

## SHORT COMMUNICATION

# Lizards assess complex social signals by lateralizing colour but not motion detection

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## ABSTRACT

Vertebrates lateralize many behaviours including social interactions. Social displays typically comprise multiple components, yet our understanding of how these are processed comes from studies that typically examine responses to the dominant component or the complex signal as a whole. Here, we examined laterality in lizard responses to determine whether receivers separate the processing of motion and colour signal components in different brain hemispheres. In *Psammophilus dorsalis*, males display colours that dynamically change during courtship and aggressive interactions. We tested the visual grasp reflex of both sexes using robotic stimuli that mimicked two signal components: (1) multiple speeds of head-bobbing behaviour and (2) multiple colours. We found no laterality in response to different motion stimuli, indicating that motion similarly attracts attention from the two visual fields across sexes. Notably, receivers showed left visual field dominance to colours, especially when males were exposed to 'aggression-specific' colours and females to 'courtship-specific' colours.

**KEY WORDS:** Courtship, Aggression, Laterality, Communication, Vision, Social interaction

## INTRODUCTION

*...both the left and the right hemisphere may be conscious simultaneously in different, even in mutually conflicting, mental experiences that run along in parallel*

Roger Wolcott Sperry, 1974 (Horowitz, 2014)

Lateralization of the brain, wherein the left and right hemispheres show independent functions in response to stimuli, has been documented in many animals, including humans (Bisazza et al., 1998a,b; Byrne et al., 2004; Galaburda et al., 1978; Rogers, 2002). Although hemispheric brain areas control opposite sides of the body, functional overlap of information between the two hemispheres can occur via commissural connections, which, when weak, result in high functional laterality for different tasks (Bisazza et al., 1998a,b). In many reptiles, amphibians and fish, processing of visual information occurs almost independently in the two brain hemispheres because of monocular vision from each eye (Greenberg, 1982) and weak commissural connections between the hemispheres (Bisazza et al., 1998a,b). To control for conflicting responses elicited by two simultaneous visual stimuli, and to


enhance processing efficiency, hemispheric dominance is therefore important (Bisazza et al., 1998a,b).

During social interactions, many animals, including lizards, use postural and colour displays to communicate (Macedonia et al., 2013; Stuart-Fox and Moussalli, 2008). Responses to social signals seem to be strongly lateralized in tetrapod vertebrates, with a consistent left-eye bias during aggressive and courtship interactions (Benelli et al., 2015; Bisazza et al., 1998a,b; Cantalupo et al., 1996; Deckel, 1995; Hews and Worthington, 2001; Hews et al., 2004). Surprisingly, even though anatomical asymmetry in brain structures exists between sexes, both males and females of several species are more reactive to competitors when they are viewed from the left visual field (Bisazza et al., 1998a,b; Hews and Worthington, 2001; Hews et al., 2004). Complex signals, however, involve multiple components and individual components could be processed independently in different hemispheres. For example, in zebra finches, different components of song are processed in different hemispheres. The left hemisphere is involved in the broad discrimination of their own song from the song of another, whereas the right hemisphere is activated when discriminating subtle harmonic differences within song structure (Cynx et al., 1992). Here, we asked whether lizards also separate the processing of social signals, such that motion and colour components are analysed in different hemispheres. Given the importance of motion and colour in both courtship and aggressive interactions for many lizards, we specifically examined whether males and females are similarly lateralized in their responses to both contextual signals.

Males of *Psammophilus dorsalis* (Gray 1831) (Fig. 1) have complex social signals that involve physiologically controlled colours that dynamically change (Batabyal and Thaker, 2017) and conspicuous behavioural displays (Deodhar and Isvaran, 2017). During the breeding season, males develop conspicuous colours on the dorsal and lateral regions of their body, which can change dynamically within minutes depending on the type of social interaction (Batabyal and Thaker, 2017). When males of *P. dorsalis* interact with females, the dorsal band changes from patchy yellow (typical neutral colour) to orange or red, while the lateral band changes from patchy orange (typical neutral colour) to black (Batabyal and Thaker, 2017). During interactions with other males, the dorsal band changes to yellow, while the lateral band changes to an even brighter orange (Batabyal and Thaker, 2017). As is typical for most agamid lizards, *P. dorsalis* also shows head bob and push-up displays during inter- and intra-sexual social interactions (Deodhar and Isvaran, 2017). In this study, we tested laterality in receiver responses to social signals with the use of robotic stimuli that mimicked two key components: (1) multiple speeds of head bobbing behaviour (slow, medium, fast) and (2) multiple colours (red, yellow, black and grey). The visual grasp reflex of receivers in response to controlled robotic stimuli exposed simultaneously in the two visual fields allowed us to determine visual field bias for movement and colour stimuli separately (Nava et al., 2012). By

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**Fig. 1.** *Psammophilus dorsalis* male assessing a potential competitor from the left visual field. Average body size and head size of an adult male are indicated (photo credit: K. Shanker, Ashoka Trust for Research in Ecology and Environment).

recording receiver responses to paired stimuli, we determined whether and to what degree complex social signal processing is lateralized, as well as whether the sexes differ in their laterality and responsiveness to signal components.

## MATERIALS AND METHODS

To test receiver responses to signal components, we designed robotic stimuli (resembling a lizard head) that closely mimicked two key aspects of the social display of *P. dorsalis* males: motion and colour (similar to Clark et al., 2017; Macedonia et al., 2013). Motion stimuli were set at one of three rates: slow (0.5 Hz=0.5 head bobs s<sup>-1</sup>), medium (1 Hz=1 head bob s<sup>-1</sup>) and fast (2 Hz=2 head bobs s<sup>-1</sup>), with an amplitude of 30 deg centred on the test lizard's nearest eye. This reflected the range of head bob speeds shown by males during male–male (medium) and male–female (fast) interactions. Each motion stimulus was paired with a stationary control stimulus of the same colour (neutral grey). The three static colour stimuli – red, black and yellow – were matched to the natural spectra seen in males of *P. dorsalis* during social interactions. Each coloured stimulus was paired with a grey control stimulus, which is not a display colour for this species. Thus, during the trials, each lizard was simultaneously exposed to two different stimuli placed in both the left and right visual fields (see Fig. S1 for experimental setup).

### Robotic stimulus design

Robotic stimuli closely mimicked two key aspects of the social display of males of *P. dorsalis*: motion and colour. To minimize the complexity of the stimuli, robots did not mimic the entire lizard body, but were a cylinder (3.5 cm diameter×4 cm length), approximately the size of a *P. dorsalis* male's head that varied in colour and moved in a manner that mimicked a typical head-bob display. To correctly match colour and motion to the natural responses of males, we first caught sexually mature males and females from the wild during the peak breeding season (April to August) and brought them to the

laboratory, where they were housed individually in a dedicated lizard housing facility. After a 24 h habituation period, males were allowed to interact undisturbed for 30 min with a conspecific male or female ( $N=20$  for each type of social interaction). These social encounters were staged in large glass terraria (95×45×30 cm) under full-spectrum lighting behind a blind, and were digitally recorded from above. From these videos, we extracted all occurrences of head-bob displays and quantified the rate of head bob, measured as the time it took for a male to lift and return his head to the original position (i.e. perform a single head bob). The speed of head-bob displays by males ranged from 1.25 to 2 Hz (1.25–2 head bobs s<sup>-1</sup>) during interactions with females and from 0.75 to 1.5 Hz (0.75–1.5 head bobs s<sup>-1</sup>) during interactions with males, with an amplitude ranging between 20 and 30 deg from the viewing conspecific.

*Psammophilus dorsalis* males also dynamically change their colours to red (dorsal and lateral regions), yellow (dorsal region only) and black (lateral region only) during social interactions (Batabyal and Thaker, 2017). To ensure that the colours on the robotic model were within the natural range and perceptually similar to the spectral reflectance of males, we used visual modelling to compare the red, yellow and black paints on the robots with the reflectance displayed by *P. dorsalis* during social interactions. Natural spectral reflectance for social colours was obtained from data published in Batabyal and Thaker (2017), and spectral reflectance for the robotic colours was measured using a spectrophotometer (Jaz Spectrometer, Ocean Optics, Largo, FL, USA; see detailed methods in Batabyal and Thaker, 2017; Zambre and Thaker, 2017). Visual modelling was done using the PAVO package in R statistical software (Maia et al., 2013) using spectral sensitivity states of the agamids *Ctenophorus ornatus* and *Ctenophorus decresii* (from Barbour et al., 2002; Yewers et al., 2015, respectively). Visual systems in diurnal lizards are conserved and therefore the spectral sensitivities of *Ctenophorus* species serve as a suitable alternative for those of *P. dorsalis*, as it is also an agamid (Olsson et al., 2013). Irradiance values for visual modelling were fixed as standard daylight irradiance conditions (D65) provided in the PAVO package. We also applied the Von Kries transformation as described in Endler and Mielke (2005) to account for light adaptation. Chromatic contrast (just noticeable differences, JNDs) between red, yellow and black obtained from averaged natural spectra of *P. dorsalis* and from the robotic stimuli indicated that lizards could detect robotic stimulus colours similar to natural spectra when viewed against a brown background (chromatic contrast of all colours against brown background; natural red dorsal: 12.79, natural red lateral: 10.92, model red: 13.11; natural yellow: 8.87, model yellow: 10.10; natural black: 10.08, model black: 8.88; see also Fig. S2). Achromatic contrast or brightness (calculated against the brown background used during the experiment) and luminance of all model colours (grey, yellow and red, except black) were also comparable (achromatic contrast: model red=23.35, model yellow=22.22, model grey=23.68, model black=30.24; see also Fig. S3 for luminance graph). Thus, the reactions of lizards to paired colour stimuli were expected to be in response to differences in hue and chroma (chromatic contrast), and not luminance or brightness.

### Housing and testing conditions

Receiver responses for motion and colour were measured during the breeding season from April to August 2015 using wild-caught adult male and female *P. dorsalis*. All animals were housed individually in glass terraria (60×30×25 cm) in a dedicated animal housing room that permitted natural temperature and light conditions. Terraria

were lined with disposable paper towels as the substratum, provided with rocks for refuge, and were covered on all sides to minimize disturbance. Lizards were acclimatized for 2 days before the start of trials. Animals were provided with live ants and field crickets daily for food and water *ad libitum* and were maintained in the laboratory for 7–9 days for the duration of the trials.

Before the start of each choice trial, lizards were allowed to bask individually under a 60 W incandescent light bulb for at least 30 min to reach preferred body temperatures before being transferred to the testing terrarium. The entire experimental setup was kept under full-spectrum lighting conditions in the laboratory (VivaLite B22, Winterbach, Germany: UV+visible+infrared wavelength), and was behind a blind to minimize disturbance. All behavioural trials were digitally recorded with an overhead camera (Cannon 600D digital SLR).

### Paired choice trials

Receiver responses were measured using a paired choice trial. We designed narrow glass testing terrariums (35×11×35 cm) that restricted the movement of a lizard such that it was facing the front throughout the trial. The front and back of the terrarium were opaque to minimize disturbance and the longer lateral sides were transparent with brown removable sliding boards. Lizards were allowed 10 min to acclimate in the testing terrarium before the beginning of each trial. After acclimation, the brown sliding boards were removed and each lizard was exposed to two stimuli simultaneously, one on each side. One robotic stimulus was placed on each of the two lateral sides of the testing terrarium with the standard brown background to mimic the natural signalling conditions (Fig. S1). Two behavioural responses were recorded during each trial: (1) the choice made by each focal animal, measured as the movement of the head in the direction of the preferred stimulus, and (2) the latency to make that choice (Nava et al., 2012).

To determine responses to motion, wild-caught males ( $N=42$ ) and females ( $N=35$ ) were given a choice between the following robotic pairs: a slow (0.5 Hz), medium (1 Hz) or fast (2 Hz) moving grey stimulus paired with a stationary grey stimulus. To quantify laterality in receiver responses to motion, we exposed all animals to the moving robotic stimuli in both the left and right visual fields, in random order with a 24 h gap between trials. Based on the results of the motion trials (see Results), we used the speed with the lowest variation in response times shown by both males and females (1 Hz) as the standard motion rate for the following colour trials. To determine responses to stimulus colour, males ( $N=40$ , for 6 colour trials) and females ( $N=33$ , for 6 colour trials) were given a choice between the following robotic pairs: a moving red, black or yellow stimulus paired with a moving grey stimulus. Similar to the motion trials, the positions of the coloured and grey stimuli were initially randomized and then switched 24 h later.

Lizards were allowed a minimum of 4 h in their home terrariums between successive trials and the same individual was tested for a maximum of 2 trials in 1 day. One set of lizards (males:  $N=42$ , females:  $N=35$ ) was exposed to all motion trials and a different set of lizards was exposed to all colour stimuli (males:  $N=40$ , females:  $N=33$ ). All capture, handling and experimental protocols were approved by the Institutional Animal Ethics Committee at the Indian Institute of Science (CAF/Ethics/394/2014)

### Statistical analyses

We first scored responses of individuals as 0 (no response) and 1 (response) based on whether they turned towards a stimulus, for all types of stimuli (3 speeds or 3 colours) and for all visual fields of

exposure (left or right). To determine whether the stimulus elicited lateralized responses (turn to one side over another), we used generalized linear mixed-effects models (R package: glmmADMB, <http://r-forge.r-project.org>) with a binomial distribution, wherein the response variable was scored as 0 or 1, and stimulus type (slow, medium, fast), sex (male or female) and visual field (left or right) were fixed factors, with lizard ID as a random effect. We first constructed a global model with sex, stimulus type and visual field of exposure as a three-way interaction factor (model 1:  $\text{Response} \sim \text{Sex} \times \text{Stimulus} \times \text{Visual\_field}$ ,  $\text{random} = 1 | \text{ID}$ ). We then contrasted simplified models with two-way interactions of the fixed factors against this global model to determine the most parsimonious model (ANOVA). An additive model of sex, stimulus type and visual field of exposure, with an additional interaction term of sex and stimulus (model 2:  $\text{Response} \sim \text{Sex} + \text{Stimulus} + \text{Visual\_field} + \text{Sex} : \text{Stimulus}$ ,  $\text{random} = 1 | \text{ID}$ ), sufficiently explained the response of lizards (ANOVA comparison of model 1 and model 2:  $P=0.761$ ).

We ran a similar glmm (glmmADMB) for colour stimuli (black, red, yellow versus grey). Responsiveness to colour was best predicted by a global model with sex, type of colour and visual field as a three-way interaction (model 1:  $\text{Response} \sim \text{Sex} \times \text{Colour} \times \text{Visual\_field}$ ,  $\text{random} = 1 | \text{ID}$ ). Removal of the three-way interaction term resulted in a significant difference between the models (model 2:  $\text{Response} \sim \text{Sex} + \text{Colour} + \text{Visual\_field} + \text{Sex} : \text{Colour} + \text{Colour} : \text{Visual\_field} + \text{Sex} : \text{Visual\_field}$ ,  $\text{random} = 1 | \text{ID}$ ; ANOVA comparison between model 1 and model 2:  $P < 0.001$ ). Thus, the three-way factor of sex×colour×visual\_field was an important predictor of whether lizards turned towards a coloured stimulus. To better understand these interactions, we separated our data into males and females and analysed sex-specific responses to colour and visual field as a two-way interaction model ( $\text{Response} \sim \text{Colour} \times \text{Visual\_field}$ ,  $\text{random} = 1 | \text{ID}$ ). For both colour and motion stimuli we performed contrasts between interacting factors in the glmm models using lsmeans (Lenth, 2016).

For those individuals that responded, we then compared the latency to respond to a moving stimulus to determine whether sex (male, female), speed of stimulus (slow, medium, fast) and visual field (left, right) affected how quickly an animal responds by using a linear mixed-effects model with individual ID as a random effect. Similarly, we compared the latency to respond to a colour stimulus using a linear mixed-effects model with sex, type of colour (black, red, yellow) and visual field as fixed factors and individual ID as a random effect (R package: lme4 and lmerTest; Bates et al., 2014; Kuznetsova et al., 2016). For these analyses, we included an interaction term between the three fixed factors and presented the *F*-test for lmer results that predicted the latency to respond (type III with Satterthwaite approximation for degrees of freedom). Where relevant, we performed *post hoc* comparisons for all interactions using lsmeans (R package lsmeans; Lenth, 2016). Variation due to individual ID was low for all tests ( $s.d. < 1.00$ ). All data analyses were performed using R studio version 3.4.2 (<http://www.R-project.org/>).

## RESULTS AND DISCUSSION

### Response to a moving stimulus

When given a choice between a moving stimulus and a stationary one, all lizards that responded chose the moving stimulus, regardless of motion speed. The response of lizards, measured as whether or not they turned to the stimulus (1 or 0), was best explained by an interaction of sex and stimulus speed, and not visual field ( $z$  ratio=1.19,  $P=0.071$ ; Table 1). When given the choice between a stationary stimulus and a slow-moving stimulus, more males than

**Table 1. Proportion of individuals that responded to different motion and colour stimuli when viewed from the left versus right visual field**

Stimulus	Type	Sex	Visual field	
			Left	Right
Motion	Slow	Female	0.57	0.51
		Male	0.95	0.83
	Medium	Female	0.85	0.77
		Male	0.95	0.83
	Fast	Female	0.77	0.60
		Male	0.73	0.59
Colour	Black	Female	<b>1</b>	<b>0.40</b>
		Male	0.77	0.72
	Red	Female	<b>1</b>	<b>0.45</b>
		Male	<b>0.92</b>	<b>0.29</b>
	Yellow	Female	0.66	0.57
		Male	<b>0.84</b>	<b>0.41</b>

Proportion data were calculated from 35 females and 42 males tested in the motion trials and 33 females and 40 males tested in the colour trials. Significant laterality (bias towards the left visual field) by males and females was seen for specific colours, as indicated in bold.

females turned towards the moving stimulus ( $z$  ratio= $-2.92$ ,  $P=0.040$ ; Fig. 2, Table 1). More females turned towards the moving stimulus when it was of medium speed compared with slow speed ( $z$  ratio= $2.79$ ,  $P=0.054$ ; Fig. 2, Table 1).

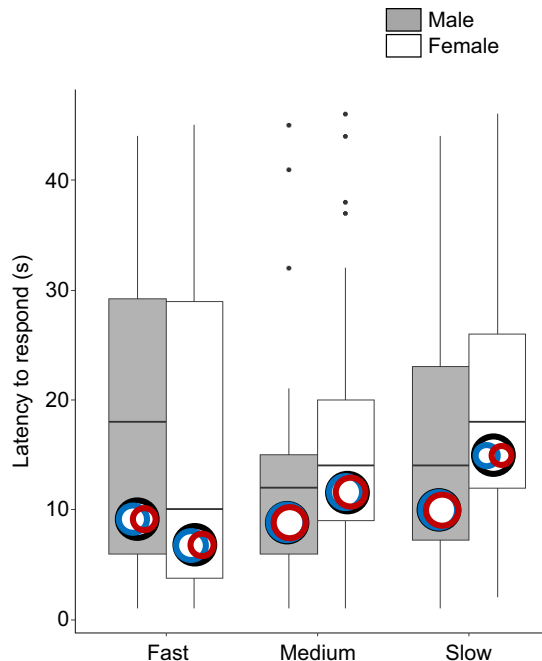
Latency to respond to a moving stimulus was significantly affected by an interaction between sex and speed of the stimulus (interaction  $F_{2,334}=3.20$ ,  $P=0.041$ ), but not the visual field ( $F_{1,334}=0.13$ ,  $P=0.717$ ). Further *post hoc* comparisons showed that males responded fastest to the medium speed compared with the

fast speed (*post hoc*  $P=0.007$ ; Fig. 2). Females responded similarly to all speeds (*post hoc*  $P>0.07$  for all pairwise comparisons; Fig. 2).

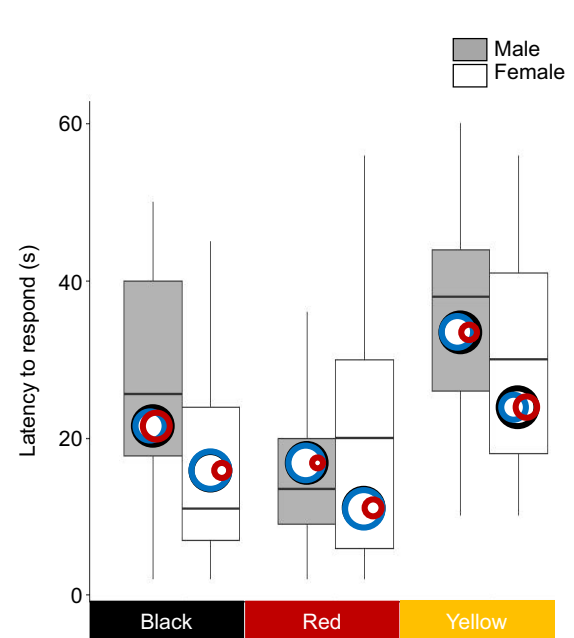
### Response to a coloured stimulus

During the colour trials, all lizards that responded turned towards the coloured stimulus over the grey one, indicating that they could detect differences between these stimuli. The proportion that responded, however, depended on the type and position of the colour stimulus, with more males and females being responsive when the coloured stimulus was in their left visual field compared with when it was in their right visual field (Table 1). When comparing sex-specific responses across colour stimuli, a greater number of males responded to red and yellow colours when they were seen from their left visual field compared with their right visual field (red:  $z$  ratio= $3.09$ ,  $P=0.001$ ; yellow:  $z$  ratio= $2.23$ ,  $P=0.025$ ; Fig. 3, Table 1). Females showed a similar visual field bias in responses to red and black colours, wherein a greater number of females responded to these colours when they were seen from their left visual field compared with their right visual field (red:  $z$  ratio= $1.97$ ,  $P=0.047$ ; black:  $z$  ratio= $3.43$ ,  $P<0.001$ ; Fig. 3, Table 1).

Latency to respond to a colour stimulus was affected by an interaction between sex and the type of colour (interaction  $F_{2,288}=4.48$ ,  $P=0.012$ ), as well as an interaction between type of colour and visual field (interaction  $F_{2,288}=4.73$ ,  $P=0.009$ ). *Post hoc* comparisons showed that males responded fastest to red compared with yellow (*post hoc*  $P=0.028$ ; Fig. 3). Latency for females to respond was similar across coloured stimuli (*post hoc*  $P>0.20$  for all pairwise comparisons; Fig. 3). Laterality, or left visual field bias, in the latency to respond was observed only for yellow stimuli for both



**Fig. 2. Latency to respond to a moving stimulus (fast, medium, slow) for the two visual fields combined.** Data are shown for males ( $N=42$ ) and females ( $N=35$ ). Boxplots show medians, quartiles, 5th and 95th percentiles and extreme values. There was no significant laterality in response to different motion stimuli, as illustrated by the inner circles within the boxplots, which represent the proportion of individuals that turned to the moving stimulus when it was in the left visual field (blue circles) compared with when it was in the right visual field (red circles). Diameters of the circles represent the proportion of individuals.



**Fig. 3. Latency to respond to a colour stimulus (black, red, yellow) for the two visual fields combined.** Data are shown for males ( $N=40$ ) and females ( $N=33$ ). Boxplots show medians, quartiles, 5th and 95th percentiles and extreme values. The inner circles within the boxplots represent the proportion of individuals that turned to the colour stimulus when it was in the left visual field (blue circles) compared with when it was in the right visual field (red circles). Diameters of the circles represent the proportion of individuals. Note that significant laterality (bias towards the left visual field) was observed for males in response to red and yellow colours and for females in response to black and red colours.

males (mean±s.e.m.: 31.54±1.84 s for left versus 44.50±1.97 s for right; *post hoc*  $P<0.001$ ) and females (23.40±1.79 s for left versus 37.42±2.20 s for right; *post hoc*  $P<0.001$ ).

Social displays in *P. dorsalis* are complex, involving dynamic changeable colours and behaviour displays. When stimulus components were separated, we found that males and females showed lateralized responses for colours and not for moving stimuli. Regardless of the speed of the stimulus, all lizards chose a moving stimulus over a stationary stimulus in both visual fields. When shown various social colours, a greater number of males and females responded when the social colour stimulus was in the left visual field than the right. Our results are in general congruence with previous evidence across taxa for right hemispheric dominance (left visual field) in social aggression, although we show for the first time that all social display colours, including courtship displays, have a left visual field bias in lizards, while motion is similarly attractive to the left and right visual fields.

Laterality was not observed for general moving stimuli in male and female lizards. This suggests that motion effectively attracts attention, probably because motion is associated with more than just social displays, and is involved in the detection of many other natural stimuli, including predator or prey movement. A variety of species are more reactive to predators seen in their left visual field than in their right (Bonati et al., 2010; Martín et al., 2010). In contrast to leftward responses for predators, animals are more likely to attack prey viewed from the right hemifield (Bonati et al., 2008; Robins et al., 2005). Though the movement pattern for conspecific displays and movement of predators or prey are different, a general motion stimulus in the environment might be sufficient to attract attention across both visual fields. Further processing of motion stimuli for precise responses might invoke laterality when the organism needs to respond with elaborate behavioural reactions (Robins and Rogers, 2004). We found that motion alone without any association with display colours elicits similar responses from the two visual hemifields, which strongly supports our hypothesis that *P. dorsalis* uses motion mainly to attract the attention of receivers. Laterality in social signal processing is only seen when motion is associated with specific display colours.

The strength of laterality in response to colour stimuli depended not only on the colour but also on the sex of the receiver. More males were lateralized when responding to red and yellow colours, while more females used lateralized responses when exposed to red and black colours. There are two key conclusions that can be drawn from these results. First, receiver responses match the context of dynamic changeable display colours of senders. We can also ascertain here that laterality shown for colour stimuli is perceived as social signal colours and not prey colours because responses of males and females towards colour stimuli are different. It is unlikely that the sexes will differ in their responses to prey stimuli, especially as dietary overlap between the sexes is high for *P. dorsalis* (Balakrishna et al., 2016). Females of *P. dorsalis* are cryptic, but males display red (dorsal band) and black (lateral band) colours during courtship interactions with females, and yellow (dorsal band) and red (lateral band) colours during competitive interactions with other males (Batabyal and Thaker, 2017). Our results support the expectation that males would be less responsive or less attracted to black whereas females would be less attracted to yellow, which are colours that are not typically displayed to them during social interactions. These sex differences suggest that responses were not generalized for all colours; instead, right brain hemisphere dominance is seen for relevant social display colours only. It is also clear that some colours elicit stronger reactions (quicker

responses) than others. For example, males responded faster to red than to yellow. We make no assertion here that the visual grasp reflex of head turning reflects preference but it does indicate attraction to a particular colour stimulus. Second, our study shows right hemispheric dominance in both males and females for all social colours. The phenomenon of right hemispheric dominance during aggressive displays has been seen in fish, birds and lizards (Bisazza et al., 1998a,b; Cantalupo et al., 1996; Hews and Worthington, 2001; Ventolini et al., 2005), but very few studies have examined laterality in both courtship and aggressive contexts for a single species (but see Cantalupo et al., 1996). In a classic experiment by Howard et al. (1980), hemispheric dominance in chicks was detected by injecting cyclohexamide or glutamate in left and right brain hemispheres, which blocked proper development (Howard et al., 1980). An elevated rate of attack and copulation was observed following injection in the left but not the right brain hemisphere, suggesting that the right hemisphere activated/enhanced attack and copulation behaviours while the left hemisphere suppressed it (Howard et al., 1980). In a similar way, right hemispheric dominance for social interactions might explain why the visual grasp reflex in *P. dorsalis* was stronger when social display colours were presented in the left visual field compared with the right.

In a recent review, Endler and Mappes (2017) highlight several weak links in animal colour research, including the fact that we still have little understanding of how animals detect and process moving colour stimuli during social interactions (Endler and Mappes, 2017). Despite immense data on the complexity and function of social signals in animals (Cuthill et al., 2017), higher-level brain processing of motion and colour signals in vertebrates remains a mystery (Endler and Mappes, 2017). We show here that complex social signals are processed as separate motion and colour components: while motion stimuli are attractive to both visual fields (hemispheres), social colours are lateralized to the right hemisphere. This is in accordance with the fact that initial detection of motion and colour are performed by different cells (rods and cones, respectively) in the retina of most animals and thus separate brain processing of functional information is not surprising. We also show that not all colours are similarly attractive to receivers. This species uses nuanced physiological colours to communicate, showing different colours in different social contexts (Batabyal and Thaker, 2017). Although receivers can detect all social colours, we found that responses are similarly nuanced and lateralized to relevant social colours only.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: A.B., M.T.; Methodology: A.B., M.T.; Formal analysis: A.B.; Investigation, A.B.; Writing - original draft: A.B.; Writing - review & editing: M.T.; Funding acquisition: M.T.

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## Supplementary information

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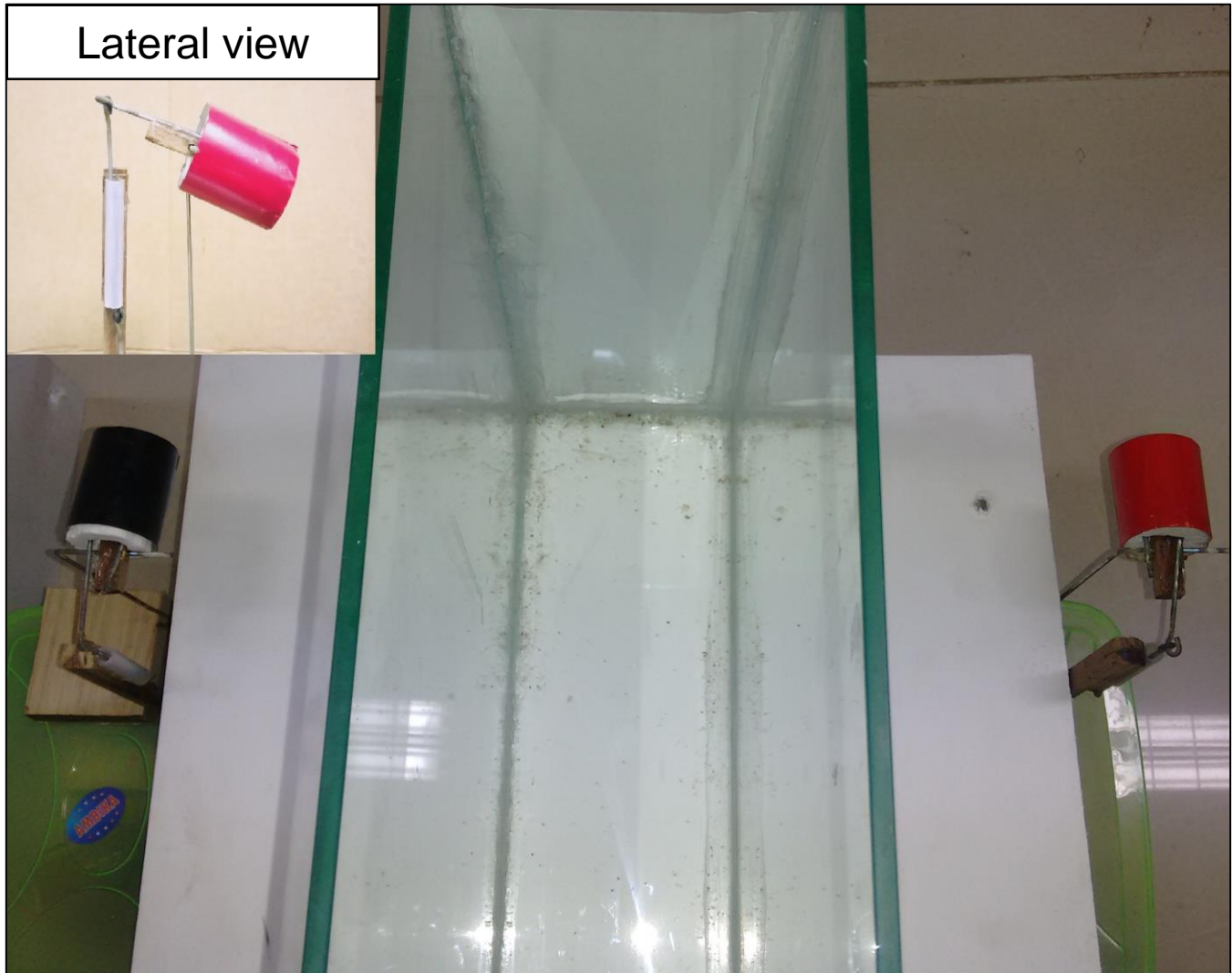


Figure S1. Experimental setup in which two stimuli were simultaneously placed on either side of the terrarium, where the test lizard was introduced. The lateral view shows the stimulus from the perspective of the test lizard.

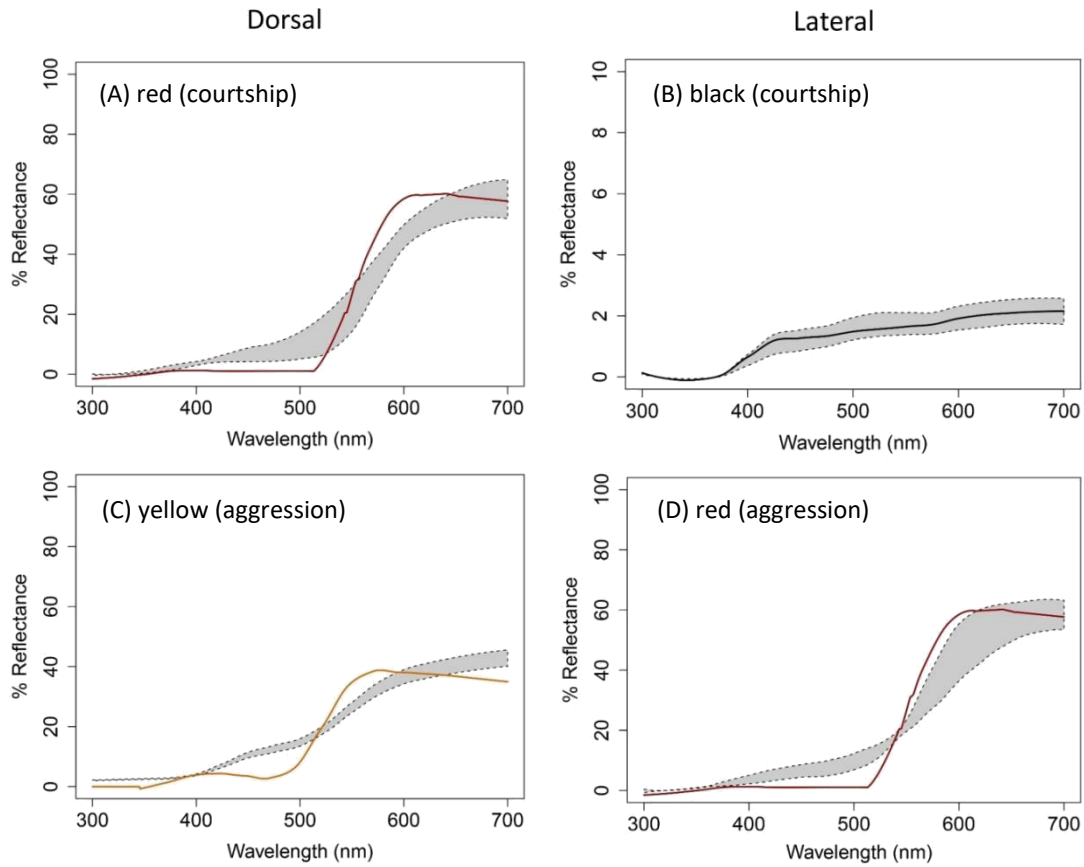


Figure S2. Typical variation in reflectance spectra in males of *P. dorsalis* during staged social interactions. Shown are the (A) red dorsal and (B) black lateral regions during courtship interactions with females, and the (C) yellow dorsal and (D) red lateral regions during aggressive interactions with males (grey spectral band; N=5 for each colour). Solid lines depict the reflectance spectra of corresponding model colours used on the robotic stimuli.



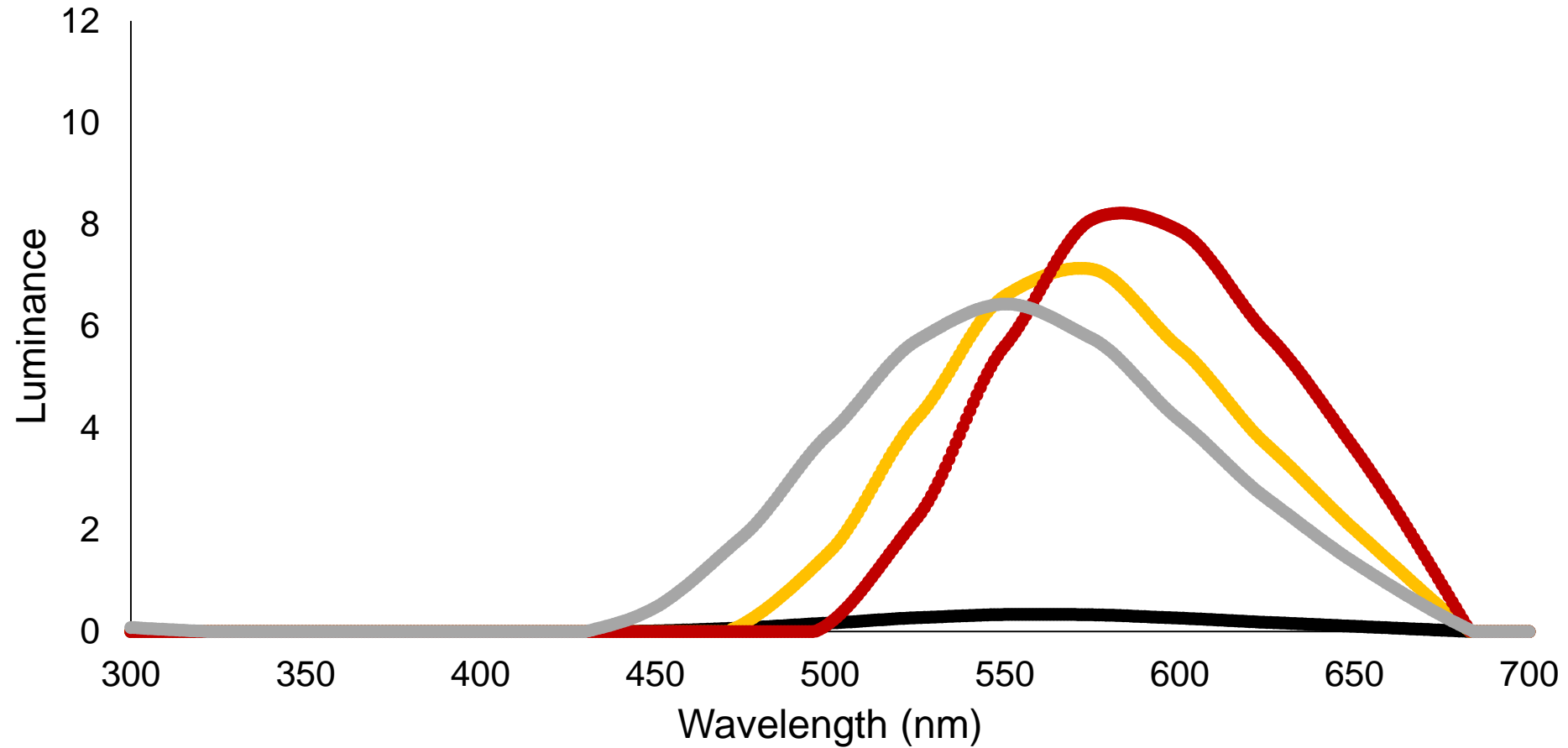


Figure S3. Luminance for all four model colours (black, grey, yellow and red) on the robotic stimuli. Luminance values were calculated as reflectance\*irradiance\*spectral sensitivity of the long wavelength sensitive cone.