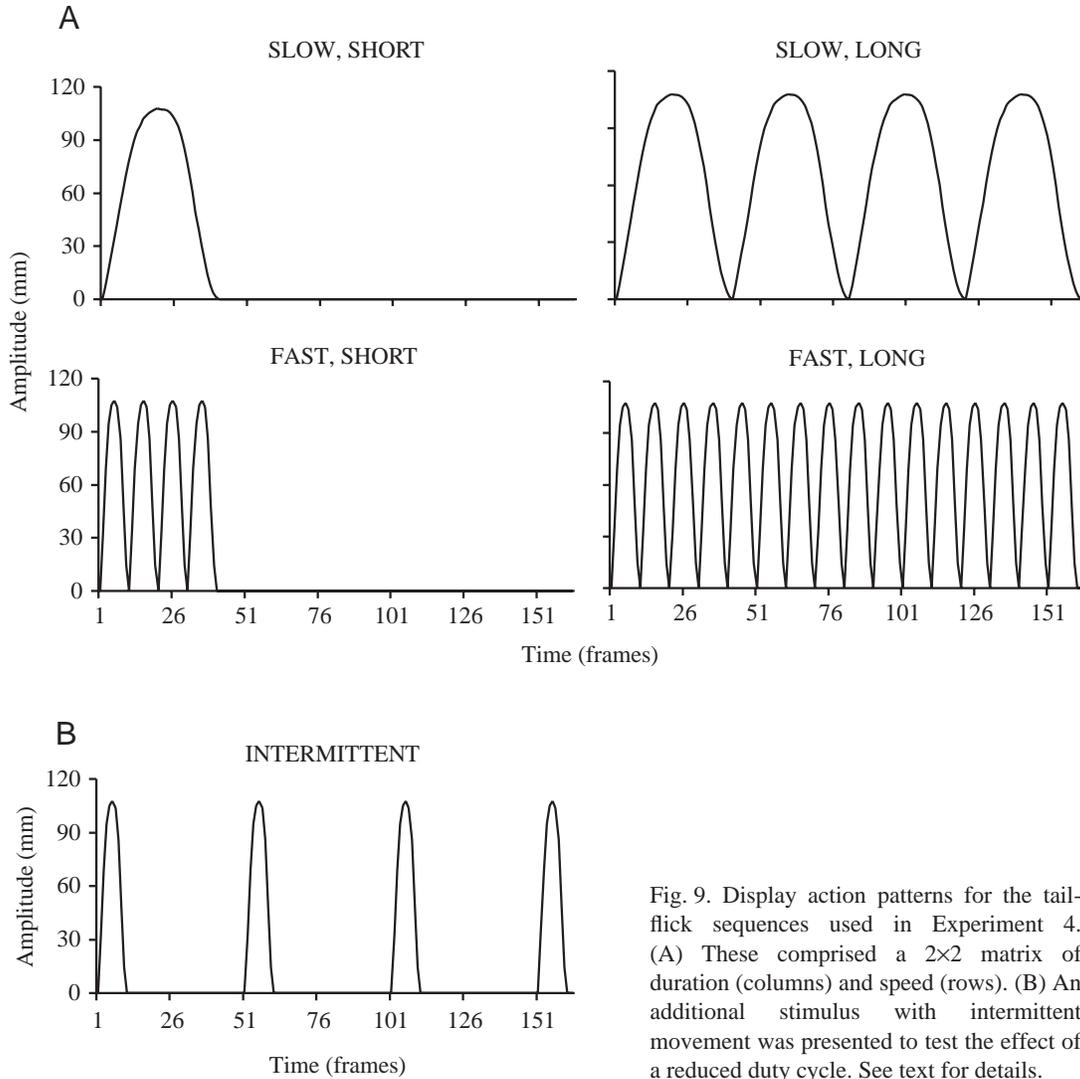In the final experiment, we explored the interaction between

Fig. 8. (A) Probability of an orienting response and (B) latency to respond to Experiment 3 sequences in which tail-flick amplitude was manipulated. Values are means + S.E.M.

A

B

Fig. 9. Display action patterns for the tail-flick sequences used in Experiment 4. (A) These comprised a 2×2 matrix of duration (columns) and speed (rows). (B) An additional stimulus with intermittent movement was presented to test the effect of a reduced duty cycle. See text for details.

tail-flick speed and duration (Fig. 9). Results suggest that this latter parameter is particularly important (Fig. 10). The probability of a response was unaffected by speed, but increased significantly when signal duration was extended. Furthermore, longer signals were equally effective, irrespective of speed. Nevertheless, there was some evidence for a subtle interaction between these two variables because the effect of duration, within speed class, was only significant for the fast tail-flick sequences.

Comparison between the INTERMITTENT stimulus, which depicted realistic pauses between tail-flicks, and the FAST,SHORT stimulus, which presented the same number of movements without breaks, suggests that pauses increase the probability of receiver response. In addition, the INTERMITTENT stimulus was as
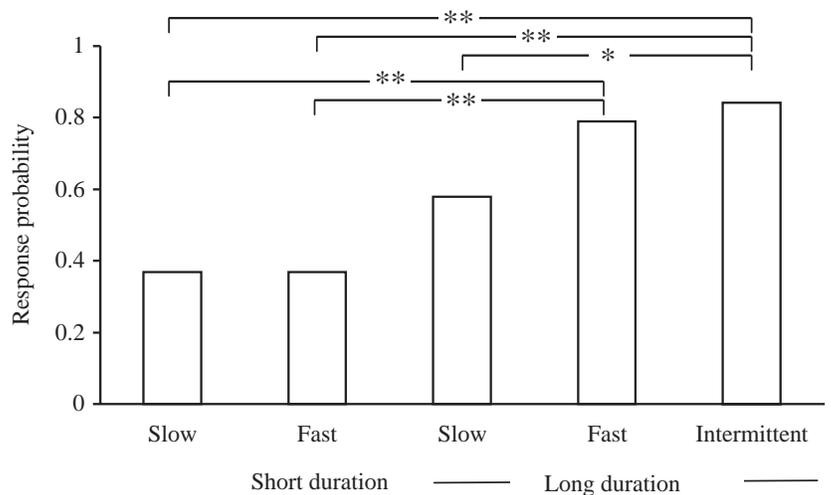

Fig. 10. Probability of an orienting response to Experiment 4 sequences, which varied in terms of speed, duration and duty cycle (*$P<0.05$; **$P<0.01$).

effective as the matched-duration FAST,LONG stimulus, suggesting that large differences in period do not affect response probability, and that there does not seem to be a cost associated with reduced duty cycle. Taken together, these results are consistent with the idea that intermittent movement is an energetically cheap strategy for achieving the efficacy benefit of increased duration.

The propensity of a signal to attract attention is an important consideration for understanding design. Some animals achieve this goal using high intensity, short duration, alerting components (Richards, 1981; Fleishman, 1992). However, both quantitative analyses of display structure (Peters and Evans, 2003), and the results of the present series of playback experiments, indicate that Jacky dragons may have evolved an alternative approach. The most effective stimulus for eliciting orienting responses was a long duration signal with low duty cycle. This finding suggests that there may be several possible solutions to the problem of engaging the intended receiver, and invites comparative study to identify the ecological and physiological factors responsible for this variation (e.g. Ord et al., 2001; Ord and Blumstein, 2002; Ord et al., 2002a).
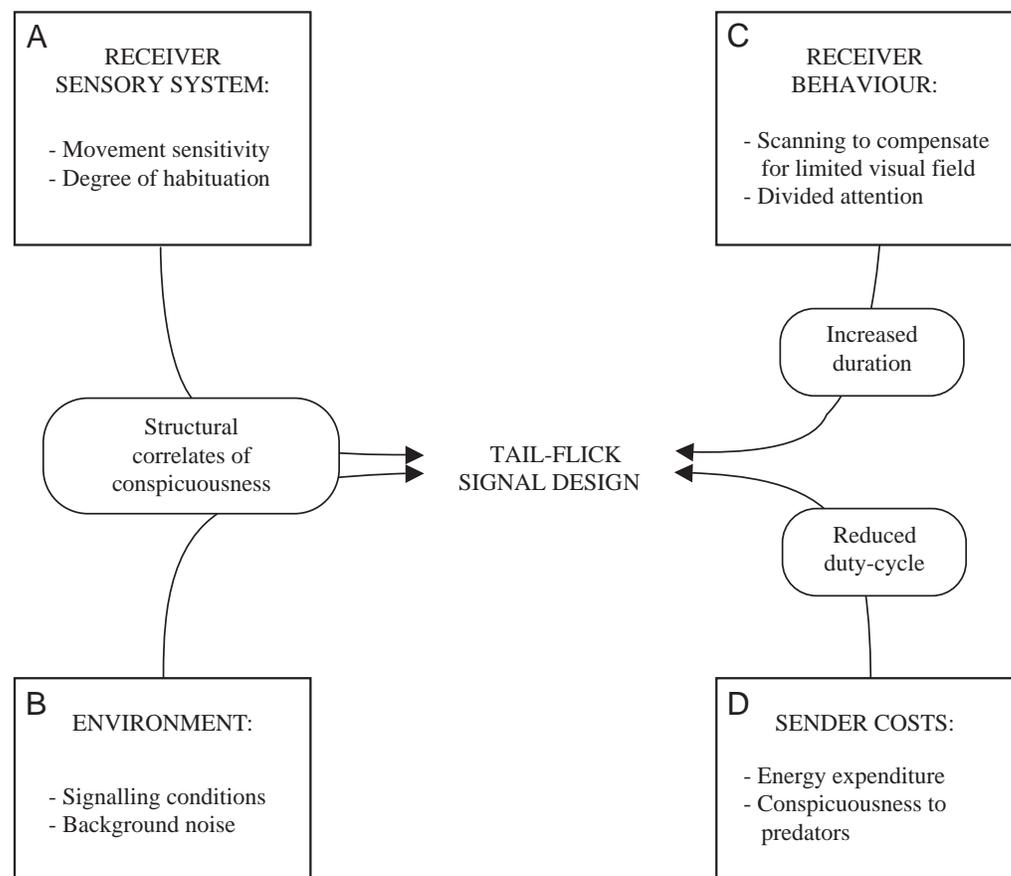
Tail-flick design: a working hypothesis

In Fig. 11 we present a preliminary model of the interactions between factors that are likely to have shaped the structure of this introductory display component. Movement-based signals are constrained by the sensory capabilities of receivers

(Fig. 11A). The evolutionary significance of perceptual processes is well documented (Endler, 1991; Guilford and Dawkins, 1991; Pagel, 1993; Dawkins and Guilford, 1996; Endler and Basolo, 1998). For example, female butterflies in the Genus *Lycaena* ensure recognition by having visual-pigment absorbance characteristics that are well matched to the wing reflectance spectra of conspecific males (Bernard and Remington, 1991). Similarly, the auditory periphery of cricket frogs *Acris crepitans* is well-matched to the call structure of their own species (Ryan et al., 1992), and the preference of female Túngara frogs *Physalaemus pustulosus* for low frequency male chucks reflects the tuning of their basilar papillae (Ryan et al., 1990b; Ryan and Rand, 1990). Studies of acoustic communication in insects and anuran amphibians have yielded many other examples of such detailed correspondence between signal structure and receiver sensory characteristics (Gerhardt and Huber, 2002). In Jacky dragons, the relative ineffectiveness of a stationary tail in Experiment 2 (Fig. 6) highlights the importance of movement for signal detection, and suggests that motion-processing constraints will probably have influenced tail-flick structure in an analogous fashion.

Signal design is also a product of the environment (Fig. 11B; Endler, 1992). Signals must be detectable to be effective, and conspicuousness is often a function of habitat characteristics. Endler (1991) demonstrated that the colour patterns of guppies *Poecilia reticulata* appear different in varying light

Fig. 11. Factors likely to have contributed to the design of the Jacky dragon tail-flick. The sensory properties of receivers (A) and the environmental conditions (B), interact to define signal conspicuousness. Important characteristics of receiver behaviour (C) include compensation for a limited (<360°) visual field by constant scanning of the environment and engagement of visual processing by other stimuli, such as predators and insect prey. These factors predict increased signal duration. Energetic cost (D) has probably selected for a reduced duty cycle. In addition, the tail-flick is less likely to compromise anti-predator responses than other motor patterns.

A
RECEIVER SENSORY SYSTEM:
- Movement sensitivity
- Degree of habituation

C
RECEIVER BEHAVIOUR:
- Scanning to compensate for limited visual field
- Divided attention

B
ENVIRONMENT:
- Signalling conditions
- Background noise

D
SENDER COSTS:
- Energy expenditure
- Conspicuousness to predators

Structural correlates of conspicuousness → TAIL-FLICK SIGNAL DESIGN ← Increased duration / Reduced duty-cycle

environments, and that this affects their relative conspicuousness to females and predators. Similarly, Leal and Fleishman (2002) have recently shown that two sympatric lizards *Anolis cooki* and *A. cristatellus* occupy different terrestrial microhabitats that ensure optimal signalling conditions for each. *Anolis cristatellus* is found in microhabitats that have low ultraviolet (UV) radiance (background light). These lizards are sensitive to UV and have UV-reflecting dewlap regions. Conversely, *A. cooki* have relatively low UV spectral sensitivity, no UV-reflecting structures in their dewlap, and occupy microhabitats that are characterised by high UV radiance. Differences between microhabitats have also promoted divergence in call structure between subspecies of cricket frogs *Acris crepitanus* (Ryan et al., 1990a).

Conspicuousness can also be enhanced through temporal adjustments in signalling behaviour. For example, guppies court early and late in the day during conditions of low light to enhance their conspicuousness to conspecifics, while minimizing detection by predators (Endler, 1991). Similarly, Panamanian katydids (Genus: *Neoconcephalus*) adjust their singing behaviour to avoid interference from sympatric congeners (Greenfield, 1988). Sensitivity to environmental noise also allows for structural change to suit signalling conditions. Amplitude compensation in noisy environments occurs in the acoustic signals of zebra finches *Taeniopygia guttata* (Cynx et al., 1998), white-lipped frogs *Leptodactylus albilabris* (Lopez et al., 1988), and budgerigars *Melopsittacus undulatus* (Manabe et al., 1998). There have been no comparable reports for movement-based displays. It is intriguing to consider whether Jacky dragons might adjust their introductory tail-flicks (e.g. by increasing duration) on windy days; this is a topic for future study.

The environment also defines the state of receiver nervous systems at the moment of signal production. Consistent background movement over long periods will cause selective habituation/adaptation. To properly understand signal perception, it is necessary to study receivers in this state, which was the rationale for incorporating a baseline period of moving vegetation playback in Experiments 2–4. It follows that signal conspicuousness should not be a simple product of the average contrast between structure and background, but rather, will vary with the recent experience of the receiver. For example, tail-flicks may be more easily recognised when recent wind conditions have been stable than when they have been variable. These examples illustrate the way in which the structural correlates of conspicuousness are defined by the interaction between environmental conditions and receiver sensory systems.

A particular problem for communication in the visual domain is that signals are not omni-directional; the probability of attracting the attention of conspecifics is constrained by receiver orientation (Fig. 11C). Physical adaptations such as laterally placed eyes (Moermond, 1981), and a high concentration of motion-sensitive cells in the periphery (Stein and Gaither, 1983), increase the likelihood of detecting salient visual motion. However, constant scanning of the environment is also necessary to obtain full coverage of the visual field. This behaviour is necessary, not only for detecting signalling conspecifics, but also insect prey and aerial predators. The attention of receivers will hence often be engaged by other functionally critical tasks. The tail-flick component is typically one or two orders of magnitude longer than the other motor patterns that comprise the push-up display of the Jacky dragon, which are very brief (ca. 500 ms; Peters and Ord, in press). The results of our playback experiments suggest that increasing signal duration will be the most effective strategy for enhancing the probability of an orienting response.

However, longer signal durations are also likely to impose costs (Fig. 11D). In many systems, energetic costs are proportional to signal duration or rate (Taigen and Wells, 1985; Ryan, 1988; Andersson, 1989; Vehrencamp et al., 1989; Eberhardt, 1994; Mappes et al., 1996; Kotiaho et al., 1998). For example, oxygen consumption by Carolina wrens *Thryothorus carolinensis* increases exponentially with greater singing rates, and is higher than for other non-flight activities (Eberhardt, 1994). Similarly, Kotiaho et al. (1998) have shown that the drumming performed by male wolf spiders *Hygrolycosa rubrofasciata* during sexual displays is more demanding than locomotion. Another important cost of highly conspicuous displays is increased predation risk (McKinney, 1965; Cade, 1975; Burk, 1982; Ryan et al., 1982; Yasukawa, 1989). For example, female Túngara frogs are attracted to the low frequency chucks of male frogs, but so are fringe-lipped bats *Trachops cirrhosus* (Ryan et al., 1982).

It seems likely that the tail-flick is better suited to sustained signalling than other motor patterns in the Jacky dragon display repertoire. The tail is a relatively light structure, but nevertheless able to sweep a large area of the visual field (Peters and Evans, 2003). The only other display motor pattern with structural characteristics that suggest equivalent conspicuousness is the body-rock, which consists of a wave travelling anterior–posterior down the lizard's body (Peters and Ord, in press). However, this involves displacing the whole mass of the animal off the substrate and is hence likely to be relatively costly. The strategy of intermittent signalling with the tail-flick clearly achieves signal efficacy comparable to that of continuous movement (Fig. 10), so this aspect of signal structure is consistent with selection for reduced energetic cost (Fig. 11D). Furthermore, because Jacky dragons face predation from both terrestrial and aerial predators in their natural habitat, they must be ready to respond to impending threats, even while signalling. Unlike other motor patterns, such as push-ups and body-rocks, which involve the legs (Peters and Evans, 2003; Peters and Ord, in press), tail-flicks probably do not compromise the capacity for rapid flight. We plan to measure both the rate of energy consumption and the changes in conspicuousness to predators associated with different displays. We anticipate that the design of this signal, as in many other systems, will reflect a trade-off between efficacy and cost.

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