

Technique for measuring speed and visual motion sensitivity in lizards

Kevin L. Woo* and Darren Burke

Macquarie University (Australia)

Testing sensory characteristics on herpetological species has been difficult due to a range of properties related to physiology, responsiveness, performance ability, and the type of reinforcer used. Using the Jacky lizard as a model, we outline a successfully established procedure in which to test the visual sensitivity to motion characteristics. We incorporated modifications to traditional operant paradigms by using three video playback systems to deliver random-dot kinematogram motion stimuli coupled with salient computer-animated secondary reinforcers representative of biologically important appetitive stimuli. This procedure has the capacity to test other visual aspects in lizards as well as other non-human species using video playback and computer-animation techniques as experimental tools.

Psychophysical studies that investigate the visual systems in various taxa are often challenging and require tedious trial-and-error testing before establishing a successful procedure (Ozlak & Wickens, 1999; Feldman & Balch, 2004). Some protocols have already been established for successful replication on similar taxa, or can provide a basis in which to test the sensory system in completely different species. However, not all available procedures are applicable to every species. Researchers must then develop a new method using basic conditioning paradigms. Limitations are also governed by the way in which the species is motivated to respond. These problematic features can be a function of the biological nature of the

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species, the types of reinforcers, or failure of the paradigm. However, it is establishing the method in measuring visual sensitivity that is critical for uncovering sensory thresholds (Derrington, Allen, & Delicato, 2004). Here, we discuss a new approach in testing the visual sensitivity to motion in the Jacky dragon (*Amphibolurus muricatus*) as a model species for testing the visual capacity in other lizard species.

The Jacky dragon is an agamid species found in southeast Australia inhabiting variable geographic ranges from coastal heathland, rocky ridges, and sclerophyll forests (Harlow & Taylor, 2000). Jacky dragons are a model species for investigating questions on visual communication due to their reliance on stereotyped visual cues (Carpenter & Ferguson, 1977; Carpenter, Badham, & Kimble, 1970) for social communication such as territoriality or mate choice. These displays range in signal strength, and it is the differences in motion characteristics that are critical to successful communication (Peters & Evans, 2003a; Peters & Ord, 2003). Understanding how the peripheral system engages in visual information from the sensory world helps us comprehend functional and cognitive actions (Endler, 1992).

Burghardt (1977) suggests that conditioning can be used as a tool to test learning phenomena and sensory processes. Although psychophysical experiments using reptilian species are not uncommon, it is establishing the right parameters that are critical for a successful protocol. Conditioning experiments involving reptilian species are notoriously difficult. Unlike mammalian or avian species, food reinforcers have unknown and unbalanced effects on the metabolism of the species (Kanarek, 1976; Castonguay, Phillips, & Collier, 1985; Plowright, Duggan, & Kruzynski, 1993). Secondly, choosing a reinforcer for the animal is highly-species dependent. For example, desert iguanas (Kreikorian, Vance, & Richardson, 1968) would prefer increased temperatures while spotted pythons (Stone, Ford, & Holtzman, 2000) would prefer shelter selection as a primary reinforcer.

In this study, we used random dot kinematograms (RDKs) to assess the visual sensitivity to salient motion as a function of motion characteristics in ecological relevant stimuli. Varying the motion parameters in RDKs has been a common tool for assessing motion sensitivity in both animal and human visual systems. RDKs engage the peripheral sensitivity of the visual system, do not represent any biological important stimulus, and have been a reliable psychophysical tool in which to measure visual sensitivity across various taxa (Curran & Braddick, 2000). In non-human taxa, RDKs have been successfully used to demonstrate psychophysical

measures of sensitivity to coherent motion in rodents (Douglas, Neve, Quittenbaum, Alam, & Prusky, 2006), ferrets (Hupfeld, Distler, & Hoffmann, 2006), pigeons (Goto, Lean, & Dittrich, 2002), macaques (Kiorpes & Movshon, 2004), cats (Burnat, Vandenbussche, & Zernicki, 2002), and owls (Willigen, Frost, & Wagner, 2003). However, to our knowledge, this is the first demonstration of the usage of RDKs to measure visual sensitivity in a lizard species.

We also used a novel secondary reinforcer to mimic visual characteristic of real invertebrates through computer animation that made the acquisition of the task possible. Previous studies using video technology has shown that pigeons (Cook & Katz, 1999) and chickens (Patterson-Kane, Nicol, Foster, & Temple, 1997) are able to discriminate key biological features such as general motor actions (Dittrich, Lea, Barrett, & Gurr, 1998) and aerial predators (Evans, Macedonia, & Marler, 1993). It has also been found that Jacky dragons respond to video images of conspecifics in biologically relevant ways (Ord & Evans, 2002; Ord, Peters, Evans, & Taylor, 2002; Peters & Evans, 2003a, 2003b; Van Dyk & Evans, 2007)

We outline a technical approach for testing motion sensitivity in the Jacky dragon, and how this procedure was shaped until a successful protocol was established. In Experiment 1A, we tested sensitivity using 100% coherent directional movement (left or right) and video footage of a lizard performing social displays as a reinforcer. In Experiment 1B, we identified the correct methodological features that allowed subjects to learn the task. We replaced the lizard reinforcer with a primary food reinforcer, and paired this with a secondary reinforcer of an ecologically appetitive stimulus of a moving computer-animated invertebrate. After having identified the successful technical aspects, we varied both the coherence and speed as a successful measure of sensitivity to visual characteristics of motion in Experiment 2. This approach may be applicable in testing other visual features in the Jacky lizard, but may also be used to comparatively test visual sensitivity in other lizard species.

EXPERIMENT 1A

METHOD

Subjects. Three male Jacky dragons collected from La Perouse and Royal National Parks in Sydney, Australia were housed in identical enclosures. Subjects were held in enclosures (55 x 85 x 95 cm) that were

placed on trolleys that allowed subjects to be moved into the testing area. Each enclosure was decorated with wooden branches and stumps for perches, native leaf litter, and Sydney sand substrate. Subjects were fed live crickets (Family Gryllidae) that were dusted with vitamin supplements (RepCal, Victoria, Australia) twice a week and were provided with water *ad libitum* in small bowls, except during testing periods. Lizards were maintained under a 14:10 h L/D cycle with additional heat lamps (125 W Spotone, Phillips, NSW, Australia) for 10 hours per day and ultraviolet (UV) lamps (300W Ultra-Vitalux, Osram, NSW, Australia) were illuminated for half-an-hour in the morning (0730). Animals housed indoors require adequate UV lighting to prevent vitamin deficiencies.

Apparatus. Three video playback systems were designed for stimulus presentation (see Figure 1). Two systems consisted of an iMac (Apple Computers Inc.) with Final Cut Pro 3 for stimulus presentation that was connected to a 160Gb external LaCie d2 hard drive (Hillsboro, Oregon USA) and contained playback stimuli (i.e., lizard/invertebrates). The digital signal was sent to an advanced digital video converter (Canopus® ADVC110, Melbourne, Victoria Australia) for analog conversion for video playback and then displayed on a Sony Trinitron monitor (Series Nos. PVM-14M2A/PVM-14L2, Sony Corporation, Shinagawa, Tokyo Japan). A Canon digital camcorder with 22X optical zoom (Model No. MV650i – Canon Inc., Japan) was mounted to a stationary tripod (Gruppo Manfrotto®, Italy) behind a one-way mirror and recorded responses to stimuli directly to a Sony VHS recorder (Serial No. SLV-EZ717AS). Recording images were sent to a colour viewfinder (NEC, Serial No. 1892, Kanagawa, Japan). The central system consisted of an iMac connected to a LaCie hard drive containing RDK stimuli. The digital signal was sent through a Sony MiniDV digital video recorder (GV-D300E) PAL player then to the Sony Trinitron (PVM-14N5A) colour display monitor. At 7.5 seconds from the start of the dots display, an electronically generated sound cue was sent to a Sony MiniDV and recorded onto VHS. Video playback was adjusted for PAL-DV standard (5:1 compression; horizontal resolution 575 lines; 25 frames/s).

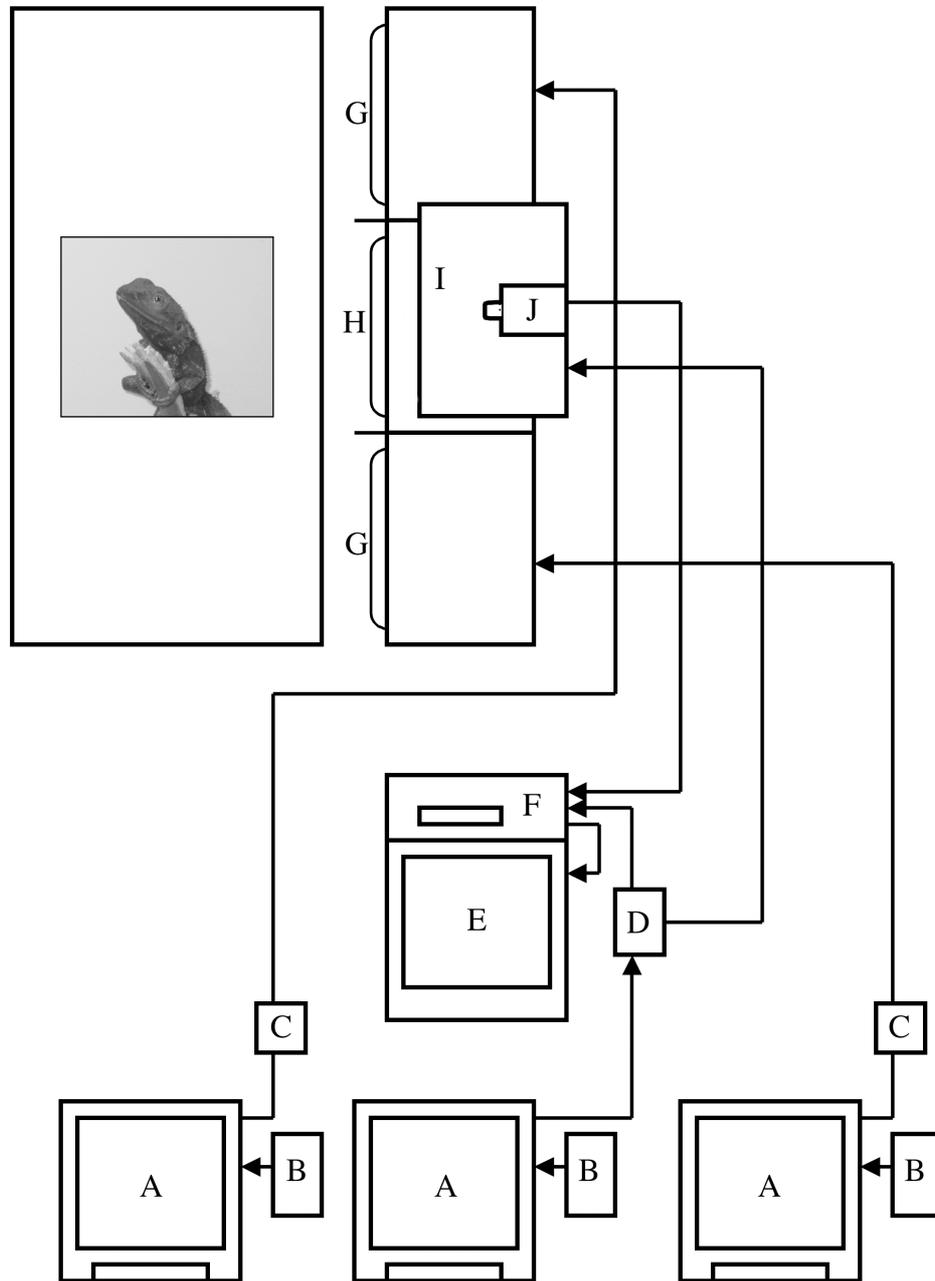


Figure 1. Schematic diagram of playback system: a) iMac; b) LaCie drive; c) ADVC Canopus box; d) Sony MiniDV recorder; e) viewfinder monitor; f) VHS recorder; g) display monitors for secondary reinforcers; h) central monitor for RDKs; i) one-way mirror; and j) digital camcorder behind one-way mirror.

Stimuli

Random-Dot Kinematograms. Random-dot kinematograms (RDKs) were created using Visual Programming under UNIX (VPixx V1.79, VPixx Technologies Inc. 2002; see Figure 2). A visual field of 200 dots at 5 x 5 pixels per dot was created. VPixx allowed us to insert various speeds in degrees per second ($^{\circ}/s$) and directional coherence (% of RDKs moving left or right). RDKs were exported out of VPixx as Motion JPEG-B files and converted to Final Cut Pro movies. RDKs were then rendered using Final Cut Pro 3 (Apple Computers Inc., Cupertino, CA, USA) for video playback. Coherence RDKs were created at speeds 5 $^{\circ}$, 20 $^{\circ}$, and 80 $^{\circ}/s$ while coherence was held constant at 100%.

Dots were presented for a total of 15 seconds. At 7.5 seconds, an electronically generated sound cue imbedded into the audio track signified the presentation of the reinforcer (i.e., lizard or invertebrate) either to the left or the right of the subject. The sound cue was only audible on the recorded VHS.

Primary Reinforcer – Lizards. Archive lizard display footage was all filmed indoors (see Ord & Evans, 2002). Subject responses to live lizards were filmed using a Canon digital video camcorder (Model No. MV650i). One hundred and twenty-seven clips ranging from nine seconds to two minutes were selected. The first 7.5 seconds showed a blank perch to match the initial 7.5 seconds of only displaying dots. Lizard displays (see Figure 6a) also ranged from inactive (i.e., lizard basking on perch) to active (i.e., highly aggressive display). The duration of these clips ranged from nine seconds to two minutes. Each clip was modified using Final Cut Pro 3 to allow for a cross-fade at 7.5 s from empty perch to a displaying lizard (see Figure 3a). Presentation of stimuli was randomized to prevent habituation.

Procedure. Each subject was given one speed. Subjects tested at 5 $^{\circ}/s$ and 20 $^{\circ}/s$ were tested for 36 block trials each (360 trials) of 10 trials each, while subject tested at 80 $^{\circ}/s$ was only tested with 30 block trials (300 trials) totalling 1080 trials. The direction of the moving dots was randomized across all individual trials. However, within each block trial encompassed five trials of dots moving left and five trials of dots moving right. Intertrial intervals (ITIs) time ranged from 30-60 s.

Statistical Analysis. We recorded orientation to the correct monitor before the appearance of a secondary reinforcer and latency to respond during the initial 7.5 seconds of dot movement. Initial coherence trials recorded orientation behaviour, and we used a three-factor repeated

measures ANOVA to examine the main effect of orientation to RDKs, acquisition dots, and lizard displays, as well as an interaction between these variables. Friedman ANOVA was used to assess any significant differences within speed for each variable, as well as each individual variable across speeds.

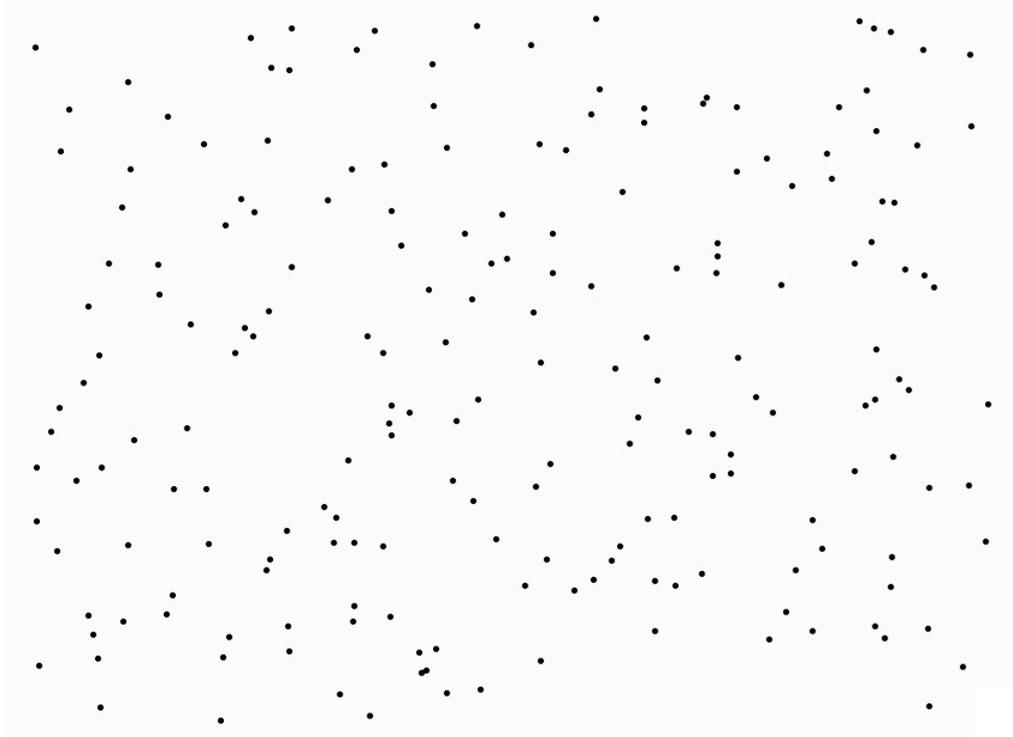


Figure 2. Field of RDKs designed for experimental stimuli.

RESULTS AND DISCUSSION

The initial switch to coherence measures showed a greater improvement in learning, but demonstrated a greater salience between the stimuli types. Comparing across the three orientation measures showed a significant main effect of speed [$F(2, 338) = 11.53, p < .05$] and response [$F(2, 338) = 2469.35, p < .05$], with an interaction evident between these patterns [$F(2, 338) = 6.43, p < .05$]. Figure 4 shows the response differences across the orientation to the RDKs, acquisition dots, and lizards. There were significant differences in orientation responses within individual speeds: 5°/s [$\chi^2(2, N = 340) = 514.21, p < .05$], 20°/s [$\chi^2(2, N = 340) =$

453.35, $p < .05$], and 80°/s [$\chi^2(2, N = 340) = 559.19, p < .05$]. There were also significant differences within the type of response measures: to the RDKs only [$\chi^2(2, N = 340) = 22.17, p < .05$], acquisition [$\chi^2(2, N = 340) = 18.74, p < .05$], and lizard [$\chi^2(2, N = 340) = 11.66, p < .05$]. However, these results do not demonstrate that subjects were able to learn the contingency, but were able to respond to the different types of stimuli.

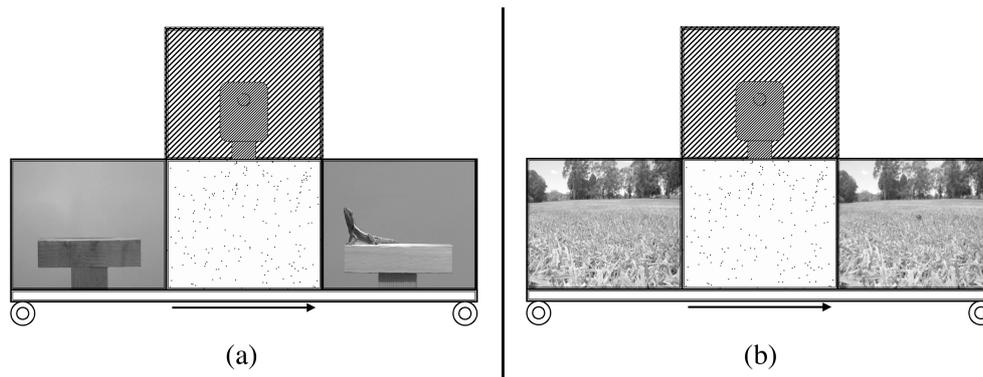


Figure 3. View of the playback rig from the subjects' point of view: a) initial displaying lizard as the secondary reinforcer on the right monitor; b) moving invertebrate replaced the displaying lizard as a more salient secondary reinforcer.

EXPERIMENT 1B

METHOD

Subjects. Five new and naïve male Jacky dragons collected from Lane Cove National Park in Sydney, Australia were held in three identical cubic glass terrariums (60 x 60 x 60 cm) on movable trolleys. Each enclosure was once again decorated with wooden branches and stumps for perches, native leaf litter, and Sydney sand substrate. Subjects were fed live crickets (Family Gryllidae) that were dusted with vitamin supplements (RepCal, Victoria, Australia) twice a week when not during testing and were provided with water *ad libitum* in small bowls. Lizards were again maintained under a 14:8 h L/D cycle with additional heat lamps (125 W Spotone, Phillips, NSW, Australia) for 10 hours per day and ultraviolet (UV) lamps (300W Ultra-Vitalux, Osram, NSW, Australia) were illuminated for half-an-hour in the morning (0730).

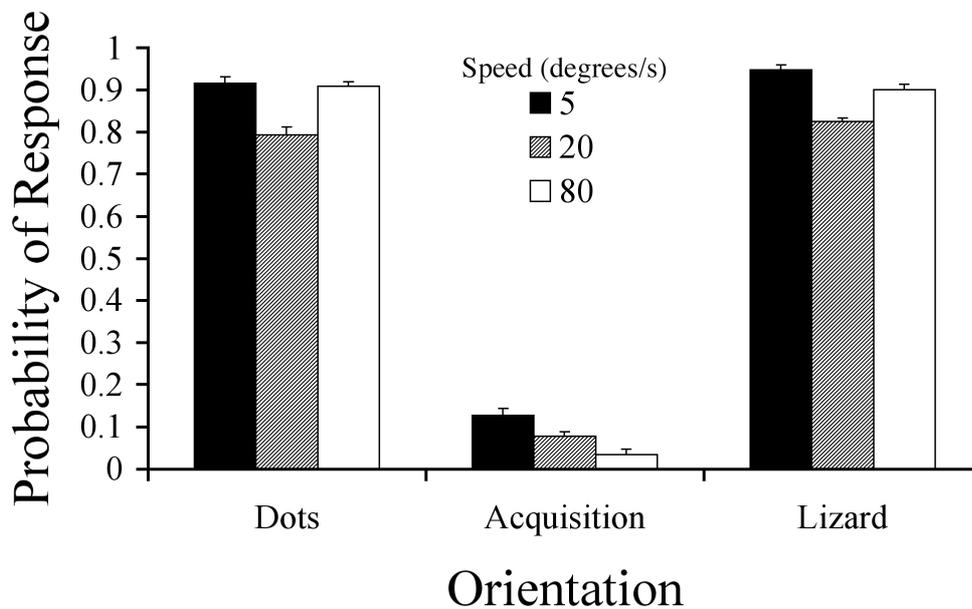


Figure 4. Orientation to elements of the conditioning paradigm showing significant differences in response levels: RDKs, acquisition dots, and lizards.

Apparatus. The same equipment was used as in Experiment 1A. However, the video camera was now mounted to the ceiling and still recorded responses from above the testing area. The cubic enclosures now situated the monitors at equal distances and angles from each other. This design forced a clear selection to a monitor by the subjects (see Figure 5).

Stimuli

Random-Dot Kinematograms. Each of the five subjects was tested at 100% coherence, randomly allocating an equal number of left- and right-moving dots patterns. Two subjects were trained at 5°/s, two subjects were trained at 20°/s, and one subject was trained at 80°/s. RDK patterns were also exported in the same manner as before. Instead of sequence immediately beginning with 5 s of moving RDKs from still dots, we modified the design so that RDK stimuli began with 2.5 s of 0% coherence,

followed by 5 s of the selected speed value with 100% coherence. By starting each sequence with 0% coherence (i.e., random noise), this provided an emphasis to the subject that the salient change to the proportion of the dots drifting either leftward or rightward; it is the direction of movement that was the important cue and not simply just the presence of movement. After 7.5 s, the RDK remained at 100% coherent motion in the appropriate direction. Each individual sequence was still 15 s in duration; however, providing the subjects with the movement of random dots before the discriminative stimuli had primed them for the trial.

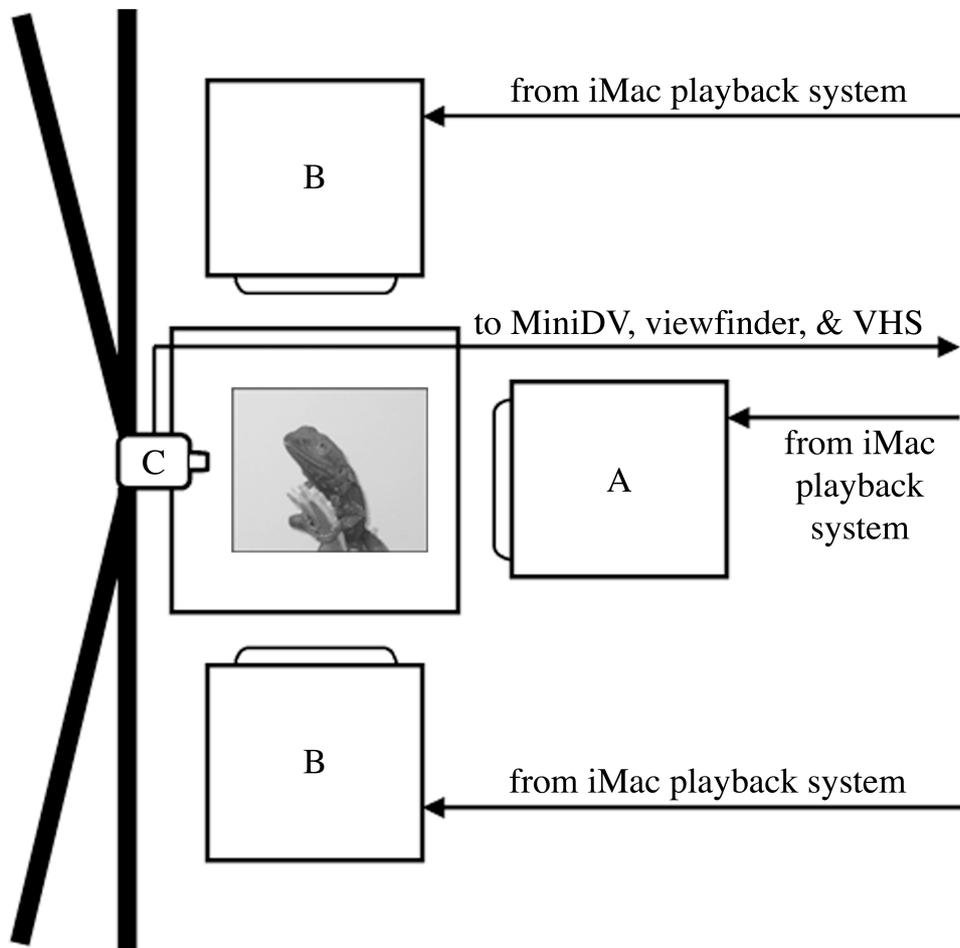


Figure 5. Schematic diagram of monitor and camera set up for the final playback rig: a) display monitors for secondary reinforcers; b) central monitor for RDKs; and c) digital camcorder.

Primary Reinforcer – Mealworm. The introduction of a primary reinforcer was implemented to motivate subjects to learn the task. Subjects were reinforced with a mealworm (*Tenebrio molitor*) using a variable reinforcement schedule. Varying the rate of reinforcement prevented habituation to the task as well as creating an appetitive stimulus. Subsequent trials reduced the reinforcement schedule to prevent satiation.

Secondary Reinforcer – Cyber-Invertebrate. Lizard displays were replaced with another appetitive secondary reinforcer of computer generated invertebrates. The movement of a stimulus resembling natural prey items is enough to elicit motivational responses from Jacky lizards (Woo, Burke, & Evans, in review). Since lizard social displays were clearly aversive, the replacement of this footage for an appetitive stimulus provided us with full control of secondary reinforcer movement and morphological characteristics.

In order to control for invertebrate movement, computer animated invertebrates were designed to mimic the movement of real invertebrates. Three computer-generated invertebrates (i.e., cricket, mite, spider) were created using Lightwave® 7.5 3D animation software (NewTek Inc., San Antonio, TX, USA; see Figure 6b-d). A still background JPEG was imported to simulate movement within a natural background (see Figure 6e). Invertebrate clips were 15 s in length, with the initial 7.5 s of still background, and the following 7.5 s presented the invertebrate on the appropriate screen (see Figure 3b). Sequences were then exported into individual JPEG image sequences, and compressed into a movie file using Final Cut Pro 3 for video playback. Fifty unique clips were designed to prevent habituation to the conditioning paradigm, and presentation was randomized. The presentation of the secondary reinforcer was coupled with the primary reinforcer.

Procedure. We manipulated the proportion of dynamic random dot stimuli that drift in a coherent direction in order to vary signal strength. Subjects were tested over five consecutive days at 20 trials per day totalling 100 trials per individual, and constituting 10 trials per block trial. Subjects maintained a variable reinforcement schedule where subjects were only reinforced for six out of 20 trials (VR6) through shaping. They were reinforced with mealworms as a primary reinforcer and paired with a secondary reinforcer of a computer-generated invertebrate. Mealworms were manually dropped in front of the correct directional monitor using the VR6. ITIs ranged from 30-60 s.

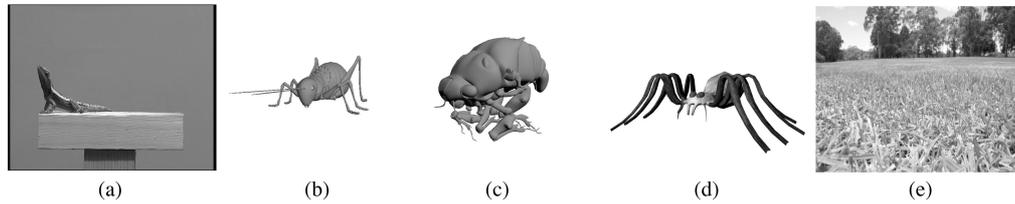


Figure 6. Secondary reinforcer and background: a) aversive lizard stimulus; b) animated cricket; c) animated mite; d) animated spider; e) background.

Statistical Analysis. We recorded orientation and latency to respond within the 5 s period in which the subjects were required to select the monitor that would present the secondary reinforcer. Both orientation and latency to response dependent measures were analysed using a two-way within-subject repeated measures ANOVA was used to assess the main effect of speed and coherence as well as test for an interaction between these to factors.

RESULTS AND DISCUSSION

Subjects were able to acquire the basic contingency using motion coherence as a dependent measure. Results show that there was a significant main effect of learning on percent correct [$F(2, 9) = 17.13, p < .05$] and latency [$F(2, 9) = 12.37, p < .05$] between speed groups (see Figure 7). There was a significant interaction between block trials and speed for accuracy [$F(2, 18) = 3.19, p < .05$] and latency [$F(2, 18) = 1.87, p < .05$].

EXPERIMENT 2

METHOD

Stimuli. The previous attempts in Experiment 1A had shown that subjects were at least interested in the RDKs. Upon modifying some technical features, we had demonstrated in Experiment 1B that subjects may acquire the basic task procedure using coherence as a discriminating visual feature. Therefore, we employed a typical psychophysical strategy by varying the characteristics of the independent variable and required the subject to demonstrate an acquisition of the task by predicting the presentation of the appetitive stimulus in a two-choice experiment.

Random-Dot Kinematograms. RDKs were once again created using VPixx. However, new speed and coherence measures were created consisting of all possible combinations of speed (0.5°, 2.5°, 5°, 10°, 20°, 40°, 80°, and 160°/s) and coherence (0%, 2.5%, 5%, 10%, 20%, 40%, 80%, and 100%) moving in a particular direction (left or right). A total of 128 stimuli were created.

RDK patterns were also exported as before. We also maintained the same RDK sequence duration and design that began with 2.5 s of 0% coherence, followed by 5 s of the discriminative stimulus (i.e., coherent directional dots), and concluding with 7.5 s where the dots became 100% coherent in the appropriate direction.

Procedure. Subjects were presented with the RDK stimuli on the central monitor. Initially, on the adjacent monitors to either side, there would be a still background. RDKs presentation began with 2.5 s of 0% coherence, followed by 5 s of the variation stimulus, and finished with 7.5 s of 100% coherence in the appropriate direction. Within the five-second interval, subjects were to predict which direction the RDKs were moving, and which monitor the secondary reinforcer would appear. This ability to predict the appearance of a salient stimulus based on the direction of moving dots indicated whether the subjects had acquired the learning contingency. Subjects were tested across four consecutive days and were given 32 trials per testing day in two block trials of 16 trials. Each subject was maintained on a VR5 schedule of reinforcement per block trial, and was reduced by one reinforcer per testing day. Subjects were reinforced with a mealworm (primary reinforcer) that was paired with the presentation of an invertebrate (secondary reinforcer) on the correct monitor. Mealworms were administered in the same fashion as in Experiment 1B. After a three-day rest period, the trials were repeated. ITIs ranged from 30-60 s. Each subject had been tested across 256 trials.

Statistical Analysis. Both orientation and latency to response dependent measures were analysed using a two-way within-subject repeated measures ANOVA was used to assess the main effect coherence.

RESULT AND DISCUSSION

We were able to establish a procedure that measured the subjects' ability to predict the appearance of an invertebrate on the appropriate directional monitor (see Figure 8). Lizards were able to use variations in both speed and coherence of the RDKs as measures to predict the appearance of an invertebrate in the correct direction using measures of accuracy [$F(7, 49) = 221.578, p < .05$] and latency [$F(7, 49) = 172.923, p < .05$]. The lizards' ability to predict direction based on these visual factors provides with a range of sensitivity to motion, and this has providing implications for resolving important ecological motion, such as social displays from conspecifics and allowing predators to exploit their poor visual ability for slow speeds (Woo et al., in review).

GENERAL DISCUSSION

Subjects were clearly unable to learn the contingency using the original methods. Despite subsequent trials and readjustment from using contrast to coherence as a measure of signal strength, subjects were still unable to acquire the contingency and displayed both submissive and escape behaviours until some parameters were changed.

A ceiling effect was produced as subjects responded to the initial onset of dots and never learned the contingency that the dots would predict a lizard in a directional monitor for both contrast and initial coherence trials. Subjects always oriented to the presentation of the dots, never predicted direction, and would orient once again to the presentation of the lizard reinforcer.

Upon completion of both of these types of trials, it was recognised that lizards as a primary reinforcer created two problems. The lizard, which displayed a random series of social communicative signals, became an aversive stimulus. The response to the archive footage of lizard displays was to produce a submissive display (i.e., head-bobbing or slow arm wave) or hyperactivity in which the subject makes an attempt to seek refuge. However, despite instituting a contingency to predict the appearance of a lizard, the subjects were never able to predict the appearance of the secondary reinforcer.

The change from an aversive stimulus to an appetitive stimulus was the first critical step in motivating the subjects to respond to the contingency. The presentation of a lizard, though a critical ecological

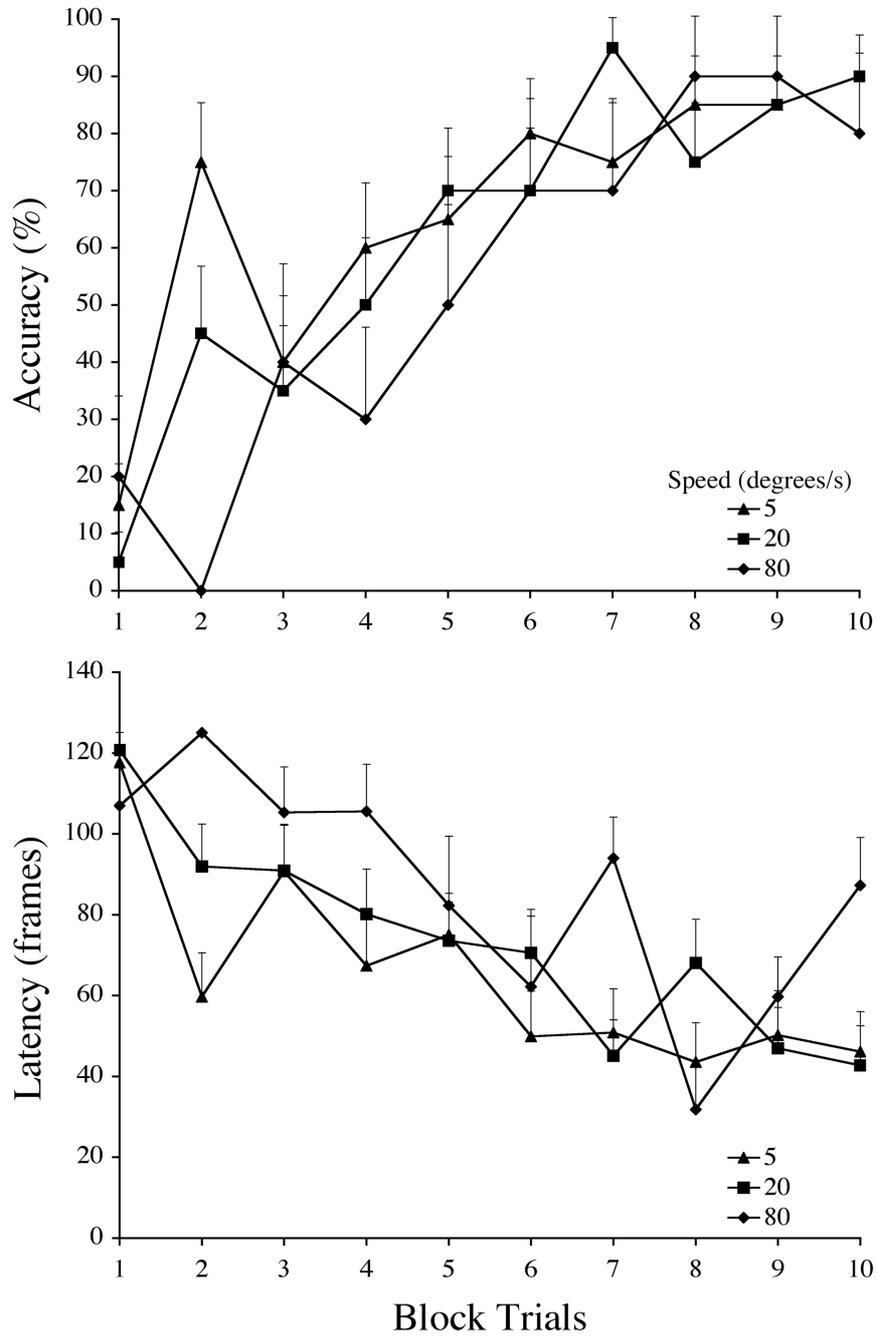


Figure 7. Performance of subjects allocated to separate speeds (5°, 20° or 80°) during pretraining coherence sessions across block trials showing an increase in mean percent correct responses (+SEM) and a decrease in latency of response (+SEM).

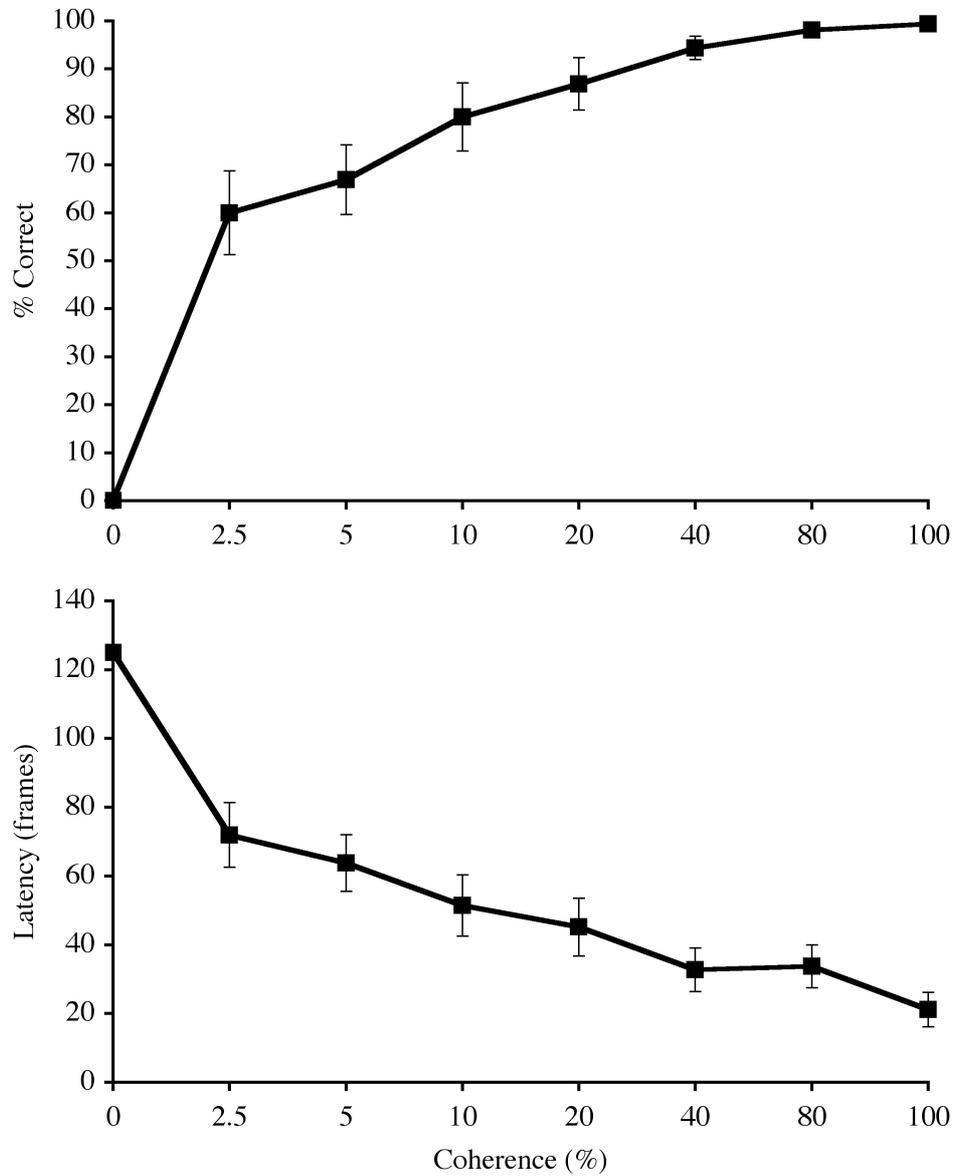


Figure 8. Main effect of coherence when collapsed across speed shows ability of subjects to use RDK characteristics as features for correct discrimination for percent correct (\pm SEM) and latency (\pm SEM).

factor, obviously produced a negative effect on behavior. Instead, the usage of invertebrate footage and eliminating the lizard displays was a key factor in establishing motivational mechanisms. Each invertebrate clip was also unique. This design prevented habituation as well as kept the subjects highly motivated. Furthermore, using a primary reinforcer on a variable schedule of reinforcement exercised the benefit of motivating the subjects. We included using a mealworm for the primary reinforcer, and an animated invertebrate mimicking natural movement patterns as the secondary reinforcer. Since little is known about Jacky lizard metabolism, subjects were placed on a decreasing variable reinforcement schedule to prevent satiation and habituation.

Secondly, the timed presentation of the dots was changed. Initial trials displayed the dots for a total of 15 s, and at 7.5 s the lizard or invertebrate was presented. However, the dots began with no movement, and then proceeded straight to a directional movement. This jitter in movement allowed the subjects to initially orient to the dots, and not acquire the contingency. When establishing coherence measures, the dots were now presented with 2.5 s of 0% coherence, followed by 5 s seconds of the independent measures, and completing with 7.5 s at 100% coherence plus the appearance of an invertebrate in the appropriate direction for the trial. This initial period had primed the subject for a directional change without causing an unnatural transition in dot movement. If the subject failed to predict the correct direction, the dots moved at 100% in the correct direction during the presentation of the secondary reinforcer. This contingency reminder exposed the subject to the correct choice.

Thirdly, the original position of the display monitors did not require the subject to maintain orientation. This was also achieved by housing the subjects in new enclosures. The new glass enclosures were cubic in design that allowed the monitors to be placed at equal distances apart and at 90° angles. By placing the monitors displaying the secondary reinforcers on opposing ends of the testing area, this forced the subject to select a direct path of orientation and maintain that position.

We established a successful psychophysical procedure to test the motion sensitivity to salient stimuli in one agamid species, the Jacky dragon, where movement is a critical component of social communication as well as interpreting important ecological information (Woo et al., in review). Having implemented many strategies to allow subjects to acquire the basic contingency of this paradigm, we found that the simplest solution was to reduce the number of potential confounds, and establish a critical motivational platform. These pivotal changes allowed the subjects to

acquire the contingency as well as remain motivated without habituating to the procedure due to varying the intensity of the reinforcers. This methodology has successfully demonstrated a potential to investigate one aspect of motion sensitivity in the Jacky lizard, but other visual aspects can be examined using this protocol such as relative sensitivity to similar motion parameters (Woo, Burke, & Peters, in review). We suggest that this methodology is also applicable to other lizard taxa as well as other non-human species.

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