This is the peer reviewed version of the following article: Frohnwieser, A., Murray, J. C., Pike, T. W. and Wilkinson, A. (2016), Using robots to understand animal cognition. Jrnl Exper Analysis Behavior, 105: 14-22., which has been published in final form at https://doi.org/10.1002/jeab.193. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. **Using Robots to Understand Animal Cognition** Anna Frohnwieser<sup>1</sup>, John C. Murray<sup>2</sup>, Thomas W. Pike<sup>1</sup> and Anna Wilkinson<sup>1</sup> <sup>1</sup> School of Life Sciences, University of Lincoln, Lincoln, UK <sup>2</sup> School of Computer Science, University of Lincoln, Lincoln, UK Correspondence to: Anna Wilkinson School of Life Science, University of Lincoln, Lincoln, LN6 7DL United Kingdom. awilkinson@lincoln.ac.uk 

# **Abstract**

 In recent years, robotic animals and humans have been used to answer a variety of questions related to behavior. In the case of animal behavior, these efforts have largely been in the field of behavioral ecology. They have proved to be a useful tool for this enterprise as they allow the presentation of naturalistic social stimuli whilst providing the experimenter with full control of the stimulus. In interactive experiments, the behavior of robots can be controlled in a manner that is impossible with real animals, making them ideal instruments for the study of social stimuli in animals. This paper provides an overview of the current state of the field and considers the impact that the use of robots could have on fundamental questions related to comparative psychology: namely, perception, spatial cognition, social cognition, and early cognitive development. We make the case that the use of robots to investigate these key areas could have an important impact on the field of animal cognition.

- Key words: Robot, Animal cognition, Perception, Spatial Cognition, Social Cognition, Developmental
- 42 Cognition

Robots have the potential to transform the field of social cognition. In particular, key features of robots can be manipulated in systematic ways to explore perception, social learning, and cognitive development in repeatable and comparable ways across the animal kingdom. In this paper, we make the case for the importance of using robots to investigate fundamental questions in the field of animal social cognition. Several reviews have been written concerning the study of social behavior using robots that consider the issues from a robotics perspective (Balch, Dellaert, & Feldman, 2006; Fong, Nourbakhsh, & Dautenhahn, 2003); biology and robotics have influenced each other to investigate and improve the intelligence and cognitive capabilities of robotic systems (Adams, Breazeal, Brooks, & Scassellati, 2000; Brooks, 1991). A separate body of work has also successfully used robots to investigate social interactions from a behavioral ecological perspective (for reviews, see Krause, Winfield, & Deneubourg, 2011; Miklósi & Gácsi, 2012; Mitri, Wischmann, Floreano, & Keller, 2013). However, these techniques also offer novel and exciting prospects for studying the cognitive mechanisms underlying a variety of complex behaviors, particularly relating to social cognition; they have yet to be exploited in the field of comparative cognition. This paper will provide an overview of the current state of the field and make the case for the use of robots to investigate a variety of questions fundamental to our understanding of animal cognition. Throughout this paper, we will be using the term 'robot' for different types of mechanical devices – from the very simple to the very complex – most of which have been described by their creators as robots. We acknowledge that there are different ways to define what constitutes a robot, but we

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#### **Perception of Social Stimuli**

As humans, we primarily rely on vision to perceive and assess other members of our species; however, animals may use a variety of different senses when evaluating novel stimuli. Understanding the sensory systems of animals and how they perceive their environment and process the information they glean from it, is a fundamental question in the field of comparative cognition. It is one that can be examined effectively using robots, but also one that is essential to understand in order to create appropriate robotic counterparts to investigate other cognitive questions.

Traditional methods for investigating the cues used by animals to mediate their social interactions generally involve exposing a test animal to a stimulus and observing its reactions, either to the stimulus alone or to changes in some of the stimulus' features. Under these circumstances, the use of live animals has inherent constraints. Bidirectional interactions between the stimulus animal and

have decided to use the term loosely for reasons of readability and simplicity.

the test animal may make the data, at best, noisy, at worst, unusable. Furthermore, to investigate key issues – such as the influence of visual and olfactory cues on conspecific recognition – one might wish to experimentally manipulate a stimulus animal's color or mask its natural odor. This is problematic with live animals as, not only is it difficult to control the stimulus of interest (e.g., an animal's natural odor may begin to mask an artificial chemical stimulus over time), but the manipulation may influence the stimulus animal's behavior, thereby making it impossible to determine what is responsible for any changes observed in the test animal's behavior (D'Eath, 1998). Consequently, it is common to use video stimuli to investigate perception in animals. Of course, this limits experiments to the visual modality; however, it does provide consistent stimuli and allows manipulation of color (e.g., Clark & Uetz, 1993; McKinnon, 1995), shape, size (e.g., McClintock & Uetz, 1996), and speed of movement (e.g., Evans, Macedonia, & Marler, 1993). Further, stimuli can readily be altered and/or additional information inserted into the video (e.g. Shashar, Rosenthal, Caras, Manor, & Katzir, 2005). To humans, video stimuli appear to be realistic representations of the real entity that they present (e.g., Spetch, Cheng, & MacDonald, 1996). However, there may be issues with the visual stimulus as it is presented. An animal's perception of a video might differ greatly from that of a human (Baldauf, Kullmann, & Bakker, 2008; Fleishman & Endler, 2000; Oliveira et al., 2000). Although some studies have revealed no differences in behavioral responses toward real animals and video images of those animals (e.g., Clark & Uetz, 1990; Ikebuchi & Okanoya, 1999; Macedonia & Stamps, 1994; Shimizu, 1998), others have shown the opposite to be true (D'Eath & Dawkins, 1996; Dawkins, Guilford, Braithwaite, & Krebs, 1996; Dawkins, 1996). Computer monitors are designed to recreate color images for human trichromatic vision and might therefore appear unrealistic to animals with a different number of cone classes or cones with different spectral sensitivity (e.g., birds, Cuthill & Bennett, 1993; reptiles, Fleishman, Loew, & Leal, 1993, and fish, McFarland & Loew, 1994; Rick, Modarressie, & Bakker, 2006). The restriction of the monitor's gamut to the human perceptual range also makes it impossible to test 'hidden' visual attributes involving ultraviolet, infrared, or polarized light (Baldauf et al., 2008; D'Eath, 1998). Motion perception may also be limited by the use of video. Although for humans around 24 frames per second are required to make motion in a video seem fluent, many animals have a higher flicker fusion threshold (see Healy, McNally, Ruxton, Cooper, & Jackson, 2013); they might thus perceive a video as a series of static, 'strobed' images. Further, videos also lack depth information (see D'Eath, 1998). Although with extensive training pigeons (Columba livia) are able to respond to changes in depth cues of two-dimensional images, such as shading patterns or texture gradients (Cavoto &

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Cook, 2006; Cook & Katz, 1999; Cook, Qadri, Kieres, & Commons-Miller, 2012; Reid & Spetch, 1998), other species might struggle to readily extract this information from two-dimensional stimuli.

The use of robots allows us to circumvent these problems. It is possible, for example, to change as many perceptual features of a robot as required; further, different modalities of perceptual cues can be presented in different combinations. Exchangeable skins or body parts allows alteration of the visual stimulus (Kubinyi et al., 2004; Macedonia, Clark, Riley, & Kemp, 2013), whilst olfactory information can be manipulated by applying chemicals or odors from real animals (Asadpour, Tâche, Caprari, Karlen, & Siegwart, 2006; Carazo, Font, & Desfilis, 2008; López & Martín, 2002). Speed and movement can also be readily altered (although realistic movement may be difficult to replicate for some species) as can auditory information, for instance by being presented via embedded speakers. Further, these cues can be manipulated individually, all together, or in different combinations, in a highly repeatable way.

### **Perception of robots**

The perceptual information that is important for a robot to be treated as a conspecific depends on the species of study. Motion, for example, seems to be a key factor in conspecific recognition, as studies comparing rats' reactions to moving and immobilized conspecifics show (Alberts & Galef, 1973). Animals' skins have been used as a basis for a number of robots (Butler & Fernández-Juricic, 2014; Fernández-Juricic, Gilak, McDonald, Pithia, & Valcarcel, 2006; Partan et al., 2010; Partan et al., 2009; Patricelli et al., 2006; Patricelli & Krakauer, 2010; Rundus et al., 2007) (see Figure 1), effectively eliminating issues relating to color and body shape. Alternatively, synthetic 'skins' and body parts can be recreated artificially, for example, by 3D printing them or by making them from latex, and also color-matching robots to live conspecifics, taking into account the reflectance spectra of color patterns present on live animals and recreating them (Macedonia et al., 2013). Replicas may be easier to create for some species than others. Care has to be taken in their design; for example, robots that are perceived to be very similar to a real conspecific, but not similar enough to be mistaken for one can evoke fearful behavior or disgust in humans. This is known as the uncanny valley effect (Mori, 1970) and has also been observed in macaques (Macaca fascicularis) presented with synthetic conspecific faces (Steckenfinger & Ghazanfar, 2009). When interacting with a robot, visual information plays an important role (e.g., Faria et al., 2010). In

particular, shape (e.g., Abaid, Bartolini, Macrì, & Porfiri, 2012; Polverino and Porfiri 2013) and color

(e.g., Göth & Evans 2004; Polverino, Phamduy, & Porfiri, 2013) appear to be crucial in mediating interactions with robots in many species. Movement patterns (Göth & Evans 2004), particularly responsiveness toward another's movement (Kopman, Laut, Polverino, & Porfiri, 2012; Polverino, Phamduy, & Porfiri, 2013), also play a key role. However, robots do not necessarily have to be visually similar to the test species: two-dimensional three-spined stickleback (*Gasterosteus aculeatus*) replicas are sufficient to recruit conspecifics to follow them (Sumpter et al 2008), and cockroaches (*Periplaneta americana*) will direct appropriate natural behaviors towards a box on wheels when cockroach semiochemicals are applied to it (Asadpour, Tâche, Caprari, Karlen, & Siegwart, 2006; Halloy et al., 2007). The salience of different cues does appear to depend on individual experience (Partan, Fulmer, Gounard, & Redmond, 2010).

Responses toward robots can be altered through administration of drugs. Caffeine, for instance, makes zebrafish (*Danio rerio*) more sensitive to a robotic conspecific's movements; ethanol causes a decrease in the fish's attraction toward a robot that was modelled after a fertile female (Ladu, Mwaffo, Li, Macrì, & Porfiri, 2015; Spinello, Macrì, & Porfiri, 2013), making this secies ideal for investigating the effects of drugs on social interactions and cognition.

### **Social Interactions**

and social dynamics. They appear to be extremely effective for this sort of task and have been used to manipulate group behavior in terms of shelter choice (cockroaches *Periplaneta americana*, Asadpour et al., 2006; Halloy et al., 2007), inter-individual distances, shoal orientation (sticklebacks *Gasterosteus aculeatus*, Faria et al., 2010), and foraging behavior (house finches *Haemorhous mexicanus*, Fernández-Juricic et al *2006*; and bees *Apis mellifera carnica*, Landgraf et al 2011; 2012). Observation of interactions with conspecifics or humans also modulates an animal's responses toward a robot (dogs *Canis lupus familiaris*, Lakatos et al 2014).

A particular focus has been the study of mating behavior; the use of robots allows investigation into the relative importance of different cues for mating success in a manner that would be impossible to study using other methods. Robots can be used to investigate the features relevant for mate choice (e.g., Patricelli et al., 2006; Patricelli & Krakauer, 2010) (Figures 1a and 1b), which then allows the manipulation of mate value. For example, visual input is important, but specific salient features—such as the size and movement of the fiddler crab (*Uca mjoebergi*) arm (Reaney, Sims, Sims, Jennions, & Backwell, 2008; Reaney, 2009) or the inflation of the Túngara frog (*Physalaemus pustulosus*) throat pouch (Klein, Stein, & Taylor, 2012; Taylor, Klein, Stein, & Ryan, 2008) (Figure 1c)—

Robots have been used extensively to investigate social interactions, with a focus on group behavior

appear to be more relevant than the use of a realistic model. This information is a crucial prerequisite to examining the costs and benefits of mate choice (e.g. Booksmythe, Detto, & Backwell, 2008).

Another good example is the study of headbobbing displays in lizards. These function as both aggressive and mating displays and can readily be elicited by a headbobbing robot (brown anolis *Anolis sangrei*, Partan et al. 2011; sagebrush lizards *Sceloporus graciosus*, Smith & Martins 2006). Use of robots can assess male competition (e.g. sagebrush lizards *Sceloporus graciosus*, Martins et al 2005), female choice (Martins et al 2005), factors that influence communication (*Anolis gundlachi*, Ord & Stamps, 2008), and even species discrimination (*Microlophus grayii* and *Microlophus indefatigabilis*, Clark et al 2015; *Anolis grahami*, Macedonia, Clark, Riley, & Kemp, 2013; Macedonia & Stamps, 1994; *Anolis gundlachi*, Ord & Stamps, 2009) (Figure 1d).

# **Spatial cognition**

We have a fairly good understanding of the mechanisms underlying spatial navigation in a number of species. Roboticists use this information to construct robots with similar 'skills' (e.g. Möller, Lambrinos, Pfeifer, & Wehner 2001) with the aim of making robots more efficient navigators. Although this work provides clear benefits for robotics research and engineering, it also offers insights into animal cognition. Robots are useful for investigating the perceptual and neurological bases for navigation and spatial cognition by replicating the mechanisms behind them or reverse engineering typical behaviors of animals (Milford, Wyeth, & Prasser, 2004).

Robots may also be useful to investigate spatial tasks in groups of animals. When searching for a food source, rats (*Rattus norvegicus*) not only remember the locations that they have previously visited, but they are also able to remember the locations that another rat has visited and avoid repeated visits to these sites (Brown, 2011; Keller & Brown, 2011). The use of robotic animals in these types of experiments would make it possible to control for many factors such as scent traces, patterns and orders of visiting the locations, as well as the behavioral interactions between animals.

### Social learning and use of social cues

The transfer of complex behavioral information (as opposed to specific stimuli, such as isolated vocalizations) between individuals has typically been studied using live animals. For example, in studies on social learning, demonstrators are often trained to perform particular behaviors and then the ability of naive observers to acquire the behavior through observation is tested. This approach has shown that a surprisingly wide variety of species can, through observation alone, acquire

sophisticated behavioral information from conspecifics with sufficient accuracy for them to repeat the behavior themselves (e.g., birds, Fritz & Kotrschal, 1999; Todt, 1975; reptiles, Kis, Huber, & Wilkinson, 2014; Wilkinson, Kuenstner, Mueller, & Huber, 2010; fish, Brown & Laland, 2003; mammals, Call, Carpenter, & Tomasello, 2005). However, the experimental paradigm of using live demonstrators imposes limitations on the ability to extract information on the mechanisms of information transmission. In particular, there is a need for demonstrators to perform behaviors with sufficient accuracy and repeatability to allow others to learn from them, and so that all observers have the potential to receive the same information. More generally, 'noise' in the information (caused, for example, by variation in the proficiency with which a demonstrator performs a task or variation in the information accessible to the naive animal, perhaps because of visual occlusion) is a factor largely outside the experimenter's control, and often extremely difficult to quantify. Therefore, although animals can undoubtedly extract relevant information in order to learn demonstrated behaviors, it is often unclear (a) whether variation in learning ability stems from the demonstrator or the learner and (b) to which specific aspects of a complex behavioral repertoire the learner is responding. Robots represent an ideal solution to these problems. They can perform realistic and repeatable behaviors under tight experimental control, thereby engendering consistency in the information available to observers (or imposing experimentally-manipulated noise on the information) and allowing specific aspects of behavior to be controlled independently. Despite the clear advances that the use of robots could bring this field, very few studies have used robots in this context. A single study has examined gaze following using a robotic counterpart and found it to be effective. European starlings (Sturnus vulgaris) focused their attention to a specific location in response to changes in the orientation behavior of a robotic bird (Butler & Fernández-Juricic, 2014) (Figure 1f). In contrast, dogs had difficulty following the pointing gestures given by a humanoid robot (Lakatos et al 2014) and performed at a significantly lower level with the pointing robot than with a pointing human, while chimpanzees interacted socially with humanoid robots, especially when the robot was imitating them (Davila-Ross et al., 2013). One possible reason for the scarcity of these sorts of studies is the fact that, although the use of robots eliminate the unreliability that comes with using a live demonstrator, other issues might arise. Replicating accurate visual information and movement is inherently difficult, and, in some cases, may lead to similar perceptual issues to those highlighted above. Further, mechanical properties such as noisy motors may also be disturbing for the animal. Nevertheless, we believe that, with advances in

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technology and in our understanding of animal perception and, with the choice of suitable model species, many of these issues can be overcome.

Clearly, much further work is necessary in this area. However, robots provide the control with which to answer mechanistic questions about information transfer; they also allow us to manipulate the quality and reliability of that information and investigate the impact of, for example, familiarity of the demonstrator, unreliable demonstrators, or partial demonstrations

### Early experience and cognitive development

Robots can also be used to study the ontogeny of cognitive and behavioral traits in animals. It is theoretically possible to fully control an animal's experiences by exposing it to one or several robotic animals from birth. It has been shown, for example, that chicks (*Gallus gallus domesticus*) will readily imprint on a robot (Gribovskiy, Halloy, Deneubourg, Bleuler, & Mondada, 2010); this can allow manipulations which may have powerful effects on cognition. Japanese quail chicks (*Coturnix japonica*) that were raised with a heated robot (simulating the hen) that was mobile for 1 h per day showed better spatial abilities and more exploration in an arena than did control birds that were exposed to an immobile heater (De Margerie, Lumineau, Houdelier, & Richard Yris, 2011) (Figure 1e). Thus, small differences in the rearing conditions can have profound effects on the development of crucial cognitive skills.

The use of robots allows investigation into the role of early experience on cognitive development in a systematic and controlled manner. Robots allow the possibility of investigating some key developmental questions and make it possible to distinguish genetic predispositions from learned behaviors. For example, the parent robot could perform behaviors that are not naturally within the animal's repertoire, behave in ways that are contradictory to how adult animals usually behave, or manipulate foraging choices.

As well as investigating the development of aspects of cognition already considered in this article, key questions relating to development of an animal's physical understanding can be investigated using robots in which these properties are manipulated. Doing so will allow the controlled examination of fundamental questions related to folk physics, including the cognitive development of concepts such as gravity, solidity, occlusion, and containment.

### Conclusions

269	Robots present an exciting prospect for future studies in the field of animal cognition. If designed
270	correctly, they would allow a fine level of control over both the information provided in experimental
271	manipulations and, potentially, the general environment that an animal experiences. Using robots in
272	behavioral experiments will allow us to gain insight into questions in comparative psychology, which,
273	until now, have not been possible to ask. This interdisciplinary work should permit novel and exciting
274	avenues of investigation and expand the boundaries of animal cognition research.
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276	References
277 278 279	Abaid, N., Bartolini, T., Macrì, S., & Porfiri, M. (2012). Zebrafish responds differentially to a robotic fish of varying aspect ratio, tail beat frequency, noise, and color. <i>Behavioural Brain Research</i> , 233(2012), 545–553. doi:10.1016/j.bbr.2012.05.047
280 281	Adams, B., Breazeal, C., Brooks, R. A., & Scassellati, B. (2000). Humanoid robots: A new kind of tool. IEEE Intelligent Systems, 15(4), 25–31. doi:10.1109/5254.867909
282 283 284	Alberts, J. R., & Galef, B. G. (1973). Olfactory cues and movement: stimuli mediating intraspecific aggression in the wild Norway rat. <i>Journal of Comparative and Physiological Psychology, 85</i> (2), 233–42.
285 286 287	Asadpour, M., Tâche, F., Caprari, G., Karlen, W., & Siegwart, R. (2006). Robot-animal interaction: Perception and behavior of insbot. <i>International Journal of Advanced Robotic Systems</i> , 3(2), 093–098. doi:10.1109/ROBIO.2005.246321
288 289 290	Balch, T., Dellaert, F., Feldman, A., Guillory, A., Isbell, C., Khan, Z., Stein, A., & Wilde, H. (2006). How multirobot systems research will accelerate our understanding of social animal behavior. <i>Proceedings of the IEEE, 94</i> (7), 1445-1463. doi:10.1109/JPROC.2006.876969
291 292 293	Baldauf, S. A., Kullmann, H., & Bakker, T. C. M. (2008). Technical restrictions of computer-manipulated visual stimuli and display units for studying animal behaviour. <i>Ethology</i> , 114, 737–751. doi:10.1111/j.1439-0310.2008.01520.x
294 295	Brooks, R. A. (1991). Intelligence without reason. In <i>Proceedings of the 12th International Joint Conference on Artificial Intelligence</i> , 569–595. doi:10.1007/BF01538672
296 297 298	Booksmythe, I., Detto, T., & Backwell, P. R. Y. (2008). Female fiddler crabs settle for less: the travel costs of mate choice. <i>Animal Behaviour</i> , <i>76</i> (6), 1775–1781. doi:10.1016/j.anbehav.2008.07.022
299 300	Brown, M. F. (2011). Social influences on rat spatial choice. <i>Comparative Cognition &amp; Behavior Reviews</i> , 6, 5–23. doi:10.3819/ccbr.2011.6002
301	Brown, C., & Laland, K. N. (2003). Social learning in fishes: a review. Fish and Fisheries, 4(3), 280-288.
302 303	Butler, S. R., & Fernández-Juricic, E. (2014). European starlings recognize the location of robotic conspecific attention. <i>Biology Letters</i> , <i>10</i> (10), 20140665. doi:10.1098/rsbl.2014.0665

304 305 306	Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: Chimpanzees ( <i>Pan troglodytes</i> ) and human children ( <i>Homo sapiens</i> ). <i>Animal Cognition</i> , 8(3), 151–163. doi:10.1007/s10071-004-0237-8
307 308 309	Carazo, P., Font, E., & Desfilis, E. (2008). Beyond "nasty neighbours" and "dear enemies"? Individual recognition by scent marks in a lizard ( <i>Podarcis hispanica</i> ). <i>Animal Behaviour</i> , 76(6), 1953–1963. doi:10.1016/j.anbehav.2008.08.018
310 311	Cavoto, B. R., & Cook, R. G. (2006). The contribution of monocular depth cues to scene perception by pigeons. <i>Psychological Science</i> , <i>17</i> , 628–634. doi:10.1111/j.1467-9280.2006.01755.x
312 313 314	Clark, D. L., Macedonia, J. M., Rowe, J. W., Stuart, M. A., Kemp, D. J., & Ord, T. J. (2015). Evolution of displays in Galápagos lava lizards: comparative analyses of signallers and robot playbacks to receivers. <i>Animal Behaviour</i> , 109, 33–44. doi:10.1016/j.anbehav.2015.08.002
315 316	Clark, D. L., & Uetz, G. W. (1990). Video image recognition by the jumping spider, <i>Maevia inclemens</i> (Araneae: Salticidae). <i>Animal Behaviour</i> , 40(5), 884-890. doi:10.1016/S0003-3472(05)80990-X
317 318	Cook, R. G., & Katz, J. S. (1999). Dynamic object perception by pigeons. <i>Journal of Experimental Psychology</i> . <i>Animal Behavior Processes</i> , 25(2), 194-210. doi:10.1037/0097-7403.25.2.194
319 320	Cook, R. G., Qadri, M. A. J., Kieres, A., & Commons-Miller, N. (2012). Shape from shading in pigeons. Cognition, 124, 284–303. doi:10.1016/j.cognition.2012.05.007
321 322	Cuthill, I. C., & Bennett, A. T. D. (1993). Mimicry and the Eye of the Beholder. <i>Proceedings of the Royal Society B: Biological Sciences</i> , 253, 203–204. doi:10.1098/rspb.1993.0103
323 324	D'Eath, R. B. (1998). Can video images imitate real stimuli in animal behaviour experiments? Biological Reviews, 73, 267–292. doi:10.1111/j.1469-185X.1998.tb00031.x
325 326	D'Eath, R. B., & Dawkins, M. S. (1996). Laying hens do not discriminate between video images of conspecifics. <i>Animal Behaviour</i> , <i>52</i> (5), 903–912. doi:10.1006/anbe.1996.0238
327 328 329	Davila-Ross, M., Hutchinson, J., Russell, J. L., Schaeffer, J., Billard, A., Hopkins, W. D., & Bard, K. A. (2013). Triggering social interactions: chimpanzees respond to imitation by a humanoid robot and request responses from it. <i>Animal Cognition</i> , 589–595. doi:10.1007/s10071-013-0689-9
330 331	Dawkins, M. S. (1996). Distance and social recognition in hens: implications for the use of photographs as social stimuli. <i>Behaviour</i> , 133(9), 663-680. doi:10.1163/156853996X00413
332 333 334	Dawkins, M. S., Guilford, T., Braithwaite, V. A., & Krebs, J. R. (1996). Discrimination and recognition of photographs of places by homing pigeons. <i>Behavioural Processes</i> , <i>36</i> (1), 27–38. doi:10.1016/0376-6357(95)00013-5
335 336 337	De Margerie, E., Lumineau, S., Houdelier, C., & Richard Yris, M. (2011). Influence of a mobile robot on the spatial behaviour of quail chicks. <i>Bioinspiration &amp; Biomimetics</i> , 6, 034001. doi:10.1088/1748-3182/6/3/034001
338 339	Evans, C. S., Macedonia, J. M., & Marler, P. (1993). Effects of apparent size and speed on the response of chickens, <i>Gallus gallus</i> , to computer-generated simulations of aerial predators.

341 342 343 344	Faria, J. J., Dyer, J. R. G., Clément, R. O., Couzin, I. D., Holt, N., Ward, A. J. W., Waters, D., & Krause, J. (2010). A novel method for investigating the collective behaviour of fish: Introducing "Robofish." <i>Behavioral Ecology and Sociobiology</i> , 64, 1211–1218. doi:10.1007/s00265-010-0988-y
345 346 347	Fernández-Juricic, E., Gilak, N., McDonald, J. C., Pithia, P., & Valcarcel, A. (2006). A dynamic method to study the transmission of social foraging information in flocks using robots. <i>Animal Behaviour</i> , 71, 901–911. doi:10.1016/j.anbehav.2005.09.008
348 349	Fleishman, L. J., & Endler, J. A. (2000). Some comments on visual perception and the use of video playback in animal behavior studies. <i>Acta Ethologica</i> , <i>3</i> , 15–27. doi:10.1007/s102110000025
350 351	Fleishman, L. J., Loew, E. R., & Leal, M. (1993). Ultraviolet vision in lizards. <i>Nature, 365,</i> 397. doi:10.1038/365397a0
352 353	Fong, T., Nourbakhsh, I., & Dautenhahn, K. (2003). A survey of socially interactive robots. <i>Robotics and Autonomous Systems</i> , 42(3-4), 143–166. doi:10.1016/S0921-8890(02)00372-X
354 355	Fritz, J., & Kotrschal, K. (1999). Social learning in common ravens, <i>Corvus corax</i> . <i>Animal Behaviour</i> , 57(4), 785–793. doi:10.1006/anbe.1998.1035
356 357 358	Göth, A., & Evans, C. S. (2004). Social responses without early experience: Australian brush-turkey chicks use specific visual cues to aggregate with conspecifics. <i>The Journal of Experimental Biology</i> , 207, 2199–2208. doi:10.1242/jeb.01008
359 360 361	Gribovskiy, A., Halloy, J., Deneubourg, J. L., Bleuler, H., & Mondada, F. (2010). Towards mixed societies of chickens and robots. <i>IEEE/RSJ 2010 International Conference on Intelligent Robots and Systems, IROS 2010 - Conference Proceedings</i> , 4722–4728. doi:10.1109/IROS.2010.5649542
362 363 364 365	Halloy, J., Sempo, G., Caprari, G., Rivault, C., Asadpour, M., Tâche, F., Saïd, I., Durier, V., Canonge, S., Amé, J.M., Detrain, C., Correll, N., Martinoli, A., Mondada, F., Siegwart, R., & Deneubourg, J. L. (2007). Social integration of robots into groups of cockroaches to control self-organized choices. <i>Science</i> , <i>318</i> (5853), 1155–1158. doi:10.1126/science.1144259
366 367 368	Healy, K., McNally, L., Ruxton, G. D., Cooper, N., & Jackson, A. L. (2013). Metabolic rate and body size are linked with perception of temporal information. <i>Animal Behaviour</i> , <i>86</i> (4), 685–696. doi:10.1016/j.anbehav.2013.06.018
369 370 371	Ikebuchi, M., & Okanoya, K. (1999). Male zebra finches and bengalese finches emit directed songs to the video images of conspecific females projected onto a TFT display. <i>Zoological Science</i> , <i>16</i> (1), 63–70. doi:10.2108/zsj.16.63
372 373	Keller, M. R., & Brown, M. F. (2011). Social effects on rat spatial choice in an open field task. <i>Learning and Motivation</i> , <i>42</i> (2), 123–132. doi:10.1016/j.lmot.2010.12.004
374 375	Kis, A., Huber, L., & Wilkinson, A. (2014). Social learning by imitation in a reptile ( <i>Pogona vitticeps</i> ). Animal Cognition, 8(1), 325-331 doi:10.1007/s10071-014-0803-7
376 377	Klein, B. A., Stein, J., & Taylor, R. C. (2012). Robots in the service of animal behavior. <i>Communicative and Integrative Biology</i> , <i>5</i> (5), 466–472. doi:10.4161/cib.21304

378 379 380	Kopman, V., Laut, J., Polverino, G., & Porfiri, M. (2012). Closed-loop control of zebrafish response using a bioinspired robotic-fish in a preference test. <i>Journal of The Royal Society Interface</i> , 10(78), 1–11. doi:10.1098/rsif.2012.0540
381 382	Krause, J., Winfield, A. F. T., & Deneubourg, J. (2011). Interactive robots in experimental biology. <i>Trends in Ecology &amp; Evolution</i> , 26(7), 369–375. doi:10.1016/j.tree.2011.03.015
383 384 385	Kubinyi, E., Miklósi, Á., Kaplan, F., Gácsi, M., Topál, J., & Csányi, V. (2004). Social behaviour of dogs encountering AIBO, an animal-like robot in a neutral and in a feeding situation. <i>Behavioural Processes</i> , 65(3), 231–239. doi:10.1016/j.beproc.2003.10.003
386 387 388	Ladu, F., Mwaffo, V., Li, J., Macrì, S., & Porfiri, M. (2015). Acute caffeine administration affects zebrafish response to a robotic stimulus. <i>Behavioural Brain Research</i> , <i>289</i> , 48–54. doi:10.1016/j.bbr.2015.04.020
389 390 391	Lakatos, G., Janiak, M., Malek, L., Muszynski, R., Konok, V., Tchon, K., & Miklósi, Á. (2014). Sensing sociality in dogs: what may make an interactive robot social? <i>Animal Cognition</i> , <i>17</i> (2), 387–397. doi:10.1007/s10071-013-0670-7
392 393 394	Landgraf, T., Oertel, M., Kirbach, A., Menzel, R., & Rojas, R. (2012). Imitation of the honeybee dance communication system by means of a biomimetic robot. <i>Biomimetic and Biohybrid Systems, Lecture Notes in Computer Science</i> , 7375, 132–143. doi:10.1007/978-3-642-31525-1_12
395 396 397	Landgraf, T., Rojas, R., Nguyen, H., Kriegel, F., & Stettin, K. (2011). Analysis of the waggle dance motion of honeybees for the design of a biomimetic honeybee robot. <i>PLoS ONE</i> , <i>6</i> (8). doi:10.1371/journal.pone.0021354
398 399 400	López, P., & Martín, J. (2002). Chemical rival recognition decreases aggression levels in male Iberian wall lizards, <i>Podarcis hispanica</i> . <i>Behavioral Ecology and Sociobiology</i> , <i>51</i> (5), 461–465. doi:10.1007/s00265-001-0447-x
401 402 403	Macedonia, J. M., Clark, D. L., Riley, R. G., & Kemp, D. J. (2013). Species recognition of color and motion signals in <i>Anolis grahami</i> : Evidence from responses to lizard robots. <i>Behavioral Ecology</i> (2013), art027. doi:10.1093/beheco/art027
404 405 406	Macedonia, J. M., & Stamps, J. A. (1994). Species recognition in <i>Anolis grahami</i> (Sauria, Iguanidae): Evidence from responses to video playbacks of conspecific and heterospecific displays. <i>Ethology</i> , <i>98</i> (3-4), 246–264. doi:10.1111/j.1439-0310.1994.tb01074.x
407 408 409	Martins, E. P., Ord, T. J., & Davenport, S. W. (2005). Combining motions into complex displays: Playbacks with a robotic lizard. <i>Behavioral Ecology and Sociobiology</i> , <i>58</i> (4), 351–360. doi:10.1007/s00265-005-0954-2
410 411 412	McClintock, W. J., & Uetz, G. W. (1996). Female choice and pre-existing bias: visual cues during courtship in two Schizocosa wolf spiders (Araneae: Lycosidae). <i>Animal Behaviour</i> , <i>52</i> (1), 167–181. doi:10.1006/anbe.1996.0162
413 414	McFarland, W. N., & Loew, E. R. (1994). Ultraviolet visual pigments in marine fishes of the family Pomacentridae. In <i>Vision Research</i> , <i>34</i> (11), 1393–1396. doi:10.1016/0042-6989(94)90138-4

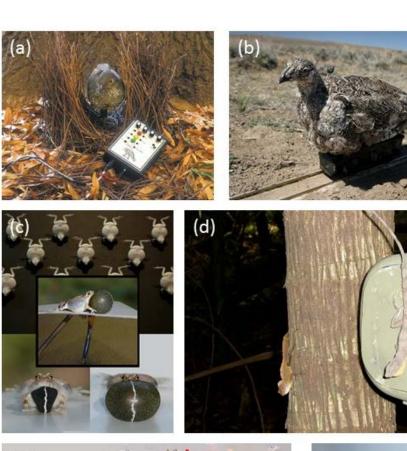
415	Mickinnon, J. S. (1995). Video mate preferences of female three-spined sticklebacks from populatio
416	with divergent male coloration. Animal Behaviour, 50(6), 1645–1655. doi:10.1016/0003-
417	3472(95)80018-2
418	Miklósi, Á., & Gácsi, M. (2012). On the utilization of social animals as a model for social robotics.
419	Frontiers in Psychology, 3(75), 1-10. doi:10.3389/fpsyg.2012.00075
420	Milford, M. J., Wyeth, G., & Prasser, D. (2004). RatSLAM: A hippocampal model for simultaneous
421	localization and mapping. IEEE International Conference on Robotics and Automation, 1, 403-
422	408. doi:10.1109/ROBOT.2004.1307183
423	Mitri, S., Wischmann, S., Floreano, D., & Keller, L. (2013). Using robots to understand social
424	behaviour. <i>Biological Reviews</i> , 88, 31–39. doi:10.1111/j.1469-185X.2012.00236.x
425	Möller, R., Lambrinos, D., Pfeifer, R., & Wehner, R. (2001). Insect strategies of visual homing in
426	mobile robots. In Webb, B., & Consilvio, T. (Eds.), Biorobotics – Methods and Applications
427	(pp.37-66). Cambridge, MA, USA: MIT Press.
428	Mori, M. (1970). The Uncanny Valley. <i>Energy</i> , 7(4), 33–35.
429	Oliveira, R. F., Rosenthal, G. G., Schlupp, I., McGregor, P. K., Cuthill, I. C., Endler, J. A., Waas, J. R.
430	(2000). Considerations on the use of video playbacks as visual stimuli: the Lisbon workshop
431	consensus. Acta Ethologica, 3(1), 61–65. doi:10.1007/s102110000019
432	Ord, T. J., & Stamps, J. A. (2008). Alert signals enhance animal communication in "noisy"
433	environments. Proceedings of the National Academy of Sciences of the United States of
434	<i>America, 105,</i> 18830–18835. doi:10.1073/pnas.0807657105
435	Ord, T. J., & Stamps, J. A. (2009). Species identity cues in animal communication. <i>The American</i>
436	Naturalist, 174(4), 585–593. doi:10.1086/605372
437	Partan, S. R., Fulmer, A. G., Gounard, M. A. M., & Redmond, J. E. (2010). Multimodal alarm behavior
438	in urban and rural gray squirrels studied by means of observation and a mechanical robot.
439	Current Zoology, 56(3), 313–326.
440	Partan, S. R., Larco, C. P., & Owens, M. J. (2009). Wild tree squirrels respond with multisensory
441	enhancement to conspecific robot alarm behaviour. Animal Behaviour, 77(5), 1127–1135.
442	doi:10.1016/j.anbehav.2008.12.029
443	Partan, S. R., Otovic, P., Price, V. L., & Brown, S. E. (2011). Assessing display variability in wild brown
444	anoles Anolis sagrei using a mechanical lizard model. Current Zoology, 57(2), 140–152.
445	Patricelli, G. L., Coleman, S. W., & Borgia, G. (2006). Male satin bowerbirds, Ptilonorhynchus
446	violaceus, adjust their display intensity in response to female startling: An experiment with
447	robotic females. <i>Animal Behaviour</i> , 71(1), 49–59. doi:10.1016/j.anbehav.2005.03.029
448	Patricelli, G. L., & Krakauer, A. H. (2010). Tactical allocation of effort among multiple signals in sage
449	grouse: An experiment with a robotic female. <i>Behavioral Ecology</i> , 21(1), 97–106.
450	doi:10.1093/beheco/arp155

451 452	Polverino, G., Phamduy, P., & Porfiri, M. (2013). Fish and robots swimming together in a water tunnel: robot color and tail-beat frequency influence fish behavior. <i>PloS One</i> , 8(10), e77589.
453	doi:10.1371/journal.pone.0077589
454	Polverino, G., & Porfiri, M. (2013). Mosquitofish (Gambusia affinis) responds differentially to a
455	robotic fish of varying swimming depth and aspect ratio. Behavioural Brain Research, 250, 133-
456	138. doi:10.1016/j.bbr.2013.05.008
457	Reaney, L. T. (2009). Female preference for male phenotypic traits in a fiddler crab: do females use
458	absolute or comparative evaluation? Animal Behaviour, 77(1), 139–143.
459	doi:10.1016/j.anbehav.2008.09.019
460	Reaney, L. T., Sims, R. A., Sims, S. W. M., Jennions, M. D., & Backwell, P. R. Y. (2008). Experiments
461	with robots explain synchronized courtship in fiddler crabs. Current Biology, 18(2), 62–63.
462	doi:10.1016/j.cub.2007.11.047
463	Reid, S. L., & Spetch, M. L. (1998). Perception of pictorial depth cues by pigeons. <i>Psychonomic Bulletin</i>
464	<i>&amp; Review, 5</i> (4), 698–704. doi:10.3758/BF03208848
465	Rick, I. P., Modarressie, R., & Bakker, T. C. M. (2006). UV wavelengths affect female mate choice in
466	three-spined sticklebacks. Animal Behaviour, 71(2), 307–313.
467	doi:10.1016/j.anbehav.2005.03.039
468	Rundus, A. S., Owings, D. H., Joshi, S. S., Chinn, E., & Giannini, N. (2007). Ground squirrels use an
469	infrared signal to deter rattlesnake predation. Proceedings of the National Academy of Sciences
470	of the United States of America, 104(36), 14372–14376. doi:10.1073/pnas.0702599104
471	Shashar, N., Rosenthal, G. G., Caras, T., Manor, S., & Katzir, G. (2005). Species recognition in the
472	blackbordered damselfish Dascyllus marginatus (Rüppell): An evaluation of computer-animated
473	playback techniques. Journal of Experimental Marine Biology and Ecology, 318(1), 111–118.
474	doi:10.1016/j.jembe.2004.12.037
475	Shimizu, T. (1998). Conspecific recognition in pigeons ( <i>Columba livia</i> ) using dynamic video images.
476	Behavior, 135(1), 43-53. doi:10.1163/156853998793066429
477	Smith, C. B., & Martins, E. P. (2006). Display plasticity in response to a robotic lizard: Signal matching
478	or song sharing in lizards? Ethology, 112(2006), 955–962. doi:10.1111/j.1439-
479	0310.2006.01253.x
480	Spetch, M. L., Cheng, K., & MacDonald, S. E. (1996). Learning the configuration of a landmark array: I.
481	Touch-screen studies with pigeons and humans. Journal of Comparative Psychology, 110(1), 55–
482	68. doi:10.1037/0735-7036.110.1.55
483	Spinello, C., Macrì, S., & Porfiri, M. (2013). Acute ethanol administration affects zebrafish preference
484	for a biologically inspired robot. Alcohol, 47, 391–398. doi:10.1016/j.alcohol.2013.04.003
485	Steckenfinger, S. A, & Ghazanfar, A. A. (2009). Monkey visual behavior falls into the uncanny valley.
486	Proceedings of the National Academy of Sciences of the United States of America, 106 (43),
487	18362–18366. doi:10.1073/pnas.0910063106
488	Sumpter, D. J. T., Krause, J., James, R., Couzin, I. D., & Ward, A. J. W. (2008). Consensus decision
489	making by fish. <i>Current Biology</i> , 18(22), 1773–1777. doi:10.1016/j.cub.2008.09.064

Taylor, R. C., Klein, B. A., Stein, J., & Ryan, M. J. (2008). Faux frogs: multimodal signalling and the value of robotics in animal behaviour. *Animal Behaviour*, *76*(3), 1089–1097. doi:10.1016/j.anbehav.2008.01.031

Todt, D. (1975). Social learning of vocal patterns and modes of their application in Grey parrots (*Psittacus erithacus*). *Zeitschrift Für Tierpsychologie*, *39*(1-5), 178–188. doi:10.1111/j.1439-0310.1975.tb00907.x

Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, 6(5), 614–616. doi:10.1098/rsbl.2010.0092



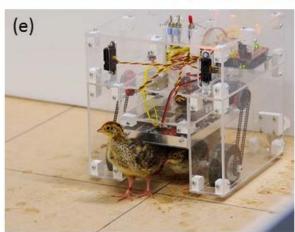




Fig.1: Examples of robots that have been used in studies interacting with animals. (a) robotic female bower bird (*Ptilonorhynchus violaceus*) with controls (Patricelli et al., 2006); (b) robotic female greater sage grouse (*Centrocercus urophasianus*) (Patricelli & Krakauer, 2010); (c) robotic túngara frog (*Physalaemus pustulosus*) (Klein et al., 2012); (d) *Anolis gundlachi* interacting with a robotic anolis (Ord & Stamps, 2008, 2009); (e) Japanese quail chicks (*Coturnix coturnix japonica*) interacting with a robotic hen (de Margerie et al., 2011); (f) robotic European starling (*Sturnus vulgaris*) (Butler & Fernández-Juricic, 2014)