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# Computer-animated stimuli to measure motion sensitivity: constraints on signal design in the Jacky dragon

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## Abstract

Identifying perceptual thresholds is critical for understanding the mechanisms that underlie signal evolution. Using computer-animated stimuli, we examined visual speed sensitivity in the Jacky dragon *Amphibolurus muricatus*, a species that makes extensive use of rapid motor patterns in social communication. First, focal lizards were tested in discrimination trials using random-dot kinematograms displaying combinations of speed, coherence, and direction. Second, we measured subject lizards' ability to predict the appearance of a secondary reinforcer (1 of 3 different computer-generated animations of invertebrates: cricket, spider, and mite) based on the direction of movement of a field of drifting dots by following a set of behavioural responses (e.g., orienting response, latency to respond) to our virtual stimuli. We found an effect of both speed and coherence, as well as an interaction between these 2 factors on the perception of moving stimuli. Overall, our results showed that Jacky dragons have acute sensitivity to high speeds. We then employed an optic flow analysis to match the performance to ecologically relevant motion. Our results suggest that the Jacky dragon visual system may have been shaped to detect fast motion. This pre-existing sensitivity may have constrained the evolution of conspecific displays. In contrast, Jacky dragons may have difficulty in detecting the movement of ambush predators, such as snakes and of some invertebrate prey. Our study also demonstrates the potential of the computer-animated stimuli technique for conducting nonintrusive tests to explore motion range and sensitivity in a visually mediated species.

**Key words**: *Amphibolurus muricatus*, Jacky dragon, motion sensitivity, random-dot kinematograms, signal evolution, virtual stimuli.

Identifying motion sensitivity and the range of motion to which a particular species is sensitive for visual discrimination is important for building a deeper understanding of the selective pressures that have shaped the evolution of visual signals in animal communication (Clifford and Ibbotson 2002). Sensitivity to moving objects is one of the primary advantages of vision (Clifford and Ibbotson 2002), with important implications across various ecological contexts (e.g., detecting food or predators, courtship, social interactions). Understanding the mechanisms that underlie motion sensitivity provides a basis in which to examine the sensory capacity involved in signal evolution of a species.

Theories of signal design suggest that the efficacy of a signal resides in its ability to: 1) propagate well and rapidly through a dynamic environment, 2) stimulate receiver sense organs, and finally

3) carry information that is meaningful to both the receiver and signaller (Guilford and Dawkins 1991, 1993; Bradbury and Vehrencamp 1998). It is now recognized that signals are shaped by evolutionary factors such as perceptual (Basolo 1990; Ryan and Rand 1993), environmental (Marchetti 1993), or social factors (Blumstein and Armitage 1997; Leal and Rodríguez-Robles 1997; Ord et al. 2002a), and eventually by the interaction between these processes (Jenssen 1977). Sensitivity to moving objects in an organism's environment is paralleled to the mechanism that exploits the visual processing system.

Here, we investigated visual sensitivity to speed and motion in the Jacky dragon *Amphibolurus muricatus*, an agamid species whose movement-based signals are characterized by complex visual displays used in social communication (Ord and Evans 2002; Ord et al. 2002b; Peters and Evans 2003a, 2003b). Similar to *Anolis* lizards (Jensen 1977; Bels 1986), Jacky dragons exhibit stereotyped aggressive signals (Carpenter et al. 1970; Peters and Ord 2003), but also produce appeasement displays (Carpenter and Ferguson 1977). Jacky lizards are highly sensitive to the motion characteristics (Peters and Evans 2003a; Woo and Rieucau 2012) and syntax (Woo and Rieucau 2015) of social signals, with those displays being designed to be conspicuous against the movement of windblown vegetation that produces environmental noise (Peters and Evans 2003a, 2003b; Woo and Rieucau 2013).

The movement-based signals of the Jacky dragon have been constrained by the selection pressures of a complex environment that were likely shaped by perceptual, environmental, and social factors (Ord et al. 2002b). Rapid and distinct movement characteristics such as direction, speed, acceleration and sweep area serve as an alerting mechanism to conspecifics (Peters and Evans 2003b). For instance, sensitivity to these motion vectors are critical to male–male interactions when competing for territory or a potential mate (Carpenter et al. 1970), and failure to perceive these signals may result in the inability to compete for resources.

Experimental research in animal behaviour has been the platform for the development of an impressive range of artificial stimuli to stage animal interactions (Noble 1939; Tinbergen and Perdeck 1951; Gallup and Capper 1970; McGregor et al. 1992; Fernandez-Juricic et al. 2006; Rieucau and Giraldeau 2009; Krause et al. 2011; Ioannou et al. 2012; Polverino and Porfiri 2013), with the ultimate aim being to insure a precise control of what focal individuals get to see or experience. Technological progress has permitted researchers to develop computer-generated animated stimuli with high degree of fidelity for both morphological and dynamic features (see e.g., Rosenthal 2000; Peters and Evans 2003a, 2003b; Saverino and Gerlai 2008; Baldauf et al. 2009; Campbell et al. 2009; Gerlai et al. 2009; Woo and Rieucau 2011, 2013, 2015; and the articles in the present issue). The computer-generated stimuli approach is becoming increasingly popular as it offers researchers with the ability to produce standardized visual stimuli while reducing the variable behaviour of life animal demonstrators during experimentations. As we intend to show in the present study, the technique can be employed to design noninvasive tests to explore motion range and sensitivity.

We employed computer-generated random-dot kinematograms (RDKs) to measure basic sensitivity to motion and sensitivity to signal speed. RDKs are a classic psychophysical tool used to measure motion thresholds in the visual system (Newsome and Paré 1988; Watamaniuk et al. 1993; Bischof et al. 1999). In humans, RDKs have successfully employed to demonstrate relationships to sensitivity to adaptation and habituation (Bex et al. 1999), global order processing (Ledgeway 1999), optic flow patterns (Clifford et al. 1999), biological motion (Grossman and Blake 1999), and discrimination between comparative vectors of motion (Curran and Braddick 2000). They also have been successfully employed to examine motion sensitivity in various animal species including Jacky dragon (Woo et al. 2009), rat and mice (Douglas et al. 2006), albino ferret *Mustela putorius furo* (Hupfeld et al. 2006), pigeon *Columba livia* (Goto et al. 2002; Ushitani et al. 2004), pigtail macaque *Macaca nemestrina* (Kiorpes and Kiper 1996; Kiorpes and Movshon 1998, 2004), domestic cat (Burnat et al. 2002), and barn owl *Tyto alba* (Willigen et al. 2003).

Previous research has demonstrated the efficiency of RDKs to produce cues that engage motion processing systems, but without triggering recognition mechanisms, since they do not resemble any biologically relevant stimulus (Curran and Braddick 2000). Therefore, the properties of RDKs allow to assess sensitivity to motion speed without cues (e.g., position or form) that might be indicative of a biologically meaningful object. We measured motion sensitivity by generating variations in RDK speed (degrees per second) and coherence (percentage of RDKs moving in the same direction). The capacity to resolve moving dots may provide insight into the operation of the visual system, and its sensitivity to speed (Vreven and Verghese 2002) and coherence (Verghese and McKee 2004) levels. Ultimately, discrimination of the RDK features may also help to identify how the visual system separates the motion patterns of ecologically relevant stimuli (Bischof et al. 1999) from irrelevant complex visual noise (Scase et al. 1996). Movement, shape, and color of the dots do not represent any biologically inherent recognition, and, therefore, the decision to use dots was justified because it did not trigger any salient responses that would be elicited at the presentation of stimulus that was inherently biological. By understanding the way motion is perceived, we can link the mechanisms associated with motion detection to biologically inherent motion vectors in the Jacky dragon visual system.

To deconstruct the parameters of motion within each display, we first examined the basic perception to movement. By measuring the visual threshold in its range of speed and coherence, we could then match motion patterns that are likely perceived by the Jacky dragon visual system. We first characterized the motion sensitivity of the Jacky dragon. Second, we measured the lizards' ability to predict the appearance of a secondary reinforcer (a computer-generated animation of 3 invertebrates: cricket, spider, and mite) based on the direction of movement of a field of drifting dots. To our knowledge, there have been no psychophysical studies that employed an instrumental learning paradigm to measure sensory thresholds in agamids. Consequently, we included the secondary reinforcers to encourage lizards to respond to a stimulus with biologically meaningful characteristics, such as the movement and morphology of prey. Once sensitivity ranges based on responses to motion and speed characteristics were established, we matched these profiles to biologically meaningful visual cues, such as different social displays, or prey and predator movements. We then considered how these salient motion patterns might have influenced the evolution of signal design.

## Materials and Methods

### Subjects

The subjects were 5 male Jacky dragons collected from La Perouse, Royal, and Lane Cove National Parks in and around Sydney, Australia, and housed in indoor facilities at Macquarie University. We fed the subjects live crickets *Acheta domesticus* that we dusted with vitamin supplements (RepCal, Victoria, Australia) twice a week. We also provided with water *ad libitum* in small bowls. Lizards were maintained under a 12:12 h L/D cycle with additional heat lamps (125W Spotone, Phillips, NSW, Australia) for 10 h per day. Ultraviolet lamps (300W Ultra-Vitalux, Osram, NSW, Australia) over the pens were illuminated for half an hour each morning to prevent vitamin deficiency. Subjects were maintained in glass terrariums (60 × 60 × 60 cm) that were placed on movable trolleys. This arrangement allowed us to better control viewing distance.

## Virtual stimuli

### *Random-dot kinematograms*

We generated a series of 200 RDKs using Visual Programming under UNIX (VPixx v1.79, VPixx Technologies Inc., 2002). Dots were 5 pixels each and placed in a 30° × 20° visual field. Each dot had a lifetime of 0.5 s. Dots were generated with variable speed and coherent motion characteristics. Speed was measured in degrees $s^{-1}$ (°/s). Coherence was defined as the proportion (%) of dots moving either leftward or rightward. We manipulated the proportion of the RDK stimulus that drifted in a coherent direction to vary signal strength. When all dots moved in the same direction (100% coherence), the motion signal was at maximum strength. The introduction of proportionally more dots moving in random directions degraded the coherent motion signal. We created a total of 128 stimuli by combining a range of speeds (0.5°, 2.5°, 5°, 10°, 20°, 40°, 80°, 160°/s), coherence values (0%, 2.5%, 5%, 10%, 20%, 40%, 80%, 100%), and 2 directions (left or right) (Figure 1).

We exported the RDKs from VPixx as Motion JPEG-B files and converted to QuickTime™ movies. RDKs were then rendered using Final Cut Pro 3 (Apple Computer Inc., Cupertino, CA, USA) for video playback. Dots were presented for a total of 15 s (Figure 1). At 7.5 s, an electronically generated marker tone embedded in the audio track signalled the presentation of a secondary reinforcer (a computer-generated invertebrate) displayed on a monitor either to the left or the right of the subject. The tone was only audible during the review of our video to indicate the conclusion of the RDKs and onset of the secondary reinforcer. The sound marker was used for scoring response latency. Each stimulus began with 2.5 s of 0% dot coherence at the respective speed. A 5.0 s response window, during which the RDKs varied in coherent motion, followed the initial sequence. At 7.5 s, the dots cross-faded (duration 0.25 s) to 100% coherence in 1 direction, maintaining current speed to prevent a startle response from the subject.

### *Secondary reinforcers: virtual invertebrates*

We created 3 types of invertebrate stimuli to use as secondary reinforcers (Figure 2). A cricket, spider, and mite were generated using Lightwave v7.5 3D animation software (NewTek Inc., San Antonio, TX, USA). Movement characteristics were matched to speed values previously known to elicit attack behaviour. We generated 50

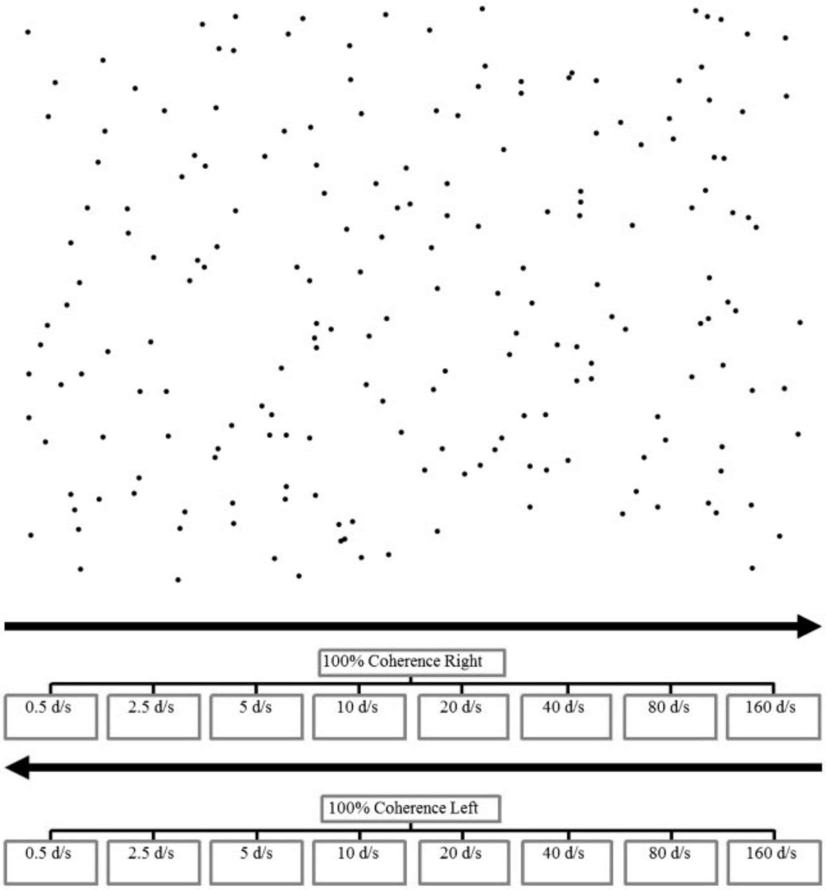

**Figure 1.** A schematic diagram to depict the RDK stimuli and the combinations in coherence, speed, and direction (right, left), as displayed to the subjects. One hundred and twenty-eight RDK combinations were displayed to the lizards, which ranged in their combination of 8 speeds (0.5°, 2.5°, 5°, 10°, 20°, 40°, 80°, 160°/s), 8 coherence values (0%, 2.5%, 5%, 10%, 20%, 40%, 80%, 100%), and 2 directions (left or right). For example, 1 possible combination for display would be an RDK stimulus that was a speed of 20°/s at 40% coherence in the left direction.

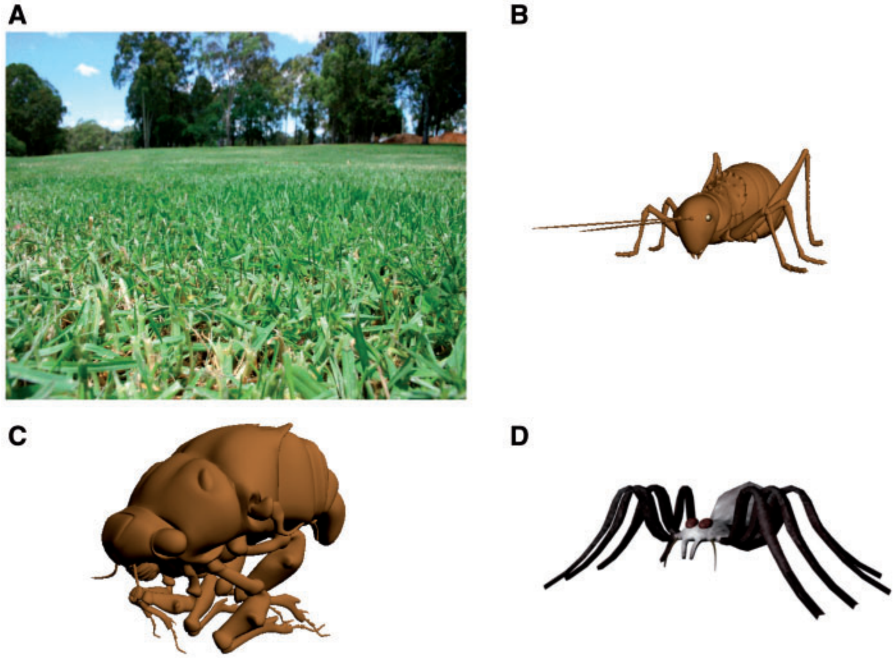

**Figure 2.** Virtual stimuli: (A) background vegetation, and the 3 computer-generated animation of (B) cricket, (C) mite and (D) spider employed as secondary reinforcers.

sequences (20 for the virtual cricket, 15 for the virtual spider, and 15 for the virtual mite) with variations in speed and motion paths to prevent habituation. We then used a video still background of grass with native flora on the horizon to simulate invertebrates in a natural environment. Lastly, we randomly assigned secondary reinforcers to our RDK stimuli.

## Equipment

We used 3 separate video playback systems for stimulus presentation. Two systems consisted of an iMac (Apple Computer Inc.) connected to an external LaCie d2 hard drive (Hillsboro, OR, USA) with Final Cut Pro 3 for presentation of playback stimuli (i.e., invertebrate or background). The digital signal was sent to a Canopus® ADVC110 (Melbourne, Victoria Australia) for analog conversion and then displayed on a Sony Trinitron monitor (Model Nos. PVM-14M2A/ PVM-14L2, Sony Corporation, Shinagawa, Tokyo, Japan). All monitors and terrariums were placed on movable trolleys. A Canon digital camcorder with 22X optical zoom (Model No. MV650i, Canon Inc., Japan) mounted to a stationary tripod (Gruppo Manfrotto®, Italy), recorded responses to stimuli directly to a Sony VCR (Sony Corporation, Shinagawa, Tokyo, Japan). Recorded images were sent to a color viewfinder so that the experimenter could monitor behaviour continuously. The third computer system consisted of an iMac connected to a LaCie hard drive that contained the RDK stimuli. The digital signal was sent through a Sony MiniDV digital video recorder (Model No. GV-D300E, Sony Corporation, Japan) PAL player and then to the Sony Trinitron color display monitor (PVM-14N5A). Video playback was adjusted for PAL-DV standard (5:1 compression; horizontal resolution 575 lines; 25 frames $s^{-1}$).

## Experimental procedure

We initially trained the 5 subjects to acquire the basic task contingency in a series of trials involving 3 speeds (5°, 20°, 80°/s), with the coherence level maintained at 100%. Lizards were tested over 5 consecutive days at 20 trials per day, totalling 100 trials per individual. Subjects were successful at learning the task during this training period (Woo 2006; Woo and Burke 2008).

During the test procedure, we tested the subjects over 4 consecutive days and each lizard was given 32 trials per day, in 2 blocks of 16 trials. To further encourage the lizards to learn the paradigm, we used a primary reinforcer of a mealworm coupled with secondary reinforcer (virtual invertebrates) that was played on the adjacent video monitor. The intervals between 2 consecutive trials ranged from 30 to 60 s.

Sensitivity to different motion characteristics was determined by measuring the subjects' reaction to a range of speeds at a variety of signal strengths. We presented the subjects with moving dots on a central monitor with 2 adjacent monitors to either side (Figure 3). Individual subjects were exposed to each of the 128 different stimuli twice, in a random order. Each trial lasted 15 s. For each trial, dots began with 2.5 s of 0% coherence, and then continued with 5 s of coherent directional dots (Figure 3). Subjects were required to respond within this period. We followed several behavioural responses including orientating response, that is, the observable redirection of the focal lizard's head towards the video sequence as defined by Peters and Evans (2003a) and similar to (Woo and Rieucau 2012, 2015), approach, or lunging attack in the direction of the correct monitor. We also measured the latency to respond to the presented stimuli. We defined response latency as the time (in seconds) it took for a focal individual to select either the left or right monitor. If no response was induced, subjects were given the longest possible latency of 5 s (e.g., 125 frames). After 7.5 s, the dots on the central monitor became 100% coherent in the appropriate direction to serve as a contingency reminder, whereupon an invertebrate appeared on the corresponding monitor.

## Analysis of image motion

We recorded and analysed several movement patterns that are ecologically relevant to Jacky dragons. Sequences included several

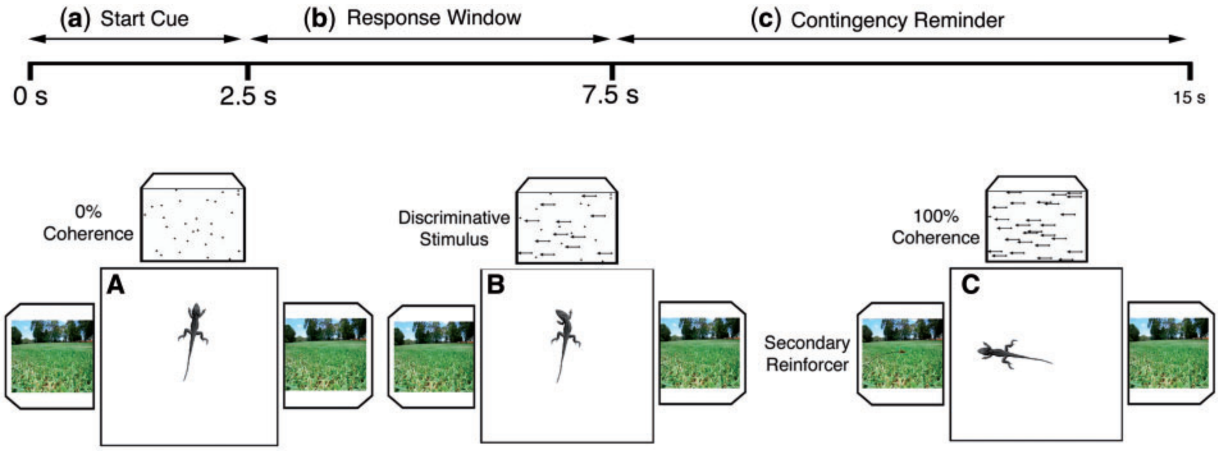

**Figure 3.** Description of the sequence of events during a test trial showing the subject orientation to the correct monitor using RDK motion characteristics.

examples of social signals, such as tail-flicks ($n = 5$), push-up body rocks (PUBRs) ($n = 6$), and slow arm waves ($n = 4$) (Ord and Evans 2002, 2003), a potential prey item (cricket *Achetus domesticus*, $n = 5$), and several snake species selected to represent ambush predators (death adder *Acanthophis antarcticus*, $n = 3$; diamond python *Morelia spilota*, $n = 3$; broad-headed snake *Hoplocephalus bungaroides*, $n = 3$; small-eyed snake *Cryptophis nigrescens*, $n = 3$). We also included examples of background vegetation movement recorded in a range of wind conditions (*Banksia* spp., $n = 9$; see Figure 4).

Over the course of several years, we filmed all display sequences with Canon digital camcorders with 22 × optical zoom mounted on stationary tripods, and cataloged them for later use. Subsequently, we extracted Jacky dragon tail-flicks, PUBRs, and slow arm waves from archival footage (Ord and Evans 2002; Ord et al. 2002a; Van Dyk and Evans 2007). We obtained cricket footage by filming individuals moving in a cardboard box lined with white paper. Snake species were selected based on sympatric distribution (Greer 1993, 1997). Three snake actions were filmed to provide an estimate of the full range of predatory movements: general locomotion and striking. We elected to analyse the stalking footage, as it would be most representative of snake predatory motion. Vegetation was filmed at various locations in La Perouse and Murramurang National Parks along the east coast of New South Wales, Australia (Peters et al. 2007). National parks were chosen based upon known geographic distribution of Jacky dragon populations. The vegetation selected was that in which lizards were known to bask. We converted all clips from Apple QuickTime$^{\text{TM}}$ movies into AVI format. Sequences were then analysed using Analysis of Image Motion (AIM; Matlab v7.1 – The MathWorks, Inc., Natick, MA). AIM is a Matlab-based optic flow movement analysis program that produces speed–time profiles of visual motion from video sequences (Peters et al. 2002; Woo and Rieucau 2008). Using AIM algorithms, we were able to summarize the speed characteristics of each movement type: social displays, prey and predator movement, and windblown vegetation (Figure 4).

### Statistical analysis

For our behavioural responses, we recorded the percent correct orientation to the appropriate monitor and latency of correct responses. We used a general linear model (GLM) analysis of variance (ANOVA) to test for a main effect of speed (8 levels: 0.5°, 2.5°, 5°, 10°, 20°, 40°, 80°, 160°/s) and coherence (8 levels: 0%, 2.5%, 5%, 10%, 20%, 40%, 80%, 100%) and the interaction between these 2 factors for both dependent variables. We then excluded 0% coherence, and used a GLM to compare the main effect of speed (8 levels: 0.5°, 2.5°, 5°, 10°, 20°, 40°, 80°, 160°/s) and coherence (7 levels: 2.5%, 5%, 10%, 20%, 40%, 80%, 100%) and the interaction between them.

We analysed the optic flow measurements using a one-way ANOVA. Least Significant Difference (LSD) post hoc test were used to compare differences between the speeds of each type of movement pattern. We plotted the average speed of each motor pattern type (± SD) across motion sensitivity results. Statistical analyses were performed using SPSS® 11 for Mac OS X (SPSS Inc., Chicago, IL, USA).

## Results

### Percent correct

We found a significant main effect of speed ($F_{7,49} = 30.58$, $P < 0.05$) and coherence ($F_{7,49} = 221.58$, $P < 0.05$), and a significant interaction between speed and coherence ($F_{7,49} = 6.67$, $P < 0.05$) on the percent of correct orienting response (Figure 5). The exclusion of 0% coherence did not affect these significant results: main effect for speed ($F_{7,42} = 30.58$, $P < 0.05$), main effect for coherence ($F_{6,42} = 43.15$, $P < 0.05$), and interaction between ($F_{6,42} = 6.04$, $P < 0.05$).

### Response latency

As dot speed increased, lizards reduced the amount of time it took to a focal lizard to select the correct monitor during the response window before levelling. We found a significant main effect of speed ($F_{7,49} = 22.43$, $P < 0.05$) and coherence ($F_{7,49} = 172.92$, $P < 0.05$), with an interaction between these factors ($F_{7,49} = 5.22$, $P < 0.05$) on the latency to respond (Figure 5). When 0% coherence was excluded, the pattern of results stayed much the same, with significant main effects for speed ($F_{7,42} = 22.43$, $P < 0.05$), coherence ($F_{2,42} = 49.88$, $P < 0.05$), and an interaction between speed and coherence ($F_{2,42} = 4.71$, $P < 0.05$).

### Optic flow analysis

Analysis of optic flow measurements revealed a significant difference in speed across all motion patterns (sample sizes: cricket = 50,

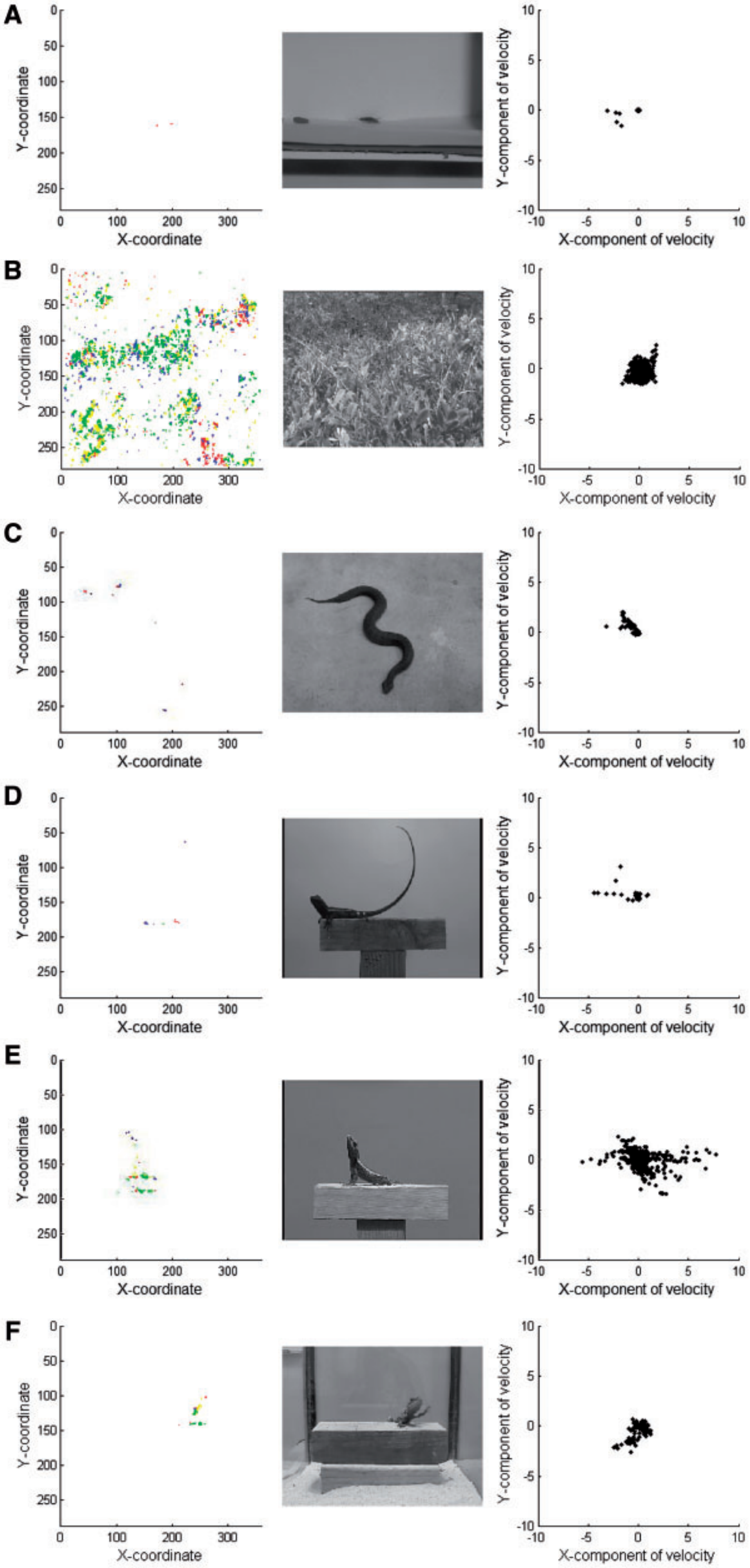

**Figure 4.** Speed profiles from the AIM for the (A) cricket, (B) background vegetation, (C) snake, (D) tail-flick, (E) PUBR, and (F) slow arm wave. Also presented representative movement of video in pixels (left panel), video image (middle panel), and velocity signature (right panel).

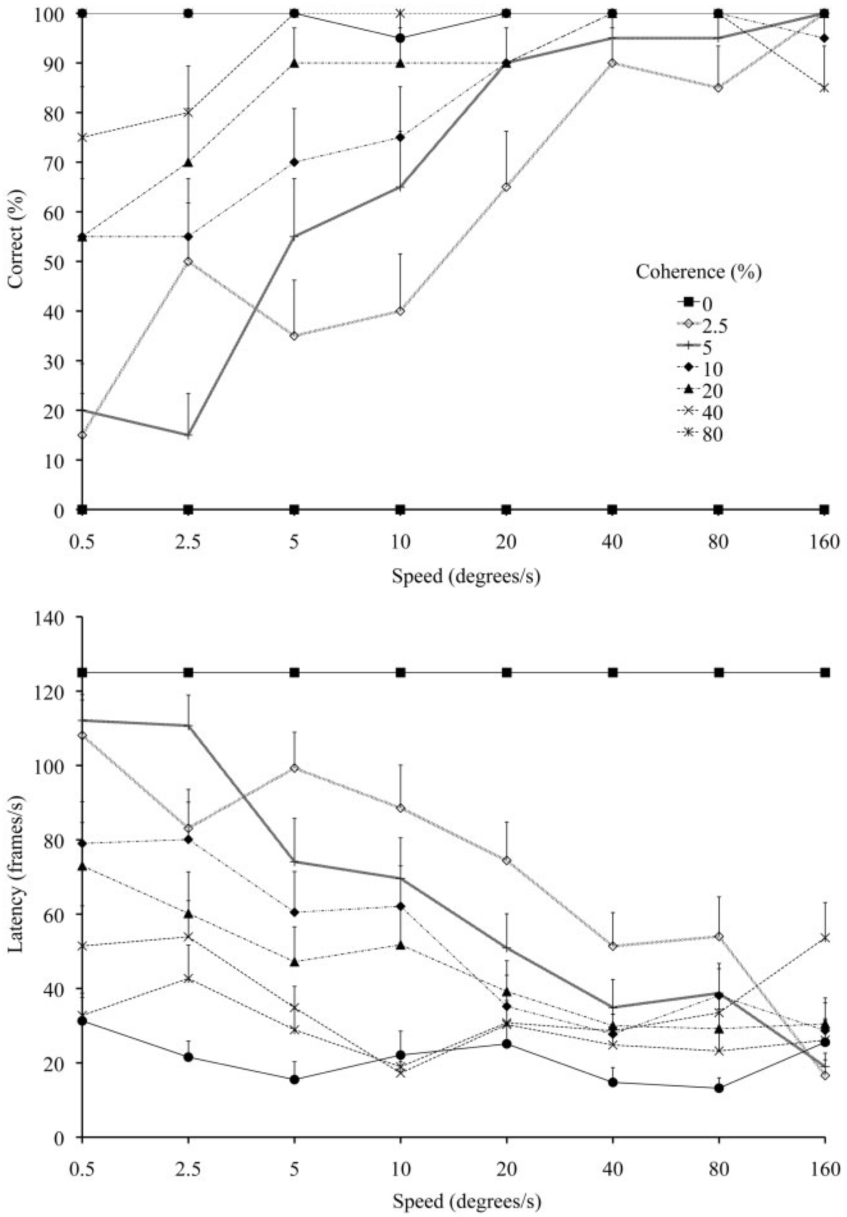

**Figure 5**. Performance of subjects across all levels of coherence as a function of speed. The upper panel shows mean percent correct responses (mean + SE) in function of speed, whereas the lower panel represents the latency of responses (mean + SE) in function of speed.

vegetation = 225, snake = 267, tail-flick = 278, PUBR = 178, slow arm wave = 202; $F_{7,1817} = 129.12$, $P < 0.05$). Post hoc tests further revealed that there was no significant speed difference between cricket and plant ($P = 0.09$), or plant and snake ($P = 0.23$). All other post hoc comparisons were statistically significant ($P < 0.05$).

## Discussion

By exploring the range of sensitivity to basic motion of the Jacky dragon, our study demonstrates that individuals can clearly resolve high-speed visual motion, but are not able to resolve movement in low sensitivity ranges. With the success of using several virtual stimuli (RDKs and computer-generated animations), our study showed that Jacky dragons are best able to detect motion at the higher end of the speed range tested (Figure 5). In particular, performance at 80 and 160°/s was almost high, as well as for coherence values >10°/s. This ability compares to the performance by rats and mice (20–80°/s; Douglas et al. 2006), pigeons (>12°/s—upper limit not tested; Bischof et al. 1999), domestic cats (15–200°/s; Burnat et al. 2002), and humans (> 0—~100°/s; Bischof et al. 1999). To detect movement at slower speeds, lizards required greater signal strength. It is, therefore, likely that Jacky dragons are sensitive to speeds that may be representative of important ecological motion.

### Sensitivity to motion

The ability of Jacky dragons to detect movement at high speeds suggests that their visual acuity may be the product of selection to perceive high levels of motion (Figure 5). This high-speed sensitivity is demonstrated by the ability of Jacky dragons to accurately resolve speeds above 20°/s. We varied the strength of the signal by manipulating the level of coherence, but sensitivity to particular speeds allowed Jacky dragons to resolve the direction of motion at both high and low coherence. Jacky dragons are known to produce highly stereotyped signals necessary to be conspicuous amongst noise from the visual field (Peters et al. 2002; Peters and Evans 2003a, 2003b; Woo and Rieucau 2013). Here, our results demonstrated that all social display speeds ranged between 20 and 40°/s. In addition, the ability to perceive dynamic social signals is not overlapped by any other motion pattern tested.

In contrast to their ability to detect high-speed motion, Jacky dragons were found to be less efficient at resolving motion speeds less than 10°/s (Figure 5). The speed of both our different virtual invertebrates and windblown vegetation was slowed to 5°/s. The speed of ground predator, such as snake, was between 2.5 and 7°/s. The speed of both the cricket and snake movement is overlapped by the motion characteristics of windblown vegetation. For predatory or prey species that need to move undetected, it is thus critical that their locomotor activity remained masked by background visual noise, such as windblown vegetation, in which Jacky dragons are least sensitive.

## Ecological correlates of speed

Our results suggest that Jacky dragon displays need to be fast, and this is an important distinction between them, and other relevant or irrelevant motion patterns (Figure 6). This is supported by previous research that showed that a high-speed tail-flick display serves as an initial alerting component to conspecifics during social communication, particularly between male aggressive interactions (Peters and Evans 2003b). Hence, the tail-flick needs to be both conspicuous and able to engage recognition mechanisms (Bradbury and Vehrencamp 1998). PUBRs, which are characterized by fast movements and a coherent trajectory, are similarly effective in eliciting orienting responses (Peters and Evans 2007). The slow arm wave, which is typically repeated at a slower rate than both the tail-flick and PUBR, is an appeasement display also known to elicit orientation responses (Peters and Ord 2003).

Lizards in a visually complex environment habituate to the movement of windblown vegetation (Woo and Rieucau 2013). Fleishman (1986) suggests that there are 2 ways in which lizards discriminate between important motion characteristics and irrelevant movements, such as windblown vegetation: 1) lizards will experience short-term habituation to present motion patterns that are common in the visual field, and 2) lizards will respond to patterns of motion that are outside the current motion patterns and, therefore, be more conspicuous. However, habituation to windblown vegetation should maximize the efficacy of important signals by highlighting the changes in display speed; the signals should be more prominent against the current motion patterns in the visual field (Fleishman 1988). Jacky dragons should perceive significant motion patterns, such as those used for communication, as the visual system is under selection pressure to accurately detect prey and predator movements. However, the motion of windblown vegetation may also mask cryptic movements that have been developed by both prey and ground predators.

Defensive behaviour by prey to avoid predation would be to decrease activity and remain motionless (Juliano and Gravel 2002).

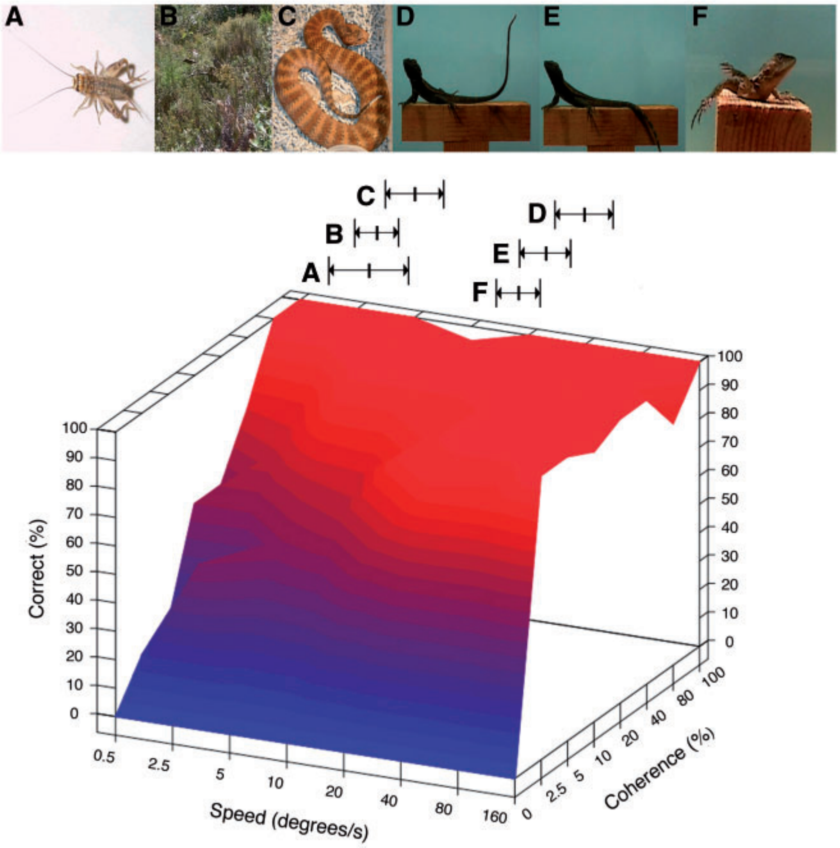

**Figure 6.** Overview of the motion sensitivity results: percentage of correct responses in function of speed and coherence as they likely correlated to the Jacky dragon's motion sensitivity regions for (A) invertebrates, (B) vegetation movement, and (C) snakes, (D) tail-flick, (E) PUBR, and (F) slow arm wave.

Cryptic behaviour decreases individual conspicuousness and attracts less attention (Marimuthu 1997), while the production of fast movement becomes a disadvantage in the presence of a predator (Hatle et al. 2002). Prey perception of predator movement, such as that of Jacky dragons, may have encouraged the development of a defensive strategy in which their own movement characteristics have been tailored to fall below the low sensitivity threshold.

There are 2 potential mechanisms by which predators could attack Jacky dragons. First, predators may undertake a passive "sit-and-wait" strategy and adopt the similar motion characteristics of natural objects that bear no threat, such as moving vegetation (Fleishman 1985). For instance, the ability for snakes to utilize moving vegetation to mask their own locomotor activity allows ground predators to move closer to prey while remaining undetected (Fleishman 1992). Thus, it is critical for snakes to increase the probability of capturing prey by drawing close enough to strike at their prey with speed and accuracy, while also minimizing mechanical demands.

### Signal design

Obtaining data about the movements to which animals are sensitive is an important part of understanding the selection pressures that have driven signal design. Selection pressures on the visual system have evolved to resolve 2 key features: shape and movement. The recognition of motor pattern displays is also critical for social interactions, as they must have been important for successful communication (Peters and Evans 2003a, 2003b). For example, the sequential structure of the display action pattern has been found to be important for signal recognition; however, reversal of the syntactical structure and manipulation of lizard morphology degraded signal recognition (Woo and Rieucau 2015). Thus, the evolution of Jacky dragon signals may be partly attributed to their capacity to discriminate morphological (Van Dyk and Evans 2007) and motion features.

Sensitivity to high-speed movements appears as a selective pressure acting on signal design in the Jacky dragon. In addition, to exploiting movement space that overlaps with predator movements, we suggest that environmental features, such as windblown vegetation, have also shaped the speed characteristics of signals. Differentiation between display and vegetation speed thus maximizes signal efficacy, as they are perceived as more conspicuous (Peters and Evans 2003a, 2003b; Peters et al. 2007). Perceptual and environmental pressures may have selected a preference for fast speed motion.

The visual system of Jacky dragons may be a product of sensory exploitation selected for high-speed motion sensitivity. Based on our study, we suggest that high-speed motion is indicative of signals that are conspicuous against the movement of windblown vegetation, and which exploit a visual system adapted to recognize fast movements. However, ground predators and prey may take advantage of the inability of Jacky dragons to resolve slow moving images to their advantage. Snakes and invertebrates adopt movement patterns that are masked by windblown vegetation, and which are outside the speeds to which Jacky dragons, and possibly other lizards, are most sensitive.

Virtual animations have been extensively employed to study the visual signal characteristics in the Jacky dragon. Our study now highlights the promising potential of this technique to experimentally explore motion range and sensitivity in this species offering new insights about the selective pressures, motion characteristics and constraints that have shaped visual signal design used in Jacky dragon communication.

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## References

Baldauf SA, Kullmann H, Thünken T, Winter S, Bakker TCM, 2009. Computer animation as a tool to study preferences in the cichlid *Pelvicachromis taeniatus*. *J Fish Biol* **75**:738–746.

Basolo AL, 1990. Female preference predates the evolution of the sword in swordtail fish. *Science* **250**:808–810.

Bels V, 1986. Analysis of the display - action - pattern of *Anolis chlorocyanus* (Sauria: Iguanidae). *Copeia* **1986**:963–970.

Bex PJ, Metha AB, Makous W, 1999. Enhanced motion aftereffect for complex motions. *Vision Res* **39**:2229–2238.

Bischof WF, Reid SL, Wylie DW, Spetch ML, 1999. Perception of coherent motion in random dot displays by pigeons and humans. *Percept Psychophys* **61**:1089–1101.

Blumstein DT, Armitage KB, 1997. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *Am Nat* **150**:179–200.

Bradbury JW, Vehrencamp SL, 1998. *Principles of Animal Communication*. Sunderland (MA): Sinauer Associates.

Burnat K, Vandenbussche E, Zernicki B, 2002. Global motion detection is impaired in cats deprived of pattern vision. *Behav Brain Res* **134**:59–65.

Campbell MW, Carter JD, Proctor D, Eisenberg ML, de Waal FBM, 2009. Computer animations stimulate contagious yawning in chimpanzees. *Proc R Soc B* **276**:4255–4259.

Carpenter CC, Badham JA, Kimble B, 1970. Behavior patterns of three species of *Amphibolurus*, Agamidae. *Copeia* **1970**:497–505.

Carpenter CC, Ferguson GW, 1977. Variation and evolution of stereotyped behavior in reptiles. In: Gans H, Tinkle DW, editors. *Biology of the Reptilia*. New York: Academic Press, 335–554.

Clifford CWG, Beardsley SA, Vaina LM, 1999. The perception and discrimination of speed in complex motion. *Vision Res* **39**:2213–2227.

Clifford CWG, Ibbotson MR, 2002. Fundamental mechanisms of visual motion detection: models, cells, and functions. *Prog Neurobiol* **68**:409–437.

Curran W, Braddick OJ, 2000. Speed and direction of locally-paired dot patterns. *Vision Res* **40**:2115–2124.

Douglas RM, Neve A, Quittenbaum JP, Alam NM, Prusky GT, 2006. Perception of visual motion coherence by rats and mice. *Vision Res* **46**:2842–2847.

Fernandez-Juricic E, Gilak N, McDonald JC, Pithia P, Valcarcel A, 2006. A dynamic method to study the transmission of social foraging information in flocks using robots. *Anim Behav* **71**:901–911.

Fleishman LJ, 1985. Cryptic movement in the vine snake *Oxybelis aeneus*. *Copeia* **1985**:242–245.

Fleishman LJ, 1986. Motion detection in the presence and absence of background motion in an *Anolis* lizard. *J Comp Physiol A* **159**:711–720.

Fleishman LJ, 1988. Sensory and environmental influences on display form in *Anolis auratus*, a grass anole from Panama. *Behav Ecol Sociobiol* **22**:309–316.

Fleishman LJ, 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.

Gallup GG Jr, Capper SA, 1970. Preference for mirror-image stimulation in finches *Passer domesticus domesticus*. and parakeets, *Melopsittacus undulatus*. *Anim Behav* **18**:621–624.

Gerlai R, Fernandes Y, Pereira T, 2009. Zebrafish *Danio rerio* responds to the animated image of a predator: towards the development of an automated aversive task. *Behav Brain Res* **201**:318–324.

Goto K, Lea SEG, Dittrich WH, 2002. Discrimination of intentional and random motion paths by pigeons. *Anim Cogn* **5**:119–127.

Greer AE, 1993. *The Biology and Evolution of Australian Lizards*. Chipping Norton: Surry Beatty & Sons.

Greer AE, 1997. *The Biology and Evolution of Australian Lizards*. Chipping Norton: Surry Beatty & Sons.

Grossman E, Blake R, 1999. Perception of coherent motion, biological motion and form-from-motion under dim-light conditions. *Vision Res* **39**:3721–3727.

Guilford T, Dawkins MS, 1991. Receiver psychology and the evolution of animal signals. *Anim Behav* **42**:1–14.

Guilford T, Dawkins MS, 1993. Receiver psychology and the design of animal signals. *Trends Neurosci* **16**:430–436.

Hatle JD, Salazar BA, Whitman DW, 2002. Survival advantages in aggregations of aposematic prey, during encounters with ambush predators. *Evol Ecol* **16**:415–431.

Hupfeld D, Distler C, Hoffman KP, 2006. Motion perception deficits in albino ferrets *Mustela putorius furo*. *Vision Res* **46**:2941–2948.

Ioannou CC, Guttal V, Couzin ID, 2012. Predatory fish select for coordinated collective motion in virtual prey. *Science* **337**:1212–1215.

Jenssen TA, 1977. Evolution of anoline lizard display behavior. *Am Zool* **17**:203–215.

Juliano SA, Gravel ME, 2002. Predation and the evolution of prey behavior: an experiment with tree hole mosquitos. *Behav Ecol* **13**:301–311.

Kiorpes L, Kiper DC, 1996. Development of contrast sensitivity across the visual field in macaque monkeys *Macaca nemestrina*. *Vision Res* **36**:239–247.

Kiorpes L, Movshon JA, 1998. Peripheral and central factors limiting the development of contrast sensitivity in macaque monkeys. *Vision Res* **38**:61–70.

Kiorpes L, Movshon JA, 2004. Development of sensitivity to visual motion in macaque monkeys. *Vis Neurosci* **21**:851–859.

Krause J, Winfield AF, Deneubourg JL, 2011. Interactive robots in experimental biology. *Trends Ecol Evol* **26**:369–375.

Leal M, Rodríguez-Robles JA, 1997. Signalling displays during predator-prey interactions in a Puerto Rican anole *Anolis cristatellus*. *Anim Behav* **54**:1147–1154.

Ledgeway T, 1999. Discrimination of the speed and direction of global second-order motion in stochastic displays. *Vision Res* **39**:3710–3720.

Marchetti K, 1993. Dark habitats and bright birds illustrate the role of environment in species divergence. *Nature* **362**:149–152.

Marimuthu G, 1997. Stationary prey insures life and moving prey ensures death during the hunting flight of gleaning bats. *Curr Sci* **72**:928–931.

McGregor PK, Dablesteen T, Shepherd M, Pedersen SB, 1992. The signal value of matched singing in great tits: evidence from interactive playback experiments. *Anim Behav* **43**:987–998.

Newsome WT, Paré EB, 1988. A selective impairment of motion perception following lesions of the middle temporal visual area (*MT*). *J Neurosci* **8**:2201–2211.

Noble GK, 1939. The experimental animal from the naturalist's point of view. *Am Nat* **73**:113–126.

Ord TJ, Blumstein DT, Evans CS, 2002a. Ecology and signal evolution in lizards. *Biol J Linn Soc* **77**:127–148.

Ord TJ, Evans CS, 2002. Interactive video playback and opponent assessment in lizards. *Behav Process* **59**:55–65.

Ord TJ, Peters RA, Evans CS, Taylor AJ, 2002b. Digital video playback and visual communication in lizards. *Anim Behav* **63**:879–890.

Peters RA, Clifford CWG, Evans CS, 2002. Measuring the structure of dynamic visual signals. *Anim Behav* **64**:131–146.

Peters RA, Evans CS, 2003a. Design of the Jacky dragon visual display: signal and noise characteristics in a complex moving environment. *J Comp Physiol A* **189**:447–459.

Peters RA, Evans CS, 2003b. Introductory tail-flick of the Jacky dragon visual display: signal efficacy depends upon duration. *J Exp Biol* **206**:4293–4307.

Peters RA, Evans CS, 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 RA, Hemmi JM, Zeil J, 2007. Signaling against the wind: modifying motion-signal structure in response to increased noise. *Curr Biol* **17**:630–636.

Peters RA, Ord TJ, 2003. Display response of the Jacky dragon *Amphibolurus muricatus* (Lacertilia: Agamidae) to intruders: a semi-Markovian process. *Austral Ecol* **28**:499–506.

Polverino G, Porfiri M, 2013. Mosquitofish *Gambusia affinis* responds differentially to a robotic fish of varying swimming depth and aspect ratio. *Behav Brain Res* **250**:133–138.

Rieucau G, Giraldeau LA, 2009. Video playback and social foraging: simulated companions produce the group size effect in nutmeg mannikins. *Anim Behav* **78**:961–966.

Ryan MJ, Rand AS, 1993. Species recognition and sexual selection as a unitary problem in animal communication. *Evolution* **47**:647–657.

Saverino C, Gerlai R, 2008. The social zebrafish: behavioral responses to conspecific, heterospecific, and computer animated fish. *Behav Brain Res* **191**:77–87.

Scase MO, Braddick OJ, Raymond JE, 1996. What is the noise for the motion system? *Vision Res* **36**:2579–2586.

Tinbergen N, Perdeck AC, 1951. On the stimulus situation releasing the begging response in the newly hatched herring gull chick *Larus argentatus argentatus* Pont. *Behaviour* **3**:1–39.

Ushitani T, Fujita K, Sato A, 2004. Perceptual organization of motions in pigeons *Columba livia*. *Jpn Psychol Res* **46**:170–181.

Van Dyk DA, Evans CS, 2007. Familiar-unfamiliar discrimination based on visual cues in the Jacky dragon *Amphibolurus muricatus*. *Anim Behav* **73**:33–44.

Verghese P, McKee SP, 2004. Visual search in clutter. *Vision Res* **44**:1217–1225.

Vreven D, Verghese P, 2002. Integration of speed signals in the direction of motion. *Percept Psychophys* **64**:996–1007.

Watamaniuk SNJ, Norberto M, Yuille AL, 1993. Dependence of speed and direction perception on cinematogram dot density. *Vision Res* **33**:849–859.

Willigen RF. v d, Frost BJ, Wagner H, 2003. How owls structure visual information. *Anim Cogn* **3**:39–55.

Woo KL, 2006. Testing visual sensitivity to the speed and direction of motion in lizards. *J Vis Exp* (**2**). Available from: http://www.jove.com/Details.htm?ID=127&VID=107.

Woo KL, Burke D, 2008. Technique for measuring speed and visual motion sensitivity in lizards. *Psicológica* **29**:135–151.

Woo KL, Burke D, Peters RA, 2009. Motion sensitivity of the Jacky dragon *Amphibolurus muricatus*: random-dot kinematograms reveal the importance of motion noise for signal detection. *Anim Behav* **77**:307–315.

Woo KL, Rieucau G, 2008. Considerations in video playback design: using optic flow analysis to examine motion characteristics of live and computer-generated animation sequences. *Behav Process* **78**:455–463.

Woo KL, Rieucau G, 2011. From dummies to computer-animated stimuli: a synthesis of techniques employed to stage animal interactions. *Behav Ecol Sociobiol* **65**:1671–1685.

Woo KL, Rieucau G, 2012. Aggressive signal design in the Jacky Dragon *Amphibolurus muricatus*: display duration affects efficiency. *Ethology* **118**:157–168.

Woo KL, Rieucau G, 2013. Efficiency of aggressive and submissive visual displays against environmental motion noise in Jacky dragon *Amphibolurus muricatus*. *Ethol Ecol Evol* **25**:82–94.

Woo KL, Rieucau G, 2015. The importance of syntax in a dynamic visual signal: recognition of Jacky dragon threat displays depends upon sequence. *Acta Ethol* **18**:255–263.