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Perception of artificial conspecifics by bearded dragons (*Pogona vitticeps*)

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Abstract: Artificial animals are increasingly used as conspecific stimuli in animal behavior research. However, researchers often have an incomplete understanding of how the species under study perceives conspecifics, and hence which features needed for a stimulus to be perceived appropriately. To investigate the features to which bearded dragons (*Pogona vitticeps*) attend, we measured their lateralized eye use when assessing a successive range of stimuli. These ranged through several stages of realism in artificial conspecifics, to see how features such as color, the presence of eyes, body shape and motion influence behavior. We found differences in lateralized eye use depending on the sex of the observing bearded dragon and the artificial conspecific, as well as the artificial conspecific’s behavior. Therefore, this approach can inform the design of robotic animals that elicit biologically-meaningful responses in live animals.

Keywords: conspecifics, bearded dragons, lateralized eye use, perception

Introduction

The use of robotic animals in behavior and cognition research is rapidly increasing (Miklósi & Gerencsér 2012; Krause et al. 2011; Mitri et al. 2013) as it allows researchers to fully control the responses of a conspecific stimulus during an interaction without having to train often unreliable or unpredictable live animals (Frohnwieser, Murray, et al. 2016). However, one of the greatest challenges in creating artificial animals for use in interactions with real animals is to understand how they are perceived by their live counterparts. To design an appropriate conspecific it is essential to investigate which features are important for them to be perceived as conspecifics.

One way of doing this is to look at behavioral markers that indicate an animal's perception of a stimulus. One of these markers is lateralized eye use, which is the predominant use of one eye over the other when observing a stimulus (Rogers 1989; Andrew 2002). In general, the left hemisphere/right eye is responsible for attention, perceptual processing and control of motor response (Rogers & Andrew 2002), while the right hemisphere/left eye controls emotions and spatial perception. Therefore, many species prefer to look at conspecifics with their left eye and use their right eye when observing other classes of stimuli, such as prey items (McKenzie et al. 1998; Bisazza et al. 1998; Bisazza et al. 1999; Karenina et al. 2013; Vallortigara et al. 1998; Racca et al. 2012; Sovrano et al. 2017). As lateralized eye use has been observed in a wide range of lizard species (Bonati et al. 2008; Bonati et al. 2010; Bonati et al. 2013; Hews & Worthington 2001; Hews et al. 2004; Deckel 1995; Deckel & Fuqua 1998; Robins et al. 2005), it may be a potentially useful tool for evaluating how animals categorize stimuli representing conspecifics. It also seems to be a useful tool to examine differentiation of conspecifics and other stimuli in bearded dragons, as females (but not males) prefer to use their left eye when viewing videos of conspecifics (Frohnwieser et al. 2017). Therefore, we used this method to investigate which visual features of an animal were important for it to be perceived as a conspecific lizard. While olfaction has been shown to aid conspecific perception in lizards (e.g. Carazo et al. 2008), bearded dragons showed little behavioral responses to scent of conspecifics (Frohnwieser et al. unpublished data). Therefore, we focussed on manipulating four key areas of visual perception: shape, eyes, color and movement.

Shape: We tested the animals' response to differently shaped stimuli, ranging from abstract objects to 3D scanned replicas of conspecifics. Shape is an important factor in the recognition of conspecifics in many animals and it has been shown that other species are able to discriminate conspecifics from objects that are shaped similarly to them (Palmer et al. 2006). Bearded dragons change shape by extending their necks into 'beards' and flattening their bodies in agonistic situations (Brattstrom 1971), indicating that shape is an important signal in this species.

Eyes: The presence of eyes has been found to be a highly salient stimulus in many vertebrate species (Emery 2000). For example, the presence or absence of eyes plays a crucial role in eliciting lateralized eye use in fish (Karenina et al. 2013), and both red-footed tortoises (*Chelonoidis carbonaria*) (Wilkinson et al. 2010) and bearded dragons (Siviter et al. in press) will follow the gaze of conspecifics.

Color: Bearded dragons have characteristic patterns on their skin that vary between individuals, and they can change the darkness of their skin according to temperature or affective state (Fan et al. 2014; Smith et al. 2016; De Velasco & Tattersall 2008). Therefore, the skin color of other bearded dragons might hold valuable information for conspecifics, such as how to approach each other and whether to expect aggression, or information about a location's temperature. Thus the color and brightness of a conspecific is an important signal and may influence how it is perceived by the animals.

Movement: Movement has been shown to aid the perception of conspecifics. For example, medaka fish (*Oryzias latipes*) exhibit more shoaling behaviour in the presence of dots that move in a way that is similar to the movement conspecifics (Nakayasu & Watanabe 2014). In antagonistic context, both male and female bearded dragons show a dominance display, known as head bobbing, which is a highly stereotypic, rapid up and down movement of the head (Brattstrom 1971; Frohnwieser, Willmott, et al. 2016). Males also exhibit it during their mating display. Because head bobbing is a key component of the visual communication of bearded dragons, we tested the response of observing bearded dragons to the head bobbing of an artificial conspecific.

To investigate what features are necessary for an object to be perceived as a conspecific we systematically manipulated the salient features highlighted above. In addition, we compared the behavior of male and female animals. Bearded dragons are territorial and show aggression towards unfamiliar conspecifics, that can lead to major injuries and is most common between males (Rowland 2009). Females are generally smaller and might therefore be at greater risk of injuries, while at the same time might be mated by males. On the other hand, males are most aggressive towards each other and risk injury when meeting other males, while females usually do not pose a threat. Therefore, it is likely that there is a difference in how males and females perceive and respond to conspecifics of either sex, with males likely showing more aggression and females likely showing more caution towards male conspecifics.

We expected bearded dragons to show a greater relative left eye preference towards 1) models of conspecifics than towards random objects; 2) towards stimuli with eyes than without eyes; 3) towards naturally colored models than towards gray ones; and 4) towards moving than stationary robots. We furthermore expected females to show more lateralization towards conspecific stimuli than males, as was shown in a previous study using video stimuli (Frohnwieser et al. 2017). Finally, we expected males to exhibit antagonistic behaviour towards head bobbing robots, such as head bobbing themselves or approaching the stimulus.

Materials and Methods

For this study 13 adult bearded dragons were used, five of which were males and eight of which were females. The animals were kept in groups of two to three animals in vivaria, with males housed only with females to avoid male-male aggression. They received fruit and vegetables daily, live food three times per week and water ad libitum, and heat lamps and UV lamps were provided in each vivarium. All animals were handled by humans on a daily basis. All work was carried out with ethical approval from the University of Lincoln, UK.

The experiment took place in a rectangular arena (length: 100cm, width: 40, height: 60cm) that was divided into two equal compartments (each measuring 50x40x60cm) by a wire mesh screen (40x60cm), which was hidden behind an additional opaque screen (40x60cm) at the start of each trial (Figure 1). One compartment contained the live focal animal and the other held the stimulus. The stimulus compartment was lined with black fabric to minimize reflections off the walls of the arena. All trials were recorded via an overhead camera, and in relevant trials, a Philips PicoPix Pocket Projector was used to project colors onto the stimuli.

Figure 1 Experimental setup, consisting of a rectangular arena divided into two compartments, an opaque screen, mesh, a projector and one of the stimuli.

Stimuli

All animals were presented with the following stimuli: (a) an empty background, (b) arbitrary objects, (c) the same objects with eyes, (d) a female 3D printed model bearded dragon without eyes, (e) the same model with eyes, (f) a male 3D printed model bearded dragon without eyes, (g) the same model with eyes, (h) a taxidermied female bearded dragon, (i) a female model bearded projected with various different colors and shades of gray, (j) a stationary robotic bearded dragon, and (k) a head bobbing robotic bearded dragon (Figure 2). These are described in more detail below:

The object stimuli, a bottle (22cm x 9cm x 6cm), a paper roll (23.5cm x 4cm x 4cm), a piece of wood (26cm x 17cm x 6cm) and a rectangular cardboard box (11.5cm x 8cm x 8cm), were spray painted white using white matt spray paint (Valspar Paint & Primer; see Figure S1 for reflectance spectrum). These were presented with and without eyes attached to them. The eyes were used from a colored photograph of a bearded dragon, printed and attached to the objects using white Bostik Blu-Tack, which could be removed and reattached easily without leaving any residue (Figure 2). Each animal was assigned one of the objects at random.

The female model (34cm x 15cm x 4.5cm) consisted of a life sized, 3D printed model of a bearded dragon. A naturally deceased bearded dragon was taxidermied and scanned using a NextEngine Desktop 3D Scanner Model 2020i. The scan was then printed using a Formlabs Form1+ 3D printer in Formlabs white resin and spray painted white using the same white matt spray paint as the object stimuli. Like the objects this model was presented with and without eyes attached to it. The taxidermied bearded dragon was also used as one of the stimuli.

For the male model (33cm x 16cm x 7.5cm) a scan of a live bearded dragon was taken using an iSense scanner attached to an iPad with a Z-resolution of 0.5mm, which was then 3D printed and spray painted white. This model was also presented with and without eyes.

For the robotic stimuli, a new 3D scan of a live male bearded dragon was taken using an iSense scanner attached to an iPad with a Z-resolution of 0.5mm. This scan then modified in Google Sketchup to allow for articulation of the head. The modified model was 3D printed and a servo motor was placed inside, using a Femtoduino Arduino clone board to control the servo to provide the movement of the head. We used marker-based motion capture of live bearded dragons to measure head bobbing motion accurately (Frohnwieser, Willmott, et al. 2016). The robot (34.5cm x 15.5cm x 10cm) had eyes and was projected onto in medium bearded dragon skin color (Figure 3), and was presented to each animal exhibiting the head bobbing behavior and being stationary. To control for the noise of the servo motors two identical robots were built, so one could be used during stationary trials, hidden from the animal's view but clearly audible. Each animal was randomly assigned one robot, which it was presented with in both trials.

Figure 2 Stimuli used in the experiment to investigate the influence of shape, eyes, color and motion; not to scale.

To test for the influence of color, we projected colored light (using a Philips PicoPix Pocket Projector) onto the white female model in order to simulate the chromatic appearance of live animals. Specifically, the colors projected onto the model were designed to produce a metameric match for those measured spectrophotometrically, in terms of bearded dragons' color perception (i.e., to the viewing animal the light reflecting from the model resulted in the same relative pattern of photoreceptor stimulation, and hence produced colors that appeared perceptually identical, to that produced by viewing live conspecifics; (Fleishman et al. 1998; Smith & Pokorny 1995). Following Pike (2017), we used an optimisation procedure to identify RGB input values that, when projected onto the white model under a particular adapting background illumination, resulted in a color that (to viewing bearded dragons) mimicked the natural skin color of conspecifics. This required knowledge of the output radiance of the projector in response to given RGB input values (Figure S2a) and the spectral output of the adapting background illumination, as well as standardized reflectance measurements from the skin of live animals and from the white model (Figure S1), and estimates of the spectral sensitivity functions of the bearded dragons' long- (L), medium- (M) and short wavelength-sensitive (S) cones.

Reflectance measurements were obtained from the dorsal surface of live bearded dragons, and the white model, using a Jaz UV-visible spectrometer coupled with a UV-VIS Deuterium-Tungsten Halogen light source (Ocean Optics, Dunedin, FL). The tip of the fibre-optic probe was housed in a hollow, black plastic sheath with an angled tip that contacted the animal's skin at 45° (following Uy & Endler 2004), and we used a spectrally flat 99% reflecting Spectralon standard (Labsphere, North Sutton, NH) and a dark current reading to standardize each scan. Measurements were taken from a ca. 3 mm diameter circle within the wavelength range 400-700 nm (the effective output range of the projector). Ten replicate measurements were taken from different locations on each of 23 individuals, which included the animals used as test subjects in this study, and averaged across wavelengths to produce a single spectrum for each animal. These spectra were further averaged to produce a spectrum representative of a ‘typical’ bearded dragon, the color of which we reproduced on the model.

In the absence of data specifically for bearded dragons, photoreceptor spectral sensitivity functions were estimated using published information for the closely-related tawny dragon lizard (*Ctenophorus decresii*), which is comparable with that of other diurnal lizards (Barbour et al. 2002; Bowmaker et al. 2005; Loew et al. 2002; Macedonia et al. 2009). This species has three classes of single cones with peak sensitivities (λ_{max}) at 569 nm (L), 495 nm (M) and 436 nm (S) (Yewers et al. 2015). Spectral sensitivity functions were constructed using the photopigment nomogram provided by Govardovskii et al. (2000) and incorporating data on the transmission spectrum across the pre-retinal media (Yewers et al. 2015) (Figure S2b).

The color projected onto the white model occupied almost exactly the same location in bearded dragon chromaticity space to that estimated for the averaged color of live conspecifics, suggesting that they would be perceived as the same color (Figure 3). However, because bearded dragons can vary the perceived brightness of their coloration dynamically, we tested this color at three different intensities: light, medium and dark. These were arbitrarily chosen, but likely to be within the range presented by live animals. As an achromatic comparison, we also projected the model with bearded dragon gray (i.e. a color that lay at the centre of chromaticity space; Figure 3), again at the three different intensities.

Figure 3 The position of the dorsal coloration of each of 23 live bearded dragons (semi-transparent gray circles) in a bearded dragon chromaticity space, in which the three apices of the triangle represent stimulation of the long (L), medium (M) and short (S) wavelength-sensitive cones in isolation (Kelber et al. 2003), after adaptation to the background radiance. The average of these colors is denoted by the white triangle, which is also the location occupied by the virtual color we projected onto the white model. The achromatic point, and hence the location of the 'gray' projected color, is denoted by the cross.

Figure S1 Reflectance spectrum of the white model bearded dragon, as a function of wavelength.

Figure S2 (a) Relative spectral radiance of the projector, for red (solid line), green (dashed line) and blue (dotted line), as a function of wavelength, normalized to the peak output of the red LED. (b) Spectral sensitivities of the cones of a typical bearded dragon, L (solid line), M (dashed line) and S (dotted line), as a function of wavelength. Each cone type has been normalised so that they produce an equal response to white light over the given wavelength range.

Procedure

All animals were habituated to the arena before starting the experiment. They were considered habituated when they readily explored and ate food inside the arena.

Each animal was given one trial per day. The order in which the stimuli were presented and the order in which the animals were tested was randomized. Animals were placed in compartment A (Figure 1) and left to habituate for 30 seconds before the opaque screen was lifted, allowing them to see the stimulus through the mesh. Each trial lasted one minute and was recorded via an overhead camera.

Data analysis

Videos were coded using Solomon coder (© András Péter; version beta 15.11.19) to the nearest 0.2 seconds and the observed behaviors were: eye used to watch the stimulus, tongue flicking, moving away from the stimulus, approaching the stimulus, head bobbing and arm waving. However, head bobbing and arm waving were not observed during the experiment, while the other behaviors – tongue flicking and locomotion – occurred too infrequently to allow meaningful statistical analysis. Ten percent of videos were coded by a second observer and inter observer reliability for eye use was high (Spearman's correlation: $r_s = 0.96$, $p < 0.001$).

To compare eye use between conditions, the ratio of the amount of time the left eye was used compared to the right eye use was calculated for each trial (left eye use / (left eye use + right eye use)). We used separate linear mixed-effects models (implemented using the 'lme' function in the 'nlme' package for R 3.4.1; Pinheiro et al. 2016) to test for differences in relative left eye use between particular groups of stimuli, allowing us to test for differences according to stimulus shape, the presence or absence of eyes, colour, and movement. Each model contained the arcsine-square root transformed proportion of time using the left eye as the dependent variable, fixed effects of stimulus type and subject sex (and their interaction), and a random effect term of subject identity.

The normality of the models' residuals was confirmed using frequency histograms, and in all analyses the alpha level was set at 0.05.

Results

Shape

There was no evidence that bearded dragons showed a difference in relative eye use when looking at the models of male or female conspecific stimuli compared to arbitrary objects ($F_{2,24} = 1.58$, $p = 0.226$), no evidence for differences in response as a function of sex ($F_{1,16} = 0.296$, $p = 0.593$), and no interaction between sex and stimulus type ($F_{2,24} = 1.40$, $p = 0.265$; Figure 4).

Eyes

There was no effect of stimulus type (stimuli with eyes or stimuli without eyes) ($F_{1,71} = 0.56$, $p = 0.458$), sex ($F_{1,16} = 2.33$, $p = 0.146$) or the interaction between sex and stimulus type ($F_{1,71} = 1.01$, $p = 0.319$) on the subjects' relative eye use (Figure 4).

Color

There was no evidence that subjects showed a difference in relative eye use when looking at naturally colored model conspecifics, gray model conspecifics, or the taxidermied specimen ($F_{2,92} = 2.16$, $p = 0.121$), no effect of sex ($F_{1,14} = 0.27$, $p = 0.612$) and no interaction between sex and stimulus type ($F_{2,92} = 1.29$, $p = 0.281$; Figure 4).

Movement

Regarding relative eye use when viewing a stationary robot compared with a moving robot, there was a significant interaction between subject sex and stimulus type ($F_{1,12} = 8.39$, $p = 0.013$), with male subjects using their left eye signifiantly more than females when viewing the stationary robot

($F_{1,12}$ = 6.16, p = 0.029) and significantly more when viewing the stationary robot compared to the moving robot ($F_{1,4}$ = 17.83, p = 0.013). Females showed no significant preference for either stimulus type ($F_{1,8}$ = 0.0006, p = 0.981; Figure 4).

Figure 4 Box plots showing the amount of time males and females spent looking at the stimuli with their left eyes compared to their right eyes for each condition (median ± interquartile range, minimum and maximum). A value of 0 indicates exclusive use of the right eye; a value of 1 exclusive use of the left eye. The horizontal dotted line indicates chance level.

Discussion

The present study investigated lateralized eye use in bearded dragons when exposed to artificial stimuli, ranging from biologically irrelevant objects to taxidermied conspecifics. We found no differences in eye use when observing these stimuli, irrespective of changes in shape or color, or the presence or absence of eyes.

When comparing animals of different sexes, males used their left eye more than females when looking at a stationary robot. This stimulus was created from scans of male bearded dragons, had eyes and was presented in natural coloration. It therefore presented a combination of all investigated stimuli, which, in cummulation may have led male animals to perceive it as a conspecific. Their preference shifted towards the right eye when the robot was moving, which contradicts studies in other species which found a left eye preference when perceiving biological motion (Rugani et al. 2015). The motion the robot performed was head bobbing, which is a highly stereotypic display in bearded dragons and used in agonistic and mating interactions (Frohnwieser, Willmott, et al. 2016; Brattstrom 1971). Therefore, this behavior likely serves as a signal that differs depending on the receiver, with males perceiving it as a threat to their territory, while females mostly experience it in a mating context (Brattstrom 1971). It has been shown in other vertebrate species that a left eye preference exhibited towards conspecifics can shift towards the right eye, when stimuli cause strong arousal, such as offspring being touched by strangers or when inspecting predators (Rogers et al. 1994; Bisazza et al. 1999). Therefore, in our study, head bobbing might have been perceived as threatening by male bearded dragons more so than by females, causing males to shift from a left eye to a non-significant right eye preference. On the other hand, most research in lizards using live conspecifics has shown a left eye preference in agonistic contexts (Hews & Worthington 2001; Hews et al. 2004). Therefore, it remains unclear which mechanisms underlie this behavior in bearded dragons.

Previous research in bearded dragons using videos of live conspecifics showed that females exhibited a left eye bias towards conspecifics while males did not, and both sexes used their left eye significantly longer when viewing moving stimuli rather than stationary (Frohnwieser et al. 2017). These stimuli were non-threatening, as all recorded animals were females and did not exhibit head bobbing. Therefore, the differences found in eye use between males and females are likely caused by context, behaviour and sex of the observed conspecific. However, further studies, possibly with a greater sample size, are needed to investigate this in more detail.

In conclusion, the present study gives insights into the factors that are important to bearded dragons when processing conspecific stimuli. It reveals that motion may play an important role in conspecific recognition in this species. However, the relevant features are likely to vary between species and, as was observed in this case, between sexes of the same species. These results can aid the development of artificial animals in future studies, while improving our understanding of the perception of conspecifics in general.

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References

Andrew, R.J., 2002. Behavioural development and lateralization. In *Comparative Vertebrate Lateralization*. Cambridge University Press, pp. 157–205.

Barbour, H.R. et al., 2002. Retinal characteristics of the ornate dragon lizard, *Ctenophorus ornatus*. *Journal of Comparative Neurology*, 450(4), pp.334–344.

Bisazza, A. et al., 1998. Lateralization of detour behaviour in poeciliid fish: The effect of species, gender and sexual motivation. *Behavioural Brain Research*, 91, pp.157–164.

Bisazza, A., De Santi, A. & Vallortigara, G., 1999. Laterality and cooperation: mosquitofish move closer to a predator when the companion is on their left side. *Animal behaviour*, 57(5), pp.1145–1149.

Bonati, B. et al., 2010. Lateralization in the escape behaviour of the common wall lizard (*Podarcis muralis*). *Behavioural Brain Research*, 207(1), pp.1–6.

Bonati, B., Csermely, D. & Romani, R., 2008. Lateralization in the predatory behaviour of the common wall lizard (*Podarcis muralis*). *Behavioural processes*, 79(3), pp.171–174.

Bonati, B., Csermely, D. & Sovrano, V.A., 2013. Looking at a predator with the left or right eye: asymmetry of response in lizards. *Laterality*, 18(3), pp.329–339.

Bowmaker, J.K., Loew, E.R. & Ott, M., 2005. The cone photoreceptors and visual pigments of chameleons. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 191(10), pp.925–932.

Brattstrom, B.H., 1971. Social and Thermoregulatory Behavior of the Bearded Dragon, *Amphibolurus barbatus*. *Copeia*, 1971(3), pp.484–497.

Carazo, P., Font, E. & Desfilis, E., 2008. Beyond “nasty neighbours” and “dear enemies”? Individual recognition by scent marks in a lizard (*Podarcis hispanica*). *Animal Behaviour*, 76(6), pp.1953–1963.

Deckel, A.W., 1995. Laterality of aggressive responses in Anolis. *Journal of Experimental Zoology*, 272(3), pp.194–200.

Deckel, A.W. & Fuqua, L., 1998. Effects of serotonergic drugs on lateralized aggression and aggressive displays in *Anolis carolinensis*. *Behavioural Brain Research*, 95(2), pp.227–232.

Emery, N.J., 2000. The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24, pp.581–604.

Fan, M., Stuart-Fox, D.M. & Cadena, V., 2014. Cyclic colour change in the bearded dragon *Pogona vitticeps* under different photoperiods. *PLoS ONE*, 9(10), p.e111504.

Fleishman, L.J. et al., 1998. Colour perception and the use of video playback experiments in animal behaviour. *Animal behaviour*, 56(4), pp.1035–1040.

Frohnwieser, A. et al., 2017. Lateralized Eye Use Towards Video Stimuli in Bearded Dragons (*Pogona vitticeps*). *Animal Behavior and Cognition*, 4(3), pp.340–348.

Frohnwieser, A., Willmott, A.P., et al., 2016. Using marker-based motion capture to develop a head bobbing robotic lizard. In E. Tuci et al., eds. *Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*. Cham: Springer International Publishing, pp. 12–21.

Frohnwieser, A., Murray, J.C., et al., 2016. Using robots to understand animal cognition. *Journal of the Experimental Analysis of Behavior*, 105(1), pp.14–22.

Govardovskii, V.I. et al., 2000. In search of the visual pigment template. *Visual Neuroscience*, 17(4), pp.509–528.

Hews, D.K., Castellano, M. & Hara, E., 2004. Aggression in females is also lateralized: left-eye bias during aggressive courtship rejection in lizards. *Animal Behaviour*, 68(5), pp.1201–1207.

Hews, D.K. & Worthington, R.A., 2001. Fighting from the right side of the brain: left visual field preference during aggression in free-ranging male tree lizards (*Urosaurus ornatus*). *Brain, behavior and evolution*, 58(6), pp.356–361.

Karenina, K.A., Giljov, A.N. & Malashichev, Y.B., 2013. Eye as a key element of conspecific image eliciting lateralized response in fish. *Animal Cognition*, 16(2), pp.287–300.

Kelber, A., Vorobyev, M. & Osorio, D., 2003. Animal colour vision--behavioural tests and physiological concepts. *Biological reviews of the Cambridge Philosophical Society*, 78, pp.81–118.

Krause, J., Winfield, A. & Deneubourg, J.L., 2011. Interactive robots in experimental biology. *Trends in ecology & evolution*, 26(7), pp.369–375.

Loew, E.R. et al., 2002. Visual pigments and oil droplets in diurnal lizards. *The Journal of experimental biology*, 205, pp.927–938.

Macedonia, J.M. et al., 2009. Conspicuousness of Dickerson's collared lizard (*Crotaphytus dickersonae*) through the eyes of conspecifics and predators. *Biological Journal of the Linnean Society*, 97(4), pp.749–765.

McKenzie, R., Andrew, R.J. & Jones, R.B., 1998. Lateralization in chicks and hens: new evidence for control of response by the right eye system. *Neuropsychologia*, 36(1), pp.51–58.

Miklósi, Á. & Gerencsér, L., 2012. Potential application of autonomous and semi-autonomous robots in the study of animal behaviour. In *2012 IEEE 3rd International Conference on Cognitive Infocommunications (CogInfoCom)*. pp. 759–762.

Mitri, S. et al., 2013. Using robots to understand social behaviour. *Biological Reviews*, 88, pp.31–39.

Nakayasu, T. & Watanabe, E., 2014. Biological motion stimuli are attractive to medaka fish. *Animal Cognition*, 17(3), pp.559–575.

Palmer, M.E., Calvé, M.R. & Adamo, S.A., 2006. Response of female cuttlefish *Sepia officinalis* (Cephalopoda) to mirrors and conspecifics: Evidence for signaling in female cuttlefish. *Animal Cognition*, 9(2), pp.151–155.

Pike, T.W., 2017. Discrimination of signal carotenoid content using multidimensional chromatic information. *Behavioral Ecology*, p.arx136.

Pinheiro, J. et al., 2016. nmle: Linear and Nonlinear Mixed Effects Models. *R package version 3.1-128. URL: https://CRAN.R-project.org/package=nlme*.

Racca, A. et al., 2012. Reading faces: Differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. *PLoS ONE*, 7(4), pp.1–10.

Robins, A. et al., 2005. Lateralized predatory responses in the ornate dragon lizard (*Ctenophorus ornatus*). *NeuroReport*, 16(8), pp.849–852.

Rogers, L.J., 1989. Laterality in animals. *International Journal of Comparative Psychology*, 3, pp.5–25.

Rogers, L.J. & Andrew, R.J., 2002. *Comparative Vertebrate Lateralization* L. J. Rogers & R. Andrew, eds., Cambridge University Press.

Rogers, L.J., Ward, J.P. & Stanford, D., 1994. Eye dominance in the small-eared bushbaby, *Otolemur garnettii*. *Neuropsychologia*, 32(2), pp.257–264.

Rowland, M., 2009. Veterinary care of bearded dragons. *In Practice*, 31(10), pp.506–511.

Rugani, R. et al., 2015. Brain asymmetry modulates perception of biological motion in newborn chicks (*Gallus gallus*). *Behavioural Brain Research*, 290, pp.1–7.

Smith, K.R. et al., 2016. Colour change on different body regions provides thermal and signalling advantages in bearded dragon lizards. *Proceedings of the Royal Society B: Biological Sciences*, 283(1832), p.20160626.

Smith, V.C. & Pokorny, J., 1995. Chromatic-discrimination axes, CRT phosphor spectra, and individual variation in color vision. *Journal of the Optical Society of America. A*, 12(1), pp.27–35.

Sovrano, V.A., Quaresmini, C. & Stancher, G., 2017. Tortoises in front of mirrors: Brain asymmetries and lateralized behaviours in the tortoise (*Testudo hermanni*). *Behavioural Brain Research*.

Uy, J.A.C. & Endler, J.A., 2004. Modification of the visual background increases the conspicuousness of golden-collared manakin displays. *Behavioral Ecology*, 15(6), pp.1003–1010.

Vallortigara, G. et al., 1998. Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *Neuroreport*, 9(14), pp.3341–3344.

De Velasco, J.B. & Tattersall, G.J., 2008. The influence of hypoxia on the thermal sensitivity of skin colouration in the bearded dragon, *Pogona vitticeps*. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 178(7), pp.867–875.

Wilkinson, A. et al., 2010. Gaze following in the red-footed tortoise (*Geochelone carbonaria*). *Animal Cognition*, 13(5), pp.765–769.

Yewers, M.S. et al., 2015. Spectral sensitivity of cone photoreceptors and opsin expression in two colour-divergent lineages of the lizard *Ctenophorus decresii*. *Journal of Experimental Biology*, 218, pp.1556–1563.

SUPPLEMENTARY MATERIALS

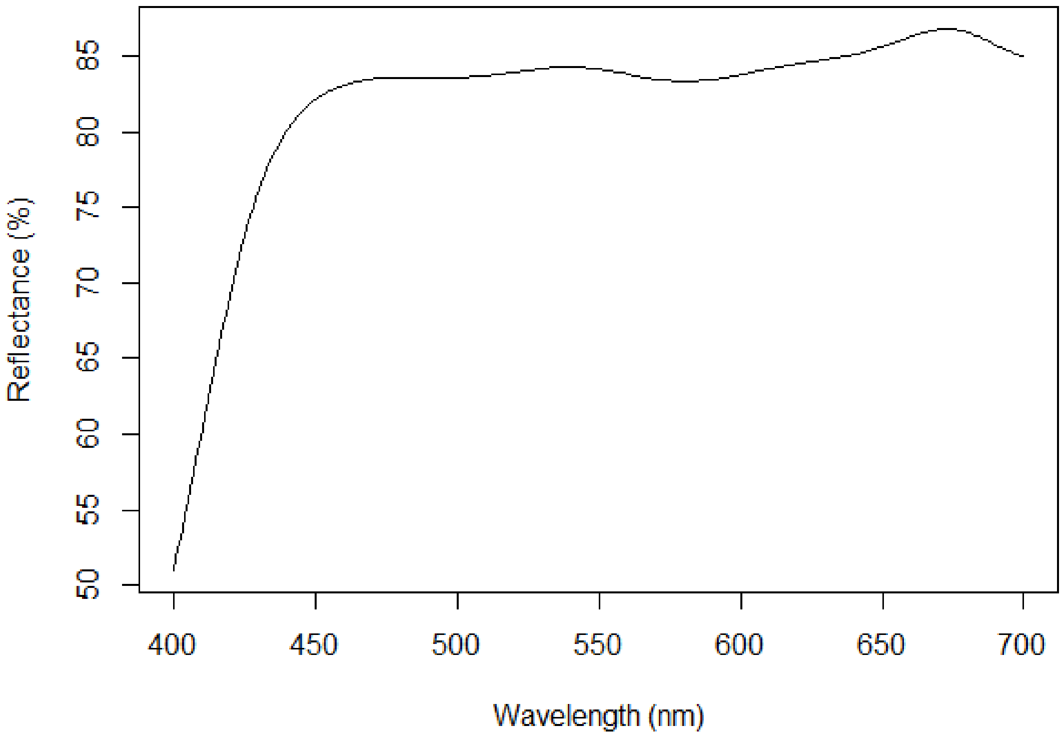

Figure S1 Reflectance spectrum of the white model bearded dragon, as a function of wavelength.

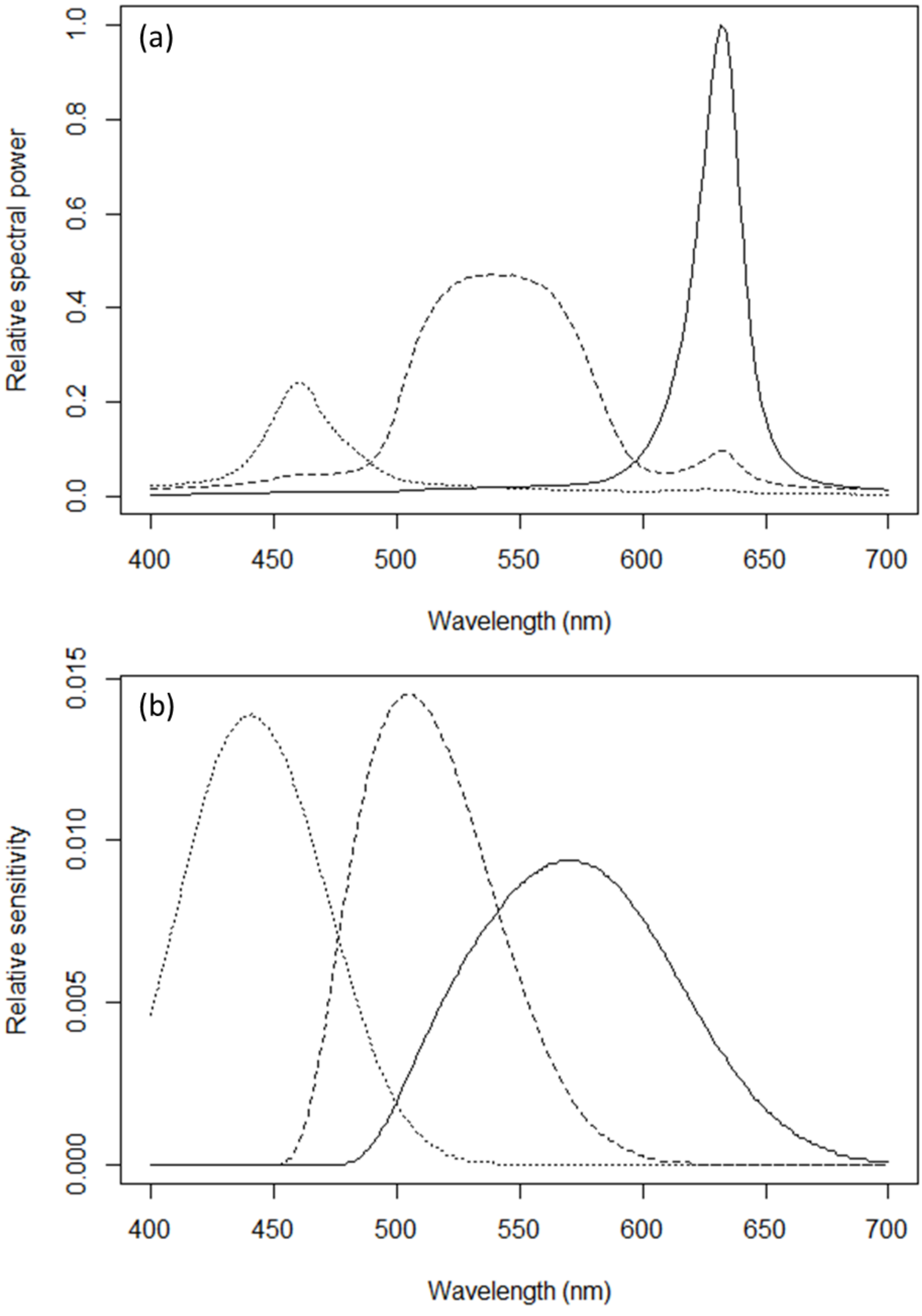

Figure S2 (a) Relative spectral radiance of the projector, for red (solid line), green (dashed line) and blue (dotted line), as a function of wavelength, normalized to the peak output of the red LED. (b) Spectral sensitivities of the cones of a typical bearded dragon, L (solid line), M (dashed line) and S (dotted line), as a function of wavelength. Each cone type has been normalised so that they produce an equal response to white light over the given wavelength range.

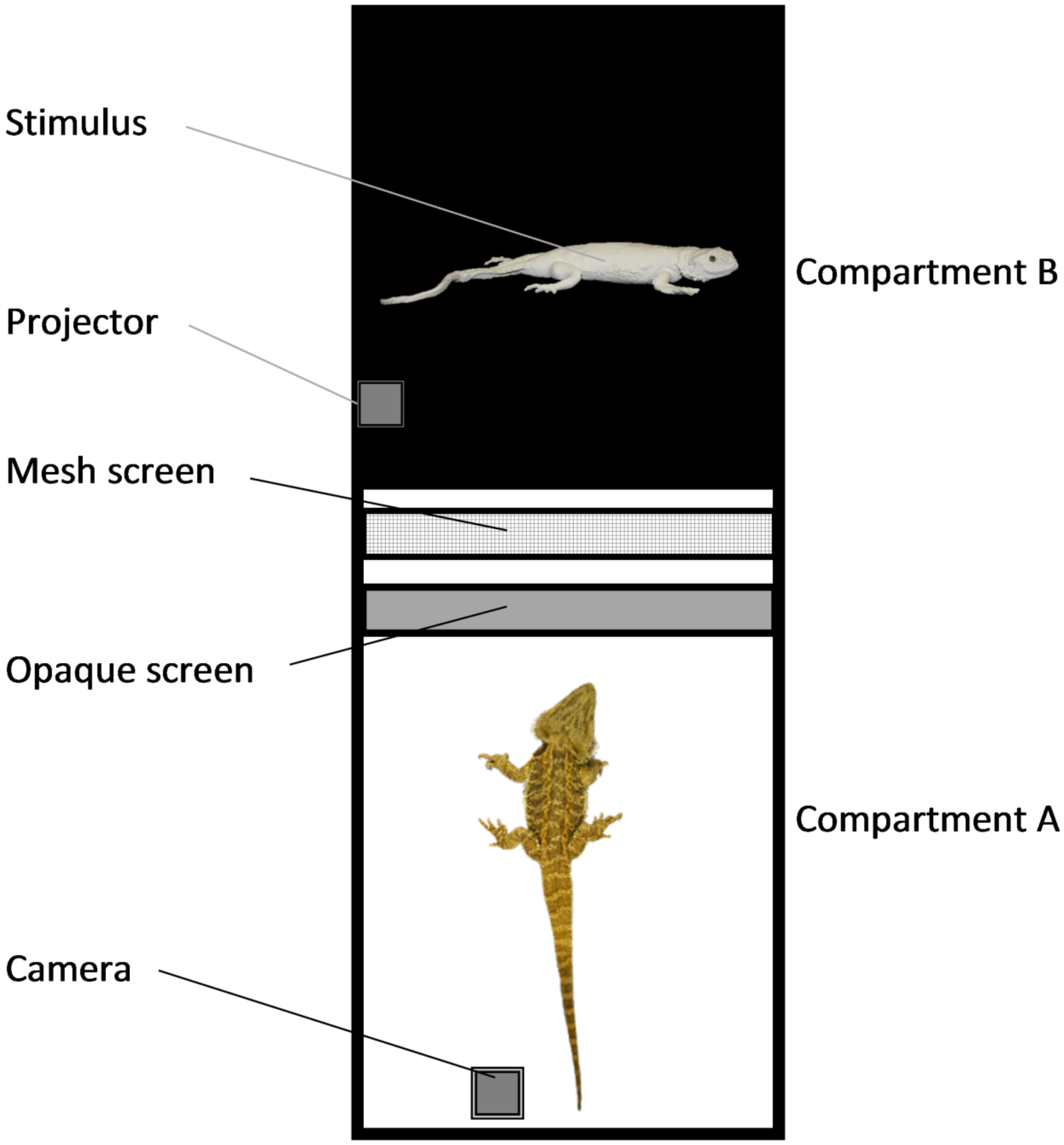

Figure 1 Experimental setup, consisting of a rectangular arena divided into two compartments, an opaque screen, mesh, a projector and one of the stimuli.

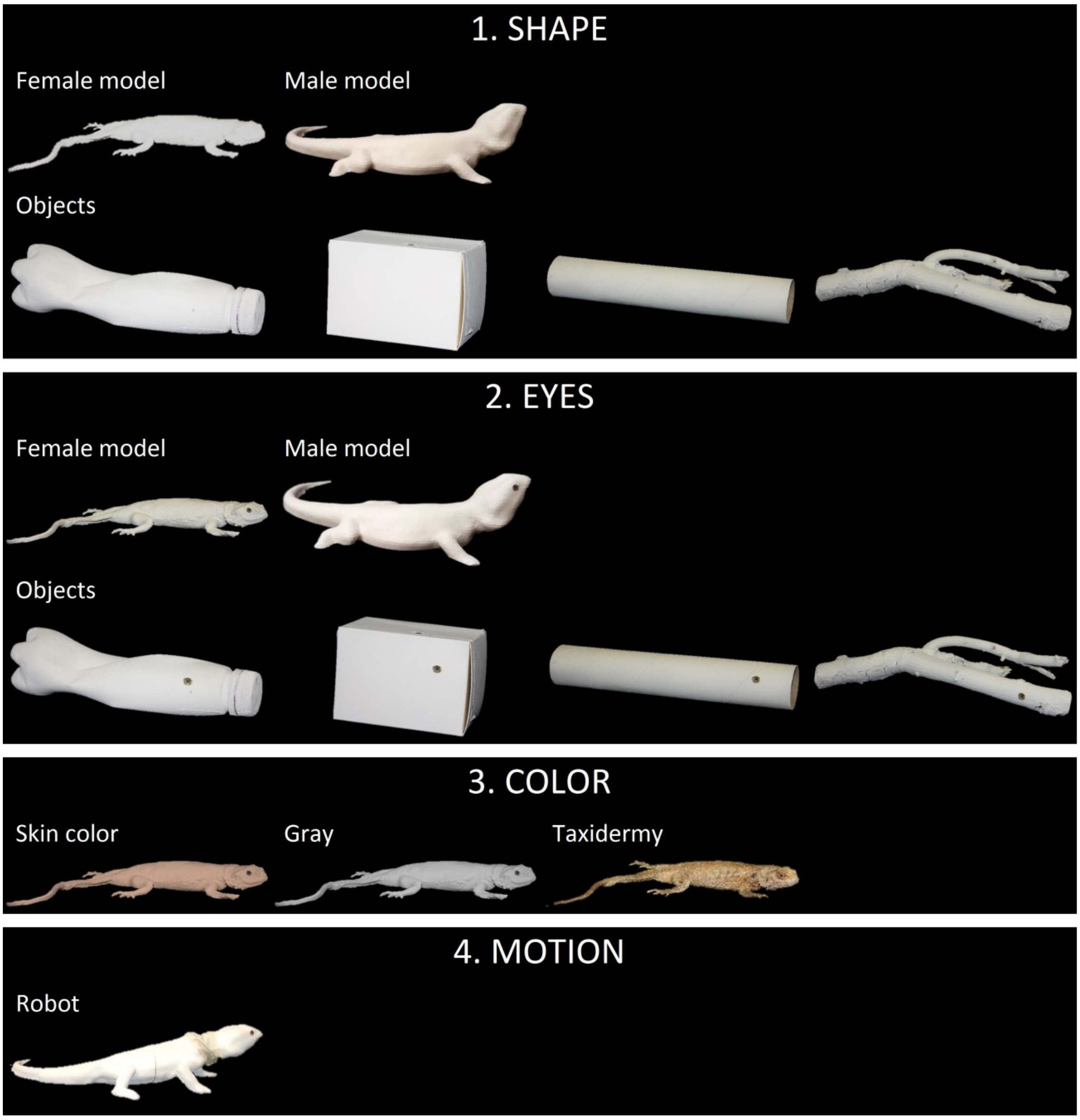

Figure 2 Stimuli used in the experiment to investigate the influence of shape, eyes, color and motion; not to scale.

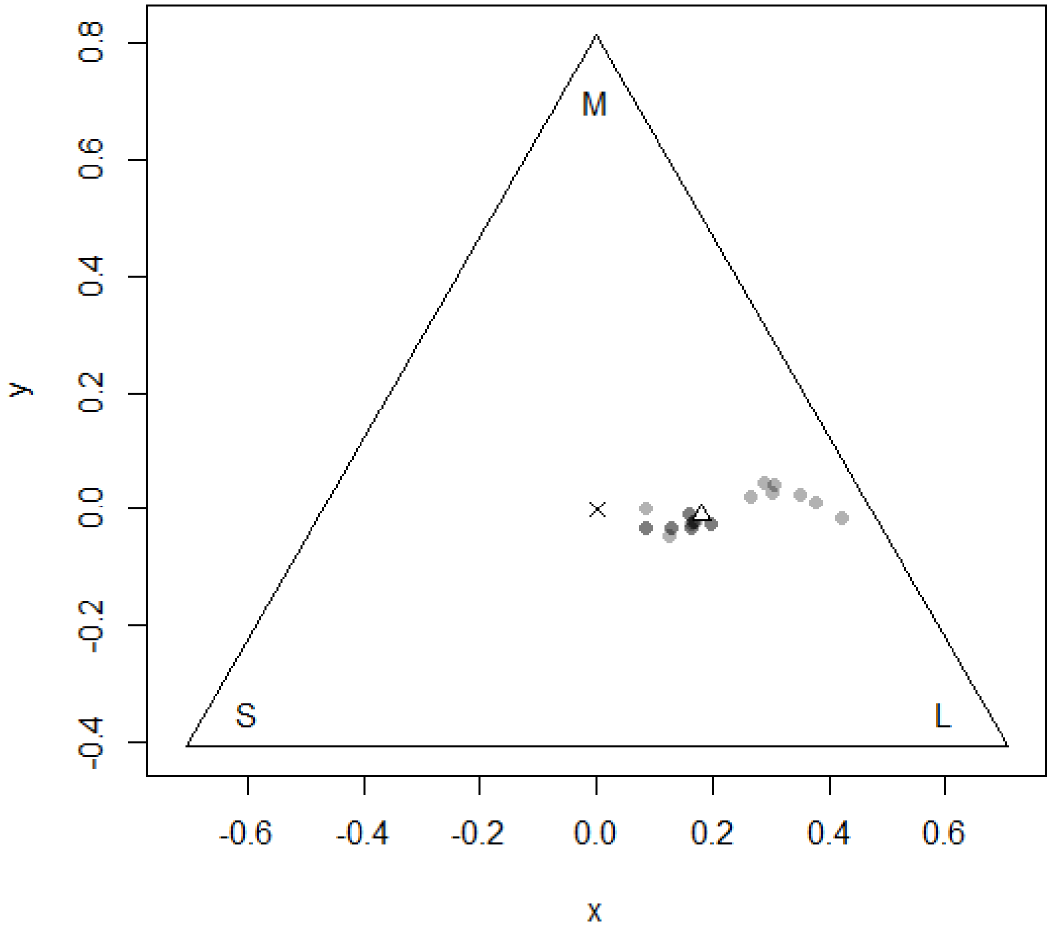

Figure 3 The position of the dorsal coloration of each of 23 live bearded dragons (semi-transparent gray circles) in a bearded dragon chromaticity space, in which the three apices of the triangle represent stimulation of the long (L), medium (M) and short (S) wavelength-sensitive cones in isolation (Kelber et al. 2003), after adaptation to the background radiance. The average of these colors is denoted by the white triangle, which is also the location occupied by the virtual color we projected onto the white model. The achromatic point, and hence the location of the 'gray' projected color, is denoted by the cross.

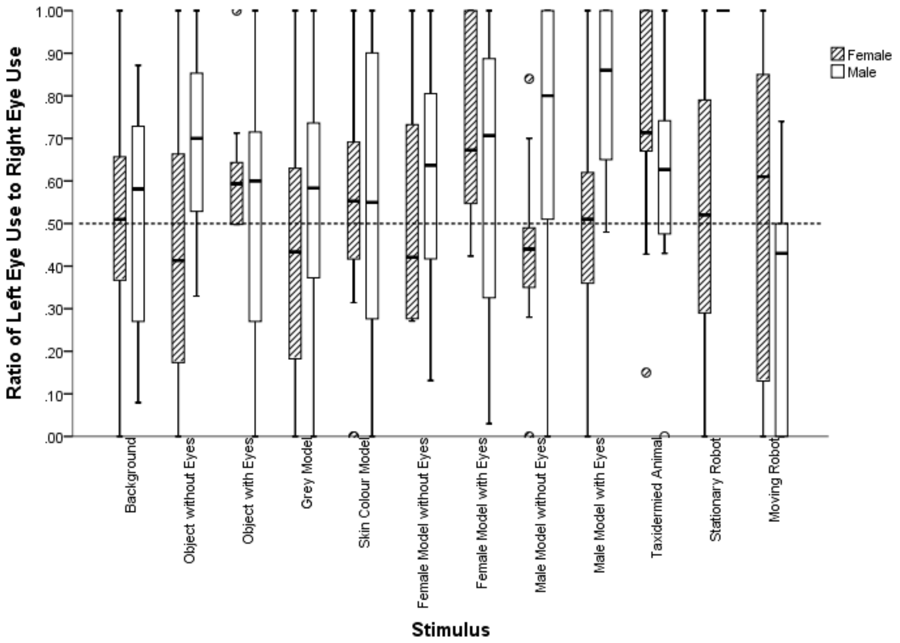

Figure 4 Box plots showing the amount of time males and females spent looking at the stimuli with their left eyes compared to their right eyes for each condition (median ± interquartile range, minimum and maximum). A value of 0 indicates exclusive use of the right eye; a value of 1 exclusive use of the left eye. The horizontal dotted line indicates chance level.