

## Motion sensitivity of the Jacky dragon, *Amphibolurus muricatus*: random-dot kinematograms reveal the importance of motion noise for signal detection

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The evolution of movement-based signals is constrained by the successful segmentation of relevant movements from motion noise by the visual system of receivers. We tested five Jacky dragons, *Amphibolurus muricatus*, a species characterized by stereotyped movement-based social signals, for their ability to discriminate the direction of drifting dots against simulated background motion noise of varying angular speeds. Results from trials with artificial (dot) backgrounds suggested that Jacky dragons are most sensitive to high-speed movement, while background movement of similar angular speeds to target stimuli reduced performance. We also found differences in accuracy between natural backgrounds comprising footage of plant motion at two independent sites. We argue that detecting salient movement depends on the particular characteristics of the surrounding motion noise, and discuss its implications for movement-based signal design.

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Signal detection within a complex environment requires effective discrimination between relevant signals and irrelevant environmental noise. Signals used in social interactions are designed to stimulate and successfully engage receiver sensory systems (Endler 1992; Endler & Basolo 1998). However, signals must also be sufficiently robust to withstand the masking effects of environmental noise (Ryan & Kime 2003).

The potential masking effect of noise has been widely considered in the context of animal signalling (Johnstone 1998). Many studies of this process have focused on auditory systems (Morton 1975; Wiley & Richards 1978; Ryan & Brenowitz 1985), such as birds (e.g. budgerigars, *Melopsittacus undulatus*; zebra finches, *Taeniopygia guttata*; canaries, *Serinus canaria*; Lohr et al. 2003), invertebrates (e.g. bush-crickets, *Steropleurus nobrei*; Stephens & Hartley 1991) and frogs (e.g. treefrogs, *Hyla ebraccata*; Wollerman & Wiley 2002; leptodactylids, *Eupsophus calcaratus*; Penna et al. 2005). Discrimination between important signals and

environmental noise has also been demonstrated in other communicative sensory modalities of animals, such as seismic (e.g. thumping in white-lipped frogs, *Leptodactylus albilabris*; Narins 1990), chemosensory (e.g. urine detection in American lobsters, *Homarus americanus*; Atema & Engstrom 1971; Atema 1995), electrical (e.g. pulses from weakly electric fish, *Eigenmannia*; Gabbiani et al. 1996) and visual (e.g. dewlap colour in *Anolis* spp.; Persons et al. 1999; Fleishman & Persons 2001).

The detection of salient movements within motion noise depends on the level of signal strength, which can be defined in terms of the combination of stimulus coherence and speed (Festa-Martino & Welch 2001). For many animals, it is the movement of wind-blown plants in the habitat that represent the primary source of environmental motion noise (Fleishman 1988a,b). It is thus critical for social interactions that signalling overcomes environmental noise across the full range of natural conditions (Fleishman 1992; Peters et al. 2008). Recent evidence from lizards has indeed shown that environmental motion is distracting (Peters 2008), and must be compensated for during signalling (Peters et al. 2007; Ord et al. 2007). However, it is not clear how segmentation of signal and noise occurs. Motion noise may be filtered by short-term habituation (Fleishman 1986), or important motion may, under certain conditions, have structural characteristics that distinguish it from noise (Peters & Davis 2006). To understand the constraints imposed

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by receiver sensory systems on movement-based signal evolution, it is critical that we identify when detection of salient movements by the visual system is compromised by the presence of background motion noise.

In this study, we measured sensitivity to motion using random-dot kinematograms (RDKs) embedded in both synthetic and plant motion noise. Widely used in signal detection experiments (Clifford et al. 1999; Curran & Braddick 2000; Watamaniuk et al. 2003), RDKs offer an ideal measure of motion sensitivity, because they engage the visual system, but do not resemble a biologically meaningful stimulus (Newsome & Paré 1988). Although most studies utilizing RDKs have focused on the human visual system, this technique has been applied successfully to measure the visual sensitivity of other animals: laboratory rats and mice (Douglas et al. 2006), albino ferrets, *Mustela putorius furo* (Hupfeld et al. 2006), pigeons, *Columba livia* (Goto et al. 2002), pigtail macaques, *Macaca nemestrina* (Kiorpes & Movshon 2004), domestic cats (Burnat et al. 2002) and barn owls, *Tyto alba* (van der Willigen et al. 2003). The use of RDKs allows for the measurement of speed sensitivity in the presence of varying coherence levels (Verghese et al. 2000; Vreven & Verghese 2002; Verghese & McKee 2004), thus providing a measure of sensitivity to important signal characteristics (Bischof et al. 1999).

We examined how Jacky dragons respond to salient visual motion against a background of irrelevant motion. These lizards produce highly stereotyped movement-based displays during social interactions (Carpenter et al. 1970; Carpenter & Ferguson 1977; Peters & Ord 2003), which they must detect against a background of wind-blown plants (Peters & Evans 2003). To investigate their ability to segregate important signals from noise, we measured their ability to accurately detect the direction of moving RDKs. We introduced our experimental protocol in an earlier study (Woo & Burke 2008), but we did not vary the signal-to-noise ratio, as background conditions were constant. Consequently here, we superimposed RDKs upon artificial backgrounds and footage of plant motion from typical Jacky dragon habitats.

## METHODS

### Subjects

Five male Jacky dragons were collected from Lane Cove National Park in New South Wales, Australia, and housed in captive facilities at Macquarie University. Although few in number, our sample size was consistent with behavioural studies that examine motion sensitivity (Coile et al. 1989; Harmening et al. 2007) and that make use of RDK stimuli (Bischof et al. 1999; Goto et al. 2002; van der Willigen et al. 2003). Each lizard was held in an individual glass terrarium (60 × 60 × 60 cm) with sand substrate, natural wooden perches and native leaf foliage. All subjects were visually isolated from each other. Lizards were maintained on a 12:12 h light:dark cycle (lights on at 0800 h). In addition, 120 W heat lamps and 300 W UV lamps were suspended above the terrariums for thermoregulation and access to UV light. Subjects were fed crickets (*Acheta domesticus*) twice a week that had been dusted with vitamin supplements (Rep-Cal<sup>®</sup> Research Labs, Los Gatos, CA, U.S.A.) and water was provided ad libitum in small plastic bowls. Room temperature was maintained at 25 ± 3 °C with minor fluctuations in temperature and relative humidity throughout the day. At the completion of the experiment, all subjects were released near the original point of capture.

### Experimental Design

In an earlier study, we developed a response-independent Pavlovian conditioning paradigm to assess motion sensitivity using

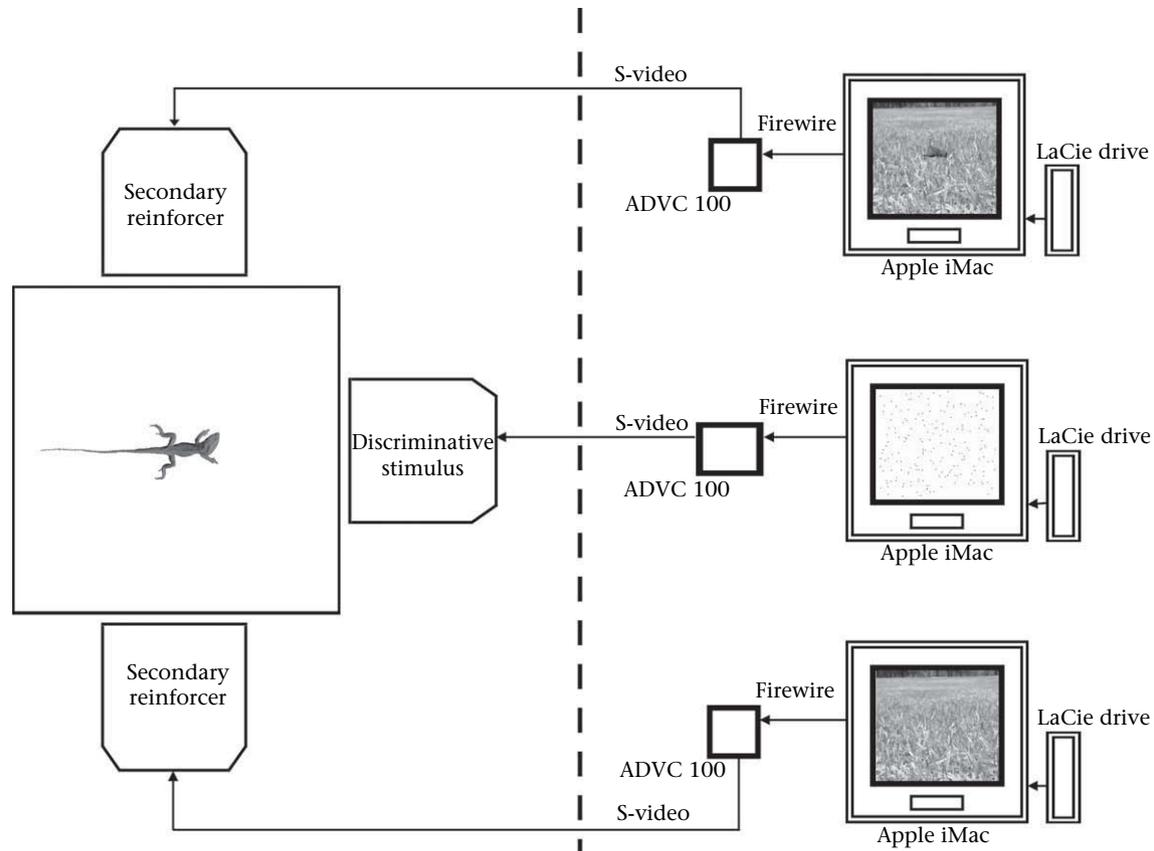
three video playback systems (Fig. 1; Woo & Burke 2008). Lizards were presented with random-dot kinematograms (RDKs) on a central monitor that predicted the appearance of a secondary reinforcer (an animated cricket) on one of two adjacent video monitors. The animated prey item had reinforcing properties because it was associated with an actual food reward during training. The direction of motion of the RDKs defined which monitor would feature the second-order reinforcer. We elected to use various computer-generated invertebrate stimuli in a second-order conditioning procedure that engaged the visual system without presenting an actual food reward. To bridge the second-order reinforcer during training, however, we presented a primary reinforcement of a mealworm (*Tenebrio molitor*), which proved to be a successful reward, using a variable reinforcement schedule. We initially began reinforcing subjects with mealworms at five random trials per block of 20. The reinforcement schedule was made leaner over subsequent blocks until lizards were given only one mealworm per block. We considered lizards to have learned the task when performance reached 75%, which took between 40 and 60 trials. All lizards had reached this criterion before participating in this experiment, during which they received primary reinforcement once per block of 20 trials.

Random-dot kinematograms were defined by the movement speed and level of coherence of a centrally located field of dots. Speed was defined as the distance over time in degrees per second (°/s), as viewed at the far edge of the enclosure (a distance of ~60 cm), while coherence reflected the percentage of RDK dots moving in a left or right direction, and is the factor used to manipulate signal strength. In Woo & Burke (2008), we tested lizards against combinations of eight speeds (0.5°, 2.5°, 5°, 10°, 20°, 40, 80°, 160°/s) and eight levels of coherence (0%, 2.5%, 5%, 10%, 20%, 40%, 80%, 100%). We examined sensitivity across these motion variables to establish the extent to which lizards can resolve moving RDKs, thus allowing us to selectively focus on the range of motion in which lizards were most sensitive. A subset of speeds and coherence levels were used in the present experiment.

We developed a standard 15 s timeline for each trial. On the centrally located monitor, the trial began with 2.5 s of the testing speed at 0% coherence (i.e. dots moving in completely random directions). This was followed by a period of 5 s where the testing speed was maintained, but the percentage of moving dots had now drifted into the test coherence level. Within this 5 s window, lizards were expected to select the left or right monitor that, soon afterwards, would feature an animated invertebrate (the second-order reinforcer). During the opening 7.5 s, both adjacent monitors showed the same looped image of a natural background (cut grass). At 7.5 s, and after the experimental speed and coherence conditions ceased, the computer-generated invertebrate appeared overlaid on the grass background on the correct monitor; no invertebrate appeared on the opposite monitor, which continued to show the natural background. At the same time as the appearance of the secondary reinforcer, the RDKs shifted to 100% coherence at the same speed, thereby identifying the correct monitor and serving as a contingency reminder to the lizards. After a further 7.5 s at 100% coherence, the animated prey item disappeared, the RDKs ceased moving and the trial ended.

### Equipment

Three video playback systems were used for stimulus presentation (Fig. 1). Two playback systems were designated as secondary reinforcers, each consisting of an Apple iMac with Final Cut Pro 3 for stimulus presentation connected to a 160 Gb external LaCie d2 hard drive. The digital signal from the iMac was sent to a Canopus<sup>®</sup> ADVC110 (Grass Valley, Inc., Burbank, CA, U.S.A.) for analogue conversion and then displayed on a Sony Trinitron colour monitor



**Figure 1.** Schematic diagram showing our experimental playback system. Lizards were housed in glass aquaria and presented with the random-dot kinematogram (RDK) stimulus on a monitor along one edge. Two monitors were located at the adjacent edges to reveal a secondary reinforcer stimulus (animated prey item). The direction of motion on the discriminative stimulus monitor indicated on which secondary reinforcer monitor a prey item would appear. Orienting in the direction of, or approach towards, the correct secondary monitor represented a correct choice.

(Model Nos. PVM-14M2A/PVM-14L2). All monitors were placed on mobile trolleys and were presented flush against the subjects' enclosure. As lizards were not constrained in their enclosures, viewing distance could vary from 5 cm next to the monitor to 60 cm at the furthest point in the enclosure. However, most lizards were positioned nearer to the monitor at a distance of approximately 10 cm. A Canon MV650i digital camcorder was mounted on a tripod directly above the terrarium and recorded responses to stimuli directly to a video-cassette recorder. Responses were also seen on a colour viewfinder. The system used for displaying the dots consisted of an iMac connected to a LaCie hard drive containing the stimuli. Digital signals were sent from the iMac to a Sony MiniDV digital recorder (GV-D300E) and then to the Sony Trinitron colour display monitor (PVM-14N5A). Video playback was adjusted for PAL-DV standard (5:1 compression; horizontal resolution 575 lines; 25 frames/s). All experimental trials were recorded directly to VHS before conversion to MPEG4 files using an EvolutionTV™ digital video recorder (Miglia Technology Ltd, Aylesbury, U.K.) for scoring.

#### Random-dot kinematograms

We generated random-dot kinematograms using Visual Programming under UNIX (VPixx v1.79, VPixx Technologies, Inc., Montreal, Quebec, Canada). In this study, we selected dot characteristics comprising four speeds (5°, 10°, 20°, 40°/s) and five directional (left or right) coherence values (5%, 10%, 20%, 40%, 80%). Noncoherently moving dots travelled in random directions with the same speed value. Manipulating the coherence and speed characteristics of the RDKs varied the relative difficulty of the discriminative task. The coherence and speed values we used in

the present study were determined in our earlier study to be within the sensitivity range of Jacky dragons (Woo & Burke 2008).

The RDK stimuli comprised 200 dots randomly positioned in a circular field (200 pixel diameter). Each dot measured five-by-five pixels, which at the typical viewing distance of 10 cm is approximately 1° of visual angle. Individual dots had a lifetime of 0.5 s, but the rebirth of dots in another part of the stimulus field ensured that coherence remained unchanged. This standard procedure prevents subjects from identifying the target direction by tracking an individual dot. RDK stimuli were created with a specified speed and coherence value. All sequences began with 0% dot coherence for 2.5 s, followed by 5 s of the experimental coherence level, and then 7.5 s of 100% coherence, all at the same experimental speed. Clips were exported into Motion JPEG B movie format from VPixx, and then combined into a single stimulus sequence in Final Cut Pro HD. At each interval, a marker tone inaudible to the lizards and fed directly to the VHS tape was included to signify a change in dot coherence for subsequent scoring.

#### Second-order conditioning using computer-generated invertebrate animations

We developed a library of appetitive stimuli to be used in a second-order conditioning paradigm. The reinforcers consisted of computer-generated animations of a moving cricket, a mite and a spider. Animations were created using Lightwave® 3D v7.5 animation software (NewTek, Inc., San Antonio, TX, U.S.A.). Fifty exemplars (20 cricket, 15 mite and 15 spider) were created with movement characteristics matched to live invertebrates. In addition to between-species variation in movement characteristics, we

incorporated within-species variation in our reinforcers set to avoid habituation to a single second-order reinforcer. All animations appeared overlaid onto a digital photo of cut grass lasting 15 s, beginning with 7.5 s of background only before the invertebrate stimulus appeared. The invertebrate appeared immediately after the discriminative stimulus had ceased, and changed to 100% coherence. Sequences were rendered in Lightwave® 3D as JPEG image sequences (375 frames) and imported into Final Cut Pro HD for final editing before being exported as movie streams for playback.

#### Background stimuli

Responses to RDKs were assessed against different backgrounds. In experiment 1, we used a homogeneous white field to examine sensitivity in the absence of motion noise. In experiment 2, we included motion noise comprising drifting dots (artificial backgrounds) and footage of wind-blown plants (natural backgrounds). The use of natural background sequences represented a shift away from traditional RDK methodology to assess sensitivity to salient motion in an ecologically relevant context (e.g. Eckert & Zeil 2001). Similarly, motion parameters set for the artificial (dot) backgrounds were based on quantitative analyses of plant image motion. We describe below the motion characteristics of the backgrounds used in experiment 2.

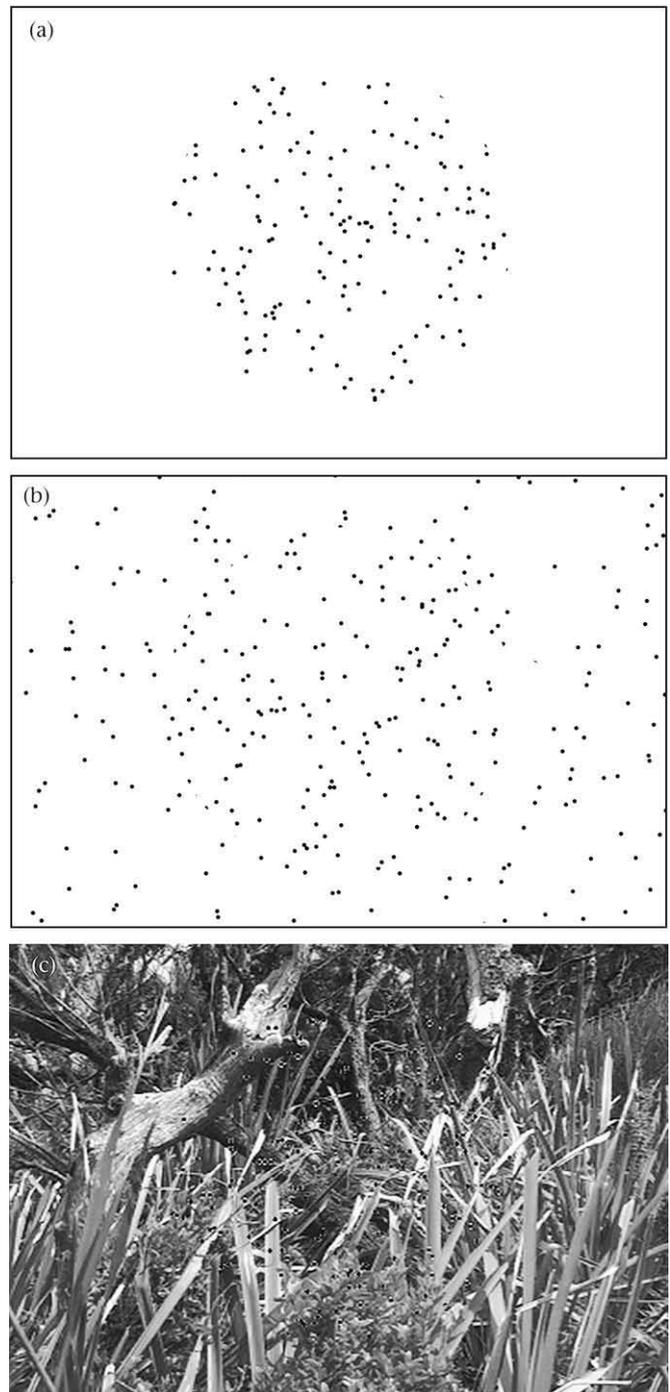
#### Experiment 1: No Motion Noise

The stimulus set comprised 40 RDKs based on the factorial combination of coherence (5 levels), speed (4 levels) and direction (left, right). All RDKs were presented within the inner 200-pixel diameter circle against a homogenous white background (Fig. 2a). Subjects were presented with stimuli in a random order on the central monitor in two blocks of 20, with an intertrial interval varying randomly between 30 and 60 s. The stimulus set was repeated in a new order on the following day.

#### Experiment 2: Artificial and Natural Motion Noise

Here, we considered sensitivity in the context of motion noise generated by artificial and natural backgrounds. Artificial backgrounds were created in VPixx as an outer field of dots (Fig. 2b) to fill the frame (DV PAL:  $720 \times 576$  pixels). Three levels of motion noise were generated based on estimates of plant image motion from a study reported elsewhere (see Peters et al. 2008). We selected two sites from this study: site 1 featured spiny-headed mat rush, *Lomandra longifolia*, in calm wind conditions ( $\sim 1.4$  m/s), and site 2 featured coastal wattle, *Acacia sophorae*, in stronger wind ( $\sim 4$  m/s). The image motions generated under these conditions were quantified using motion detection algorithms based on the gradient method (see Peters et al. 2002), and the calculated angular speed was averaged across space and time, resulting in an estimate for average angular speed for each recording. We used these image motion estimates to define the motion characteristics of artificial dots: low wind speeds at site 1 generated a slow average angular speed at a viewing distance of 10 cm of  $1.6^\circ/\text{s}$  (calm), while site 2 had an average angular speed at 10 cm of  $8.85^\circ/\text{s}$  (windy). We also created a control background sequence featuring stationary dots (still). The artificial background stimuli were created with an inner circle that consisted of the discriminative stimulus, and an outer field of dots with varying levels of motion noise: still, calm and windy.

Natural backgrounds featured the plant motion footage of *L. longifolia* (site 1) and *A. sophorae* (site 2) described above, and a static natural background using an exported frame from site 1 (control). We used the chroma key filter in Final Cut Pro HD to make



**Figure 2.** Representative frames showing random-dot kinematograms superimposed over three simulated backgrounds: (a) homogenous white; (b) artificial (dots); and (c) natural plant motion.

the white background of the RDK clips transparent and overlaid them onto footage of the natural background (Fig. 2c).

The stimulus set for experiment 2 comprised 240 RDKs created from the factorial combination of target coherence (5), speed (4) and direction (2), overlaid against the three levels of artificial and natural backgrounds. We presented the stimuli in a random order in blocks of 20, with two blocks per day over 6 consecutive days. After a break of 6 days, we presented the stimuli in the same way over the next 6 days, albeit with a new randomly generated order of presentation. Each lizard therefore viewed a total of 480 trials.

## Statistical Analysis

We used a binary response measure to score orienting towards the correct secondary reinforcer in the 5 s time window featuring the experimental speed and coherence level before the appearance of the secondary reinforcer (henceforth, accuracy); incorrect choices and the failure to make a choice within the time window were given a score of 0. We used generalized linear mixed models with a logit-link function and a binomial error distribution (GLMM; GenStat, VSN International, Oxford, U.K.) to consider variation in performance. Statistical significances of model parameters were assessed with the Wald statistic ( $\chi^2$ ), which is a large sample approximation of the  $F$  test used in the analysis of variance (McCulloch & Searle 2001). For experiment 1, we set fixed factors of coherence and speed, and used lizard identity as a random factor. Random factors in mixed models are equivalent to the block structure in the analysis of variance. We examined first the model containing fixed factors only and then added the interaction term.

We set up two models to analyse the results from experiment 2. We considered responses against artificial backgrounds using fixed factors of coherence, speed and noise level (Model 1). Direct comparison of noise level for natural backgrounds is problematic because spatiotemporal differences in plant motion might influence detection rather than the motion noise generated by plants. We therefore created a grouping variable (background), which grouped the artificial trials into one category and separated the two natural background trials (site 1, site 2). Trials featuring stationary backgrounds were excluded. The model comprised coherence, speed and background as well as interactions between each factor (Model 2). We used lizard as a random factor in both models. For both models, we started with the fixed factors before adding interaction terms to determine the appropriate model. The number of data points contributing to each model was 1200, although the composition varied slightly between the models: Model 1 included 5 levels of coherence, 4 levels of speed, 3 levels of artificial noise (still, calm, windy) and 2 target directions, with each combination repeated twice for five subjects; Model 2 included 5 levels of coherence, 4 levels of speed, 3 levels of background (artificial, site 1, site 2) and 2 target directions, repeated twice for five subjects.

We do not report latency data for either experiment. Setting nonresponse trials to the maximum stimulus duration generated a data set that mirrored accuracy, with positive and nonresponse values at opposite ends of the distribution. The alternative strategy of removing incorrect responses created an unbalanced data set, leaving model results uninterpretable.

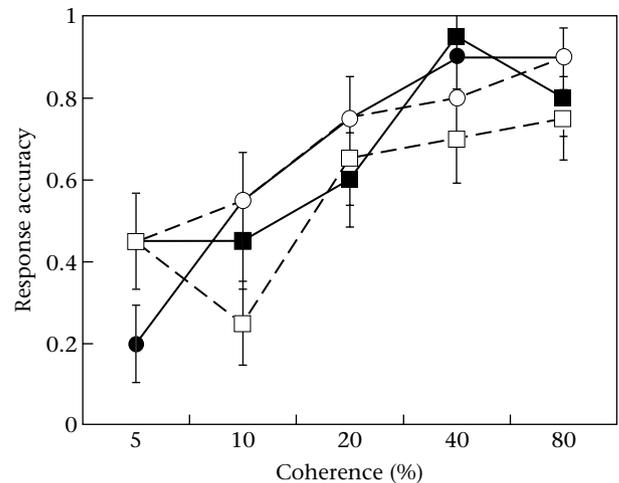
## RESULTS

### Experiment 1: No Motion Noise

Figure 3 summarizes accuracy by levels of coherence and speed for RDKs presented against a white background. Accuracy improved with increasing coherence (Wald test:  $W_4 = 53.82$ ,  $N = 200$ ,  $P < 0.001$ ) but was not influenced by RDK speed ( $W_3 = 4.72$ ,  $N = 200$ ,  $P = 0.194$ ). Improvement with greater coherence was the same for each level of speed (interaction term:  $W_{12} = 11.88$ ,  $N = 200$ ,  $P = 0.455$ ).

### Experiment 2: Artificial and Natural Motion Noise

Response accuracies viewed against artificial (dots) and natural (plants) backgrounds are shown in Fig. 4. Visual inspection of the data suggests improved performance as speed and coherence increase for both artificial and natural backgrounds, with similar trends across noise levels. We analysed separately the artificial and natural background trials. For artificial backgrounds (Model 1), the



**Figure 3.** Response accuracy (mean  $\pm$  SE) as a function of coherence level for experiment 1 in the absence of background motion; speed levels are 5° (●), 10° (○), 20° (■) and 40°/s (□).

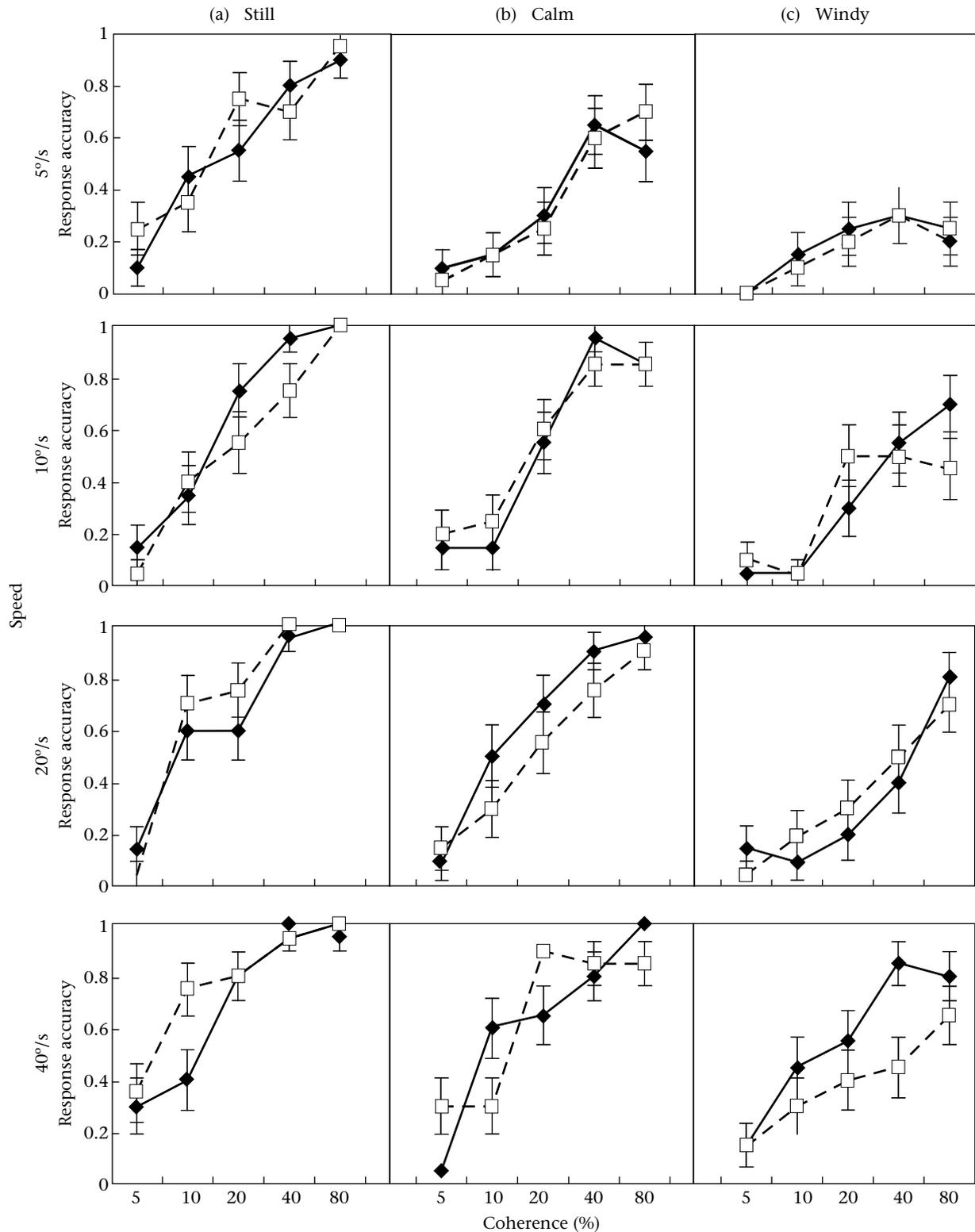
probability of a correct response increased with greater coherence and faster speeds but reduced with stronger motion noise (Fig. 5a, b and c, respectively; Table 1). The only significant interaction was between RDK speed and noise level (Fig. 6, Table 1). The improvement in performance with increasing speed was, therefore, not the same across noise conditions. Performance was particularly poor for RDKs viewed against strong motion noise (Fig. 6).

Model 2 examined performance across the different backgrounds (Fig. 4). Response accuracy varied as a function of coherence, speed and type of background noise (Fig. 5a, b and d, respectively; Table 1); there were no significant interactions.

## DISCUSSION

Random-dot kinematograms in a Pavlovian conditioning paradigm were used to assess the motion sensitivity of Jacky dragons that rely on movement for functionally critical tasks. The properties of RDK stimuli enabled us to assess sensitivity to a particular motion speed without position or form cues that might be indicative of a biologically meaningful object. During trials with artificial (dot) backgrounds (Fig. 2b) in this study, performance improved as target coherence increased and as target speed became faster (Fig. 5a and b, respectively; Table 1). However, the performance improvement with increasing target speeds depended on the level of background motion noise (Fig. 6, Table 1). Indeed, performance accuracy decreased overall when background noise became faster (Fig. 5c, Table 1). These results suggest that Jacky dragons are particularly sensitive to fast, coherent motion, but they are also susceptible to the noise conditions in which detection occurs.

Angular speed differences between the RDK stimulus and background motion noise in our study are likely to have facilitated segmentation. In experiment 1, target speed had little effect on performance because the nonmoving background contrasted sufficiently with all RDK speeds. The static background trials of experiment 2 resulted in a similar pattern of results. However, performance dropped during experiment 2 trials when we presented RDKs against a moving dot background (calm and windy; Fig. 6). This was particularly evident at the slowest target speed (5°/s). In these trials, the angular speed of motion noise encompassed the speed of RDKs. A faster target speed (10°/s) increased the separation between signal and noise during calm trials, thereby improving performance. During windy trials, however, angular speeds of signal and noise remained similar in magnitude, keeping

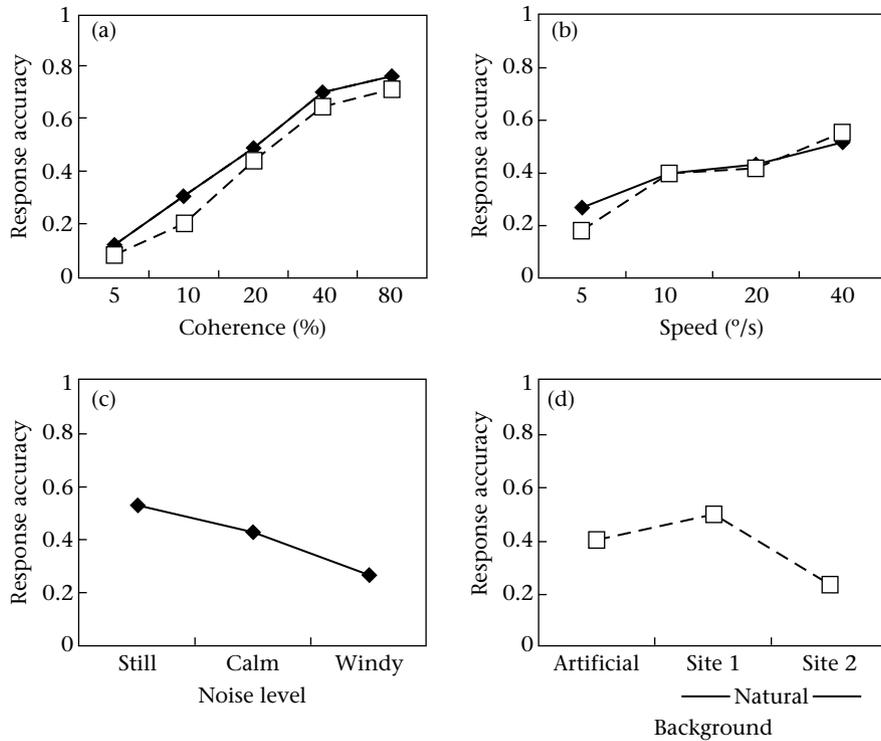


**Figure 4.** Response accuracy (mean  $\pm$  SE) by coherence, and speed for experiment 2. (a) Still conditions for the artificial ( $\blacklozenge$ ) and natural ( $\square$ ) backgrounds. (b) Slow background dot speed (artificial:  $\blacklozenge$ ) and *Lomandra longifolia* footage from site 1 (natural:  $\square$ ). (c) Fast background dot speeds (artificial:  $\blacklozenge$ ) and *Acacia sophorae* footage from site 2 (natural:  $\square$ ).

performance down. Only when RDK speed reached 40°/s were angular speeds distinct enough to improve performance.

Angular speed contrast may, therefore, be a reliable mechanism for segmenting movement-based signals from plant motion noise. This appears to be important for *Anolis* lizards, because some species generate faster displays when plant motion features higher angular speeds (Ord et al. 2007). The present data supports

such a strategy if signals can be generated with sufficient speeds to clearly contrast motion noise. However, our results also show that when the angular speeds of signal and noise are similar, detection is more difficult and that an alternative segmentation mechanism would be required. In experiment 2, strong motion noise limited performance until the target speed was approximately four times that of background motion (target speed of



**Figure 5.** Predicted values from the GLMM backtransformed to the original scale for the main effects of (a) coherence and (b) speed in Models 1 (◆) and 2 (□). Backtransformed predicted values for the main effect of (c) noise level in Model 1 and (d) background type in Model 2. See Methods for a description of the statistical models.

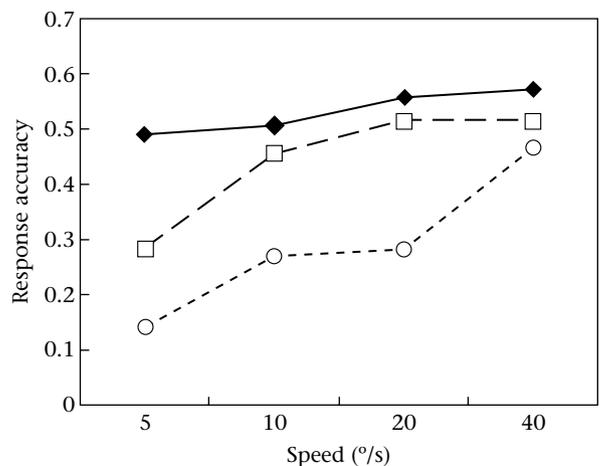
40°/s against motion noise of 8.89°/s; Fig. 6). A signal-to-noise ratio of this magnitude may not be achievable for some signals (e.g. because of physical limitations). This will be particularly true for signals that are performed in the same depth plane as plants (see Peters et al. 2008). Indeed, Jacky dragons signal in close proximity to plants and do not increase display speed to overcome greater motion noise (Peters et al. 2007). Their behaviour suggests that speed differences are not relied upon, while our data indicate that this might be because the magnitude of the signal and noise are similar. Quantitative analyses of Jacky dragon displays within their natural habitats would be required to clarify their angular speed characteristics, and possibly identify alternative segmentation mechanisms.

Replacing artificial (dot) backgrounds with footage of plant motion (Fig. 2c) changed the nature of the detection task. Unlike the dot backgrounds that are set for an entire sequence, the plant image motion was not uniform in space and time (Peters et al. 2008). Nevertheless, the correspondence between performance scores was quite striking (see Fig. 4). Results with natural backgrounds mirrored that of artificial backgrounds: performance improved with greater coherence and faster speeds (Fig. 5a and b, respectively; Table 1). The type of plant background also influenced performance (Fig. 5d, Table 1). These data suggest that the site experiencing stronger plant image motion resulted in a performance decrement. The results are confounded, however, by variation between the sites on properties other than average plant image motion conditions. Image contrast

**Table 1**  
Wald's tests for fixed effects of response accuracy for experiment 2

	Wald's	df	P
<b>Model 1: Artificial (dot) backgrounds*</b>			
Coherence (C)	271.01	4	<0.001
Speed (S)	26.91	3	<0.001
Noise level (N)	63.35	2	<0.001
S×N	26.58	6	<0.001
Interaction terms not in final model			
C×S	16.08	12	0.187
C×N	6.96	8	0.541
C×S×N	19.61	24	0.719
<b>Model 2: Natural (plant) backgrounds**</b>			
Coherence (C)	218.72	4	<0.001
Speed (S)	82.17	3	<0.001
Background (B)	46.05	2	<0.001
Interaction terms not in final model			
C×S	17.31	12	0.138
C×B	7.99	8	0.434
S×B	2.54	6	0.863
C×S×B	20.30	24	0.679

\*N = 1200; \*\* N = 1200.



**Figure 6.** Predicted values from the GLMM backtransformed to the original scale by speed and motion noise level for artificial (dot) backgrounds (Model 1) of still (◆), calm (□) and windy (○).

differences, as well as spatiotemporal variation in plant motion, are perhaps more parsimonious explanations for our findings. That differences were found at all supports our earlier conclusion for the important role of background conditions in segmenting salient visual motion from motion noise. Future work using our experimental paradigm may enable us to tease apart the relative importance of noise level at a given site from the properties that differentiate sites, such as plant structural characteristics (Wagner 1964).

We have demonstrated that random-dot kinematograms are a useful tool for assessing speed sensitivity in lizards, and this capacity may be easily extended to incorporate ecologically relevant motion characteristics. Our findings complement other studies that identified an important role of environmental motion noise for communication (Ord et al. 2007; Peters et al. 2007). By varying background conditions we have demonstrated that both noise level and the type of background can influence the segmentation of salient motion and are important selective forces influencing movement-based signal evolution.

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