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2 **Interactive Robots in Experimental Biology**
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33 Interactive robots have the potential to revolutionise the study of social behaviour because
34 they provide a number of methodological advances. In interactions with live animals the
35 behaviour of robots can be standardised, morphology and behaviour can be decoupled (so that
36 different morphologies and behavioural strategies can be combined), behaviour can be
37 manipulated in complex interaction sequences and models of behaviour can be embodied by
38 the robot and thereby be tested. Furthermore, robots can be used as demonstrators in
39 experiments on social learning. The opportunities that robots create for new experimental
40 approaches have far-reaching consequences for research in fields such as mate choice,
41 cooperation, social learning, personality studies and collective behaviour.

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45 **Introduction to interactive robots**

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47 Tinbergen [1] demonstrated that in some species of fish, birds and butterflies only simple
48 stimuli were required to elicit territorial or mating behaviour that is normally only shown in
49 response to male and female conspecifics. Insights into the mechanisms of social recognition
50 coupled with technological advances suggest that robots can be developed for use in
51 behavioural research to simulate con- and heterospecific behaviour. For the purposes of this
52 review, we define a robot as a machine that is able to physically interact with its environment
53 and perform some sequence of behaviours, either autonomously or by remote control. In
54 recent years we have witnessed the transition from robots which, once set in motion, “blindly”
55 follow a particular programme to ones that can interact with their environment, learn and even
56 adapt [2-5]. This creates many opportunities for the use of robots in experimental biology,
57 particularly when investigating social behaviour. One of the main challenges when
58 investigating social behaviour is that the behaviour of individuals is dependent on that of their
59 interaction partners. It is possible to infer certain rules or strategies from behavioural
60 observations but unless we can manipulate the behaviour of individuals, this approach
61 remains largely descriptive. One way to manipulate behaviour is to create robots that are
62 accepted as con- or heterospecific and which can be programmed to carry out specific
63 behavioural patterns. A related approach which serves the same purpose (of getting control
64 over the behaviour of one or more individuals in a group or population) is to fit a live animal
65 with interactive technology so that one animal in a group is effectively controlled as the
66 'robot' that interacts with its conspecifics. A brief overview of robots and interactive

67 technologies is provided in Table 1.

68 Here, we give an overview of interactive robotics for use in experimental biology focusing
69 on social behaviour. This approach has been successfully used across the animal kingdom
70 ranging from studies on social insects [6,7] and cockroaches [4] to fish [8], birds [9] and
71 mammals including humans [10-13]. Previous reviews on robots in biological research [14-
72 17] were less focussed on the interactive component which is a recent technological
73 development and has become an important component of studies on collective behaviour
74 [4,18-21]. We will identify important novel biological research questions that can be
75 answered with the help of interactive robots and outline new directions for future
76 developments in machine-animal interactions.

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79 **Interactive technologies**

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81 Robots and computer animations

82 Robots are not the only way to create interactions with live animals. Animations in which
83 virtual animals on a computer screen display realistic behaviours and interact with live
84 animals have become an important tool for investigating animal behaviour [22-24]. This
85 approach has provided many new insights, particularly in the areas of sexual selection and
86 prey recognition [23]. Some of the major advantages of using virtual animals (compared to
87 using real ones) are that it becomes possible to standardise the behaviour of display
88 individuals in choice experiments and to de-couple behaviour and morphology (to present
89 visual stimuli in isolation or combination). For example, this approach made it possible to
90 identify the role of male ornaments in mate choice of female swordtail fish (Xiphophorus
91 helleri) [25]. The use of animation allowed the presentation of the same behaviour by males
92 versus ones without a sword-tail but with an enlarged body to compensate for loss of surface
93 area. This decoupled morphology and behaviour and demonstrated that the sword does not
94 simply help to increase perception of male size in females.

95 However, animations with virtual animals also have many limitations because they are
96 largely restricted to the use of visual stimuli in two dimensions. Many animal interactions
97 require other or additional sensory input (for example, fish species can usually sense the
98 presence of conspecifics through the lateral line (via mechanical stimuli) and most species of
99 social insects require olfactory stimuli for social recognition) and take place in three
100 dimensions. They require the physical presence of a con- or heterospecific to fight, mate or

101 cooperate with and these types of interaction by their very nature cannot be established with a
102 virtual partner and require a robot.

103 Robots can provide solutions to some of the issues connected with virtual animals but also
104 have some potential problems of their own. Developing robots that are accepted as
105 conspecifics may not be equally straightforward in different species (depending on which
106 sensory channels are used for social recognition, the size of the species and its cognitive
107 abilities to name but a few factors) and the difficulty of implementing movements and
108 responses varies considerably. Building robots can also be time-consuming and in some cases
109 expensive and often requires collaboration with scientists in other disciplines. Despite these
110 potential problems there are in principle no limits to how realistic we can make a robot appear
111 like a con-or heterospecific in terms of its behaviour and morphology.

112

113 Smart collars and cyborgs

114 New devices such as electronic collars make it possible to get control over some aspects
115 of the behaviour of animals and therefore allow behavioural manipulations without investing
116 substantial effort to create an animation or build a robot. These devices were originally
117 developed for domestic animals which can be fitted with a “smart” collar that produces an
118 adverse stimulus (sound, odour, mild electric shock) if the animal comes too close to the
119 boundary of its designated area where a wire has been buried that communicates with the
120 collar. This technology is already commercially available for domestic dogs. However, for
121 larger scale use in cattle herding the collar usually contains a GPS unit that can determine the
122 location of the animal which is more flexible and cost-effective. An example of such work is
123 the virtual fence project which promotes the spatial control of livestock by means of smart
124 collars instead of fences [26-28]. Additionally, by making use of social hierarchies and
125 collective behaviour, only a small fraction of the total herd usually needs to be equipped [18,
126 29-30].

127 However, while it is possible to exert some influence on the behaviour of animals in this
128 way (i.e. they can be maintained in a certain area) it does not produce the kind of fine-control
129 that a robot provides. The strength of the response of the animal and its movement details
130 cannot be reliably controlled with a collar and are left to chance. This means that if the same
131 individual is given the same collar stimulus repeatedly, it may still produce a variable
132 behavioural output. In addition, there is often considerable inter-individual variation in
133 response to the collar stimuli [27]. An alternative to smart collars is the work on “cyborgs”
134 ([31-33], Box 1).

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136

137 **Making robots interactive**

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139 There are a number of common, basic requirements that must be fulfilled if interaction with
140 live animals is to be possible. The behaviour of live animals needs to be monitored (e.g.
141 through direct observation or an automated camera system) to provide the sensory basis for a
142 response by the agent (virtual animal or robot). This sensory information is used to make a
143 decision (usually made by a human observer or a computer) over how the agent should
144 respond in the next time step. Depending on what the live animal does next this can
145 potentially lead to a chain of interactions between animal and agent. Some researchers use a
146 simple remote-control system to initiate a response in the robot when they want to create an
147 interaction between live animal and robot [9]. This means the first two steps regarding
148 sensory input and decision-making (discussed above) are operated by a human observer. This
149 approach has the disadvantage that much is left to the judgement of the scientist operating the
150 robot. More sophisticated systems give the robot sensory input, a control system and
151 behavioural output so that it can make its own (standardised) decisions as to when and how to
152 interact [4]. This approach can result in an autonomous robot where the animal and the robot
153 interact without intervention from an observer [4]. As an alternative, the control system can
154 be externalised in order to allow the experimenter to change the course of an interaction
155 between robot and animal at any point (Box 2). For example, the experimenter could load a
156 new interaction sequence if the context required it.

157 Furthermore, for the analysis of robot-animal interactions and the operation of remote-
158 controlled robots, 2d or 3d tracking of robot and animal(s) is vital and usually done via digital
159 video cameras which are connected to a computer. While pattern recognition and tracking
160 have made great advances in recent years [34], fully automated tracking of multiple objects
161 (robots and/or animals) can still be surprisingly problematic under experimental conditions.

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164 **Robots in behavioural experiments**

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166 Interactive robots have the potential to revolutionise the way in which we perform
167 experimental work with animals because they provide a number of important methodological
168 advances.

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170 Manipulation of interaction sequences

171 Interactive robots allow us to investigate entire interaction sequences where formerly
172 scientists could only provide an animal with a single stimulus and then wait for a response.
173 Many if not most animal interactions involve behavioural sequences which were previously
174 difficult to test experimentally in a standardised way. Particularly relevant behavioural
175 contexts that can involve lengthy interaction sequences include cooperation, courtship and
176 agonistic behaviours and the fast-growing research area of collective behaviour.

177 Communal roosting is a wide-spread behaviour but little is known about how individuals
178 agree on a location. To investigate the mechanisms of communal shelter-seeking in
179 cockroaches (*Periplaneta americana*), robots were created that behaved like cockroaches and
180 that were accepted as conspecifics (based on their odour) by the cockroaches ([4]; Fig. 1). The
181 robots were autonomous and capable of recognising the shelters and the walls of the arena
182 and of interacting with the cockroaches. The cockroaches prefer the darker of two shelters but
183 in the presence of cockroach robots that ‘preferred’ the lighter shelter, they could be made to
184 accept the lighter one more often than they normally would. The robots, despite their
185 preference for the lighter shelter, occasionally followed the cockroaches and occupied the
186 darker one. The experiments showed that the eventual outcome (adoption of the dark or light
187 shelter) was a result of a complex interaction between robots and cockroaches. The non-linear
188 nature of the decision-making process could result in either the cockroaches or the robots
189 taking charge in the shelter selection process. Selecting a common shelter (from two
190 alternatives) involved many interactions between cockroaches and robots over an extended
191 time period.

192 Another promising area in which interaction sequences are particularly important is that of
193 mating displays where a mixture of different signals are employed and where the actions of
194 the sexes are highly interdependent. Interactive robots could provide opportunities for
195 simulating different male courtship behaviours to evaluate their effect on females and
196 likewise different female responses to male courtship [35]. An example is the elegant work by
197 Patricelli et al. [9,36] in which robotic female bowerbirds (*Ptilonorhynchus violaceus*) were
198 used to investigate male courtship behaviour. A startle response in females significantly
199 reduced the courtship intensity in males [35]. Patricelli et al. used a technique by which the
200 researcher triggered the response of the robotic female by remote-control from a hide when
201 the bowerbird male began courtship. Therefore the timing of the response was determined by
202 the experimenter and depends on his/her accuracy of judgment. Given that the experimenter’s

203 perspective (from a hide) is likely to be different from that of the female robot which has a
204 more direct and localised view, it would be an interesting challenge to provide the robot with
205 local sensors that allow it to trigger its own startle behaviour in response to details of the male
206 courtship display, may not even be perceptible by a human observer from a nearby hide.

207

208 Using robots as leaders

209 Robots can be used to explore how animals select leaders and in which contexts they are
210 willing to follow. In a study on decision-making behaviour remote-controlled fish models
211 (and later a robotic fish) were used to demonstrate that the decision of which path to choose in
212 a y-maze was based on a quorum [37]. If the robotic fish took the risky path (passing a
213 predator model) and not the safe one, it was followed by a single fish but less often by groups
214 of 2, 4 and 8 fish. To guide groups past the predator model, two (or more) robotic fish were
215 required. Three robots generated no additional following (compared to two robots) supporting
216 the idea that a quorum was already reached with two leaders. If the fish had to choose
217 between two robotic fish that were different in appearance and which moved in different
218 directions, the decision in favour of the more popular one dramatically increased as a function
219 of group size as predicted by the Condorcet theorem [38].

220

221 Robots for testing models of behaviour

222 In the case of collective behaviours of fish schools and bird flocks there is no shortage in
223 the literature of mechanistic models of these systems but a real lack of empirical data and
224 experimental tests [39]. Interactive robots should be used here to critically assess these
225 models and the assumptions they are based on. For example, in the debate on modelling
226 collective behaviour some authors proposed metric interactions (i.e. individuals respond to the
227 movements of near neighbours within a certain distance [40]) others proposed topological
228 ones (i.e. individuals respond to fixed number of near neighbours largely regardless of
229 distance [20]). To discriminate between the two model predictions a robotic fish was used that
230 performed a sudden change in direction relative to that of the rest of the shoal. From the
231 response of the shoal members it became clear that a topological model is more realistic [8].
232 This type of research required a robot that could enter a group and physically interact with its
233 members.

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236 **Conclusions and future perspectives**

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238 Selection of interactive technology

239 Interactive technology offers a whole new range of possibilities for experimental work in
240 animal behaviour. Depending on the species, the research question and the budget, different
241 options for interactive robots are available starting from lab-based systems that allow the use
242 of different robots within relatively small spaces (Box 2) to fully autonomous devices (Fig. 1).
243 The approach used in creating “cyborg” insects (Box 1) is bound to become even more
244 sophisticated in the near future and should hold interesting possibilities for experimentalists
245 that require behavioural control over one or several individuals. The strength of the cyborg
246 approach is that the animal itself is being used rather than a machine that resembles an
247 animal. Interactions in social insects could be manipulated in this way to explore open
248 questions in collective behaviour research [41-43]. For example, several projects used robotic
249 honey bees to investigate the waggle dance and the onset of information cascades [44,7].
250 However, if fine-control of a worker becomes possible through the cyborg approach this
251 could potentially open up new ways to further investigate this complex behaviour.

252 Electronic collar technology could be used to address a number of interesting questions
253 and practical conservation issues. We can test predictions from the literature [18] as to what
254 proportion in a group needs to be controlled to manipulate the whole group. In animals that
255 have social hierarchies we could experimentally explore which individuals exert the greatest
256 influence during movement decisions [45]. The applications of this technology in terms of
257 farm animals and domestic animals are clear and in some cases already widely explored.
258 However, there are two key areas where smart collar technology might be useful also for
259 wildlife management: keeping large herbivores away from valuable crops and predators away
260 from livestock. For example, one of the first free-ranging herds of European bison in
261 Germany is supposed to be restricted to a particular woodland area in this way (Witte pers.
262 commun.).

263

264 Manipulation of interaction sequences

265 We described a number of examples above in which interactive robots have been successfully
266 used to investigate animal behaviour. Particularly in the contexts of cooperation and agonistic
267 behaviour the use of interactive robots could pave the way for further progress. For example,
268 in the case of predator inspection behaviour the place of one individual could be taken by an
269 interactive robot which could follow different types of interaction programmes depending on
270 which aspect of cooperation or defection should be simulated (e.g. risk-sharing by sharing the

271 lead or return to the group). Box 2 shows that a methodology for this type of experiment
272 exists [8]. By giving the robot different identities (through different body patterns or odours)
273 it would also be possible to test whether individuals that frequently defect (while controlling
274 for other behavioural or morphological differences) are avoided as partners for predator
275 inspection in future. Furthermore, this approach could establish how many different
276 cooperation partners can actually be remembered and for how long.

277 Agonistic behaviour in the form of territorial displays of individuals is another case in
278 point. The behaviour of the rival males often strongly depends on what the opponent does
279 [46-47] and this could potentially be investigated systematically with an interactive robot. For
280 the study of winner and loser effects it might be possible to stage fights between robots that
281 mimic conspecific males and to study what the audience (i.e. males or females that watch the
282 behaviour) can learn from such interactions. The use of two robots for fight sequences would
283 allow standardisation of interactions within and between fights so that we can control what
284 each individual audience member watches at any time.

285

286 Robots to embody personality types

287 Robots could be used to experimentally decouple behaviour and morphology by
288 systematically manipulating different aspects of morphological and behavioural traits to
289 investigate their relative importance. The latter could include personality type which would
290 allow an assessment of the role of personalities in decision-making processes and in social
291 networks [48]. Social networks can be generated on the basis of interactions, spatial
292 proximity, relatedness or other factors [49]. Social network analysis provides us with many
293 new metrics to characterize the social fine-structure of populations [49-50] and therefore with
294 an opportunity to gain an understanding of the role that different personalities play in groups
295 and populations regarding the transmission of information or disease or in terms of
296 cooperation and policing of social conflicts [51,52]. How an individual can build up a certain
297 network position and what influence this position offers could be experimentally tested
298 through interactive robots providing novel insights into the social organisation of animals.

299 Different studies described the development of behavioural differentiation in groups (e.g.
300 in cases where food accessibility was made difficult). For example, a proportion of
301 individuals may specialize in stealing food from others, or in joining others that have already
302 located food [53,54]. Introducing specialized robots that mimic producer-scrounger behaviour
303 within the group might show how the proportion of different specialists is modified. Similarly
304 in insect societies, the introduction of robots as workers and how these modify the pattern of

305 division of labour could be investigated.

306

307 Robots as demonstrators

308 The cross-disciplinary study of imitation and social learning in robots, humans and animals
309 has emerged in recent years [55]. Animal behaviour experiments would benefit enormously
310 from having robotic “demonstrators” to explore the transmission process of copying
311 behaviour. The experiments on leadership in fish decision-making discussed earlier are just
312 the beginning of this new field [37,38]. We described experiments on fish (in the section
313 Using robots as leaders) in which the phenotypic characteristics of leaders were manipulated
314 to explore the willingness of conspecifics to follow but this approach could be pushed further
315 to investigate also the willingness to copy behaviours and socially learn. Furthermore, the
316 manipulation of the demonstrator’s behaviour could provide new important insights into what
317 information observers can extract from watching demonstrators (for example when exploiting
318 a food patch). Female robots could be a useful tool in experiments on mate choice copying.
319 The robot could simulate a preference for a particular male and the strength of this preference
320 could be precisely controlled in a robot so that copying behaviour from females could be
321 studied in detail. Robotic demonstrators could demonstrate behaviours with different error
322 rates which would address the question of whether it is easier to learn from individuals that
323 make mistakes.

324 Young animals can be imprinted on robots interacting with them [56]. An interesting area
325 for application is the use of robots for guiding young of the year that have been imprinted on
326 the robot (which embodies a parent) along a suitable migration route or away from danger. In
327 the past geese, cranes and other species [57] have been imprinted on costumed humans (who
328 mimic the parents species) and were trained to follow a light aircraft. This approach could
329 potentially be expanded to other species and contexts with robots that mimic the respective
330 species and can replace both humans and light aircraft.

331

332 Swarm intelligence and swarm robotics

333 In the context of collective behaviour, swarm intelligence has attracted much interest [58,
334 59]. The role of the cognitive abilities of individuals in the decision-making process of groups
335 is still relatively little understood which opens up many possibilities for experimental work.
336 How the information that individuals provide is processed could be investigated with robots
337 that inject pre-selected bits of information into the decision-making process. This is not to say
338 that this type of work can only be carried out with interactive robots. Several studies [29,60]

339 showed how trained or instructed individuals can be used to initiate new behaviours in
340 groups. However, the latter does not provide the same degree of control as robots because of
341 inter-individual and within-individual variation (e.g. due to changes in motivation).

342 Swarm robotics [61] is a rapidly expanding field of research which offers a number of
343 interesting approaches to the study of animal behaviour. Automated recognition of social
344 behaviours can be used to assess the behavioural repertoire of an individual or a species
345 (similar to classical ethograms) and to calculate transition probabilities between different
346 behaviours to develop dynamic models of the behavioural architecture of organisms [3].
347 Robots can then be used to embody these models. And going one step further, swarm robotics
348 can facilitate the study of evolutionary processes as well by mutating and evolving robot
349 social behaviour which can provide novel predictions for the study of communication and
350 adaptive behaviour [5,62,63]. Symbion is a project that goes even further by aiming to
351 model, in a self-assembling swarm of robots, generic processes within biology such as
352 morphogenesis, energy homeostasis, and immune responses to faults [64].

353 Interactive robots offer exciting new opportunities for experimental research. With the
354 help of robots complex interaction sequences can be manipulated and behaviour and
355 morphology can be decoupled. Robots can act as leaders and demonstrators and can
356 potentially even be used to embody personality types in social networks. These
357 methodological advances facilitate novel experimental work that will push the boundaries of
358 behavioural research.

359

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366 **References**

367

368 1 Tinbergen, N. (1951) *The study of instinct*. Oxford University Press

369

370 2 Winfield, A.F.T. (2009) Foraging robots. In *Encyclopaedia of Complexity and System*
371 *Science* (Meyers R.A., ed), pp. 3682–3700, Springer

372

373 3 Balch, T. *et al.* (2006) How multi-robot systems research will accelerate our understanding
374 of social animal behavior. *P. IEEE* 94, 1445-11463
375

376 4 Halloy, J. *et al.* (2007) Social integration of robots into groups of cockroaches to control
377 self-organised choices. *Science* 318, 55-1158
378

379 5 Mitri, S. *et al.* (2009) The evolution of information suppression in communicating robots
380 with conflicting interests. *Proc. Natl. Acad. Sci. U. S. A* 106, 15786-15790
381

382 6 Michelsen, *et al.* (1992) How honeybees perceive communication dances, studied by means
383 of a mechanical model. *Behav. Ecol. Sociobiol.* 30, 143-150
384

385 7 Landgraf, T. *et al.* (2008) Design and development of a robotic bee for the analysis of
386 honeybee dance communication. *Appl. Bion. Biom.* 5, 157-164
387

388 8 Faria, J.J. *et al.* (2010) A novel method for investigating the collective behaviour of fish:
389 introducing “Robofish”. *Behav. Ecol. Sociobiol.* 64, 1211-1218
390

391 9 Patricelli, G.L. *et al.* (2002) Male displays adjusted to female's response - Macho courtship
392 by the satin bowerbird is tempered to avoid frightening the female. *Nature* 415, 279-280
393

394 10 Vaughan, R. *et al.* (2000) Experiments in automatic flock control. *Robo. Auton. Syst.* 31,
395 109-117
396

397 11 Ishii, H. *et al.* (2006) Experimental study on task teaching to real rats through interaction
398 with a robotic rat. *Lect. Not. Comp. Sci.* 4095, 643-654
399

400 12 Walters, M.L. *et al.* (2008) Avoiding the uncanny valley: robot appearance, personality
401 and consistency of behavior in an attention-seeking home scenario for a robot companion.
402 *Auton. Robot.* 24, 159-178
403

- 404 13 Dautenhahn, K. *et al.* (2009) KASPAR - A Minimally Expressive Humanoid Robot for
405 Human-Robot Interaction Research. Special Issue on "Humanoid Robots", *App. Bion. Biom.*
406 6: 369-397
407
- 408 14 Webb, B. (2000) What does robotics offer animal behaviour? *Anim. Behav.* 60, 545-558
409
- 410 15 Holland, O. and McFarland, D. (2001) *Artificial Ethology*. Oxford University Press
411
- 412 16 Knight, J. (2005) Animal behaviour: When robots go wild. *Nature* 434, 954-955
413
- 414 17 Webb, B. (2008) Using robots to understand animal behavior. *Adv. Stud. Behav.* 38, 1-58
415
- 416 18 Couzin, I.D. *et al.* (2005) Effective leadership and decision-making in animal groups on
417 the move. *Nature* 433, 513-516
418
- 419 19 Buhl, J. *et al.* (2006) From disorder to order in marching locusts. *Science* 312, 1402-1406
420
- 421 20 Ballerini, M. *et al.* (2008) Interaction ruling animal collective behavior depends on
422 topological rather than metric distance: Evidence from a field study. *Proc. Natl. Acad. Sci. U.*
423 *S. A.* 105, 1232-1237
424
- 425 21 Nagy, M. *et al.* (2010) Hierarchical group dynamics in pigeon flocks. *Nature* 464, 890-893
426
- 427 22 D'Eath, R.B. (1998) Can video images imitate real stimuli in animal behaviour
428 experiments? *Biol. Rev.* 73, 267-292
429
- 430 23 Baldauf, S.A. *et al.* (2008) Technical restrictions of computer-manipulated visual stimuli
431 and display units for studying animal behaviour. *Ethology* 114, 737-751
432
- 433 24 Moiseff, A. and Copeland, J. (2010) Firefly Synchrony: A behavioral strategy to minimize
434 visual clutter. *Science* 329, 181
435
- 436 25 Rosenthal, G.G. and Evans, C.S. (1998) Female preference for swords in *Xiphorhynchus helleri*
437 reflects a bias for large apparent size. *Proc. Natl. Acad. Sci. U. S. A.* 95, 4431-4436

438
439 26 Tiedemann, A. *et al.* (1999) *Electronic (fenceless) control of livestock*. Techn. Report
440 PNW-RP-510, United States Department of Agriculture, Forest Service
441
442 27 Butler, Z. *et al.* (2006) From robotics to animals: virtual fences for controlling cattle. *Int. J.*
443 *Robot. Res.* 25, 485-508
444
445 28 Schwager, M. *et al.* (2008) Data-driven identification of group dynamics for motion
446 prediction and control. *J. Field Robot.* 25, 305–324
447
448 29 Dyer, J.R.G. *et al.* (2009) Leadership, consensus decision making and collective behaviour
449 in human crowds. *Philos. Trans. Roy. Soc. B* 364, 781-789
450
451 30 Conradt, L. *et al.* (2009) “Leading according to need” in self-organizing groups. *Am. Nat.*
452 173, 304-312
453
454 31 Sato, H. *et al.* (2009) Remote radio control of insect flight. *Front. Integr. Neurosci.* 3, 24.
455 doi: 10.3389/neuro.07.024.2009
456
457 32 Sato, H. and Maharbiz, M.M. (2010) Recent developments in the remote radio control of
458 insect flight. *Front. Neurosci.* 4, 199. doi: 10.3389/fnins.2010.00199
459
460 33 Maharbiz, M.M. and Sato, H. (2010) Cyborg beetles, *Sci. Am.* 303, 94-99
461
462 34 Correll, N. (2006) SwisTrack: A Tracking Tool for Multi-Unit Robotic and Biological
463 Systems. *IEEE/RSJ International Conference on Intelligent Robots and Systems 2006*, 2185-
464 2191
465
466 35 Reaney, L.T. (2009) Female preference for male phenotypic traits in a fiddler crab: do
467 females use absolute or comparative evaluation? *Anim. Behav.* 77, 139–143
468
469 36 Patricelli, G.L. *et al.* (2006) Male satin bowerbirds, *Ptilonorhynchus violaceus*, adjust their
470 display intensity in response to female startling: an experiment with robotic females. *Anim.*
471 *Behav.* 71, 49-59

472
473 37 Ward, A.J.W. *et al.* (2008) Quorum decision-making facilitates information transfer in fish
474 shoals. *Proc. Natl. Acad. Sci. U. S. A.* 105: 6948-6953
475
476 38 Sumpter, D.J.T. *et al.* (2008) Consensus decision-making by fish. *Current Biology* 18:
477 1773-1777
478
479 39 Krause, J. and Ruxton, G.D. (2011) Living in groups: selected topics. In: *Social behaviour:*
480 *Genes, ecology and evolution* (Szekeley T, Moore A, Komdeur J eds). Cambridge University
481 Press, Cambridge
482
483 40 Couzin, I.D. *et al.* (2002) Collective memory and spatial sorting in animal groups. *J.*
484 *Theor. Biol.* 218, 1-11
485
486 41 Camazine, S. *et al.* (2001) *Self-organization in biological systems*, Princeton University
487 Press
488
489 42 Sumpter, D.J.T. and Pratt, S.C. (2009) Quorum responses and consensus decision making.
490 *Philos. Trans. R. Soc. B* 364, 743-753
491
492 43 Conradt, L. and List, C. (2009) Group decisions in humans and animals: a survey. *Philos.*
493 *Trans. Roy. Soc. B* 364, 719-742
494
495 44 Kirchner, W.H. and Towne, W.F. (1994) The sensory basis of the honeybees dance
496 language. *Sci. Am.* 270, 74-80
497
498 45 King, A.J. *et al.* (2008) Dominance and affiliation mediate despotism in a social primate.
499 *Curr. Biol.* 18, 1833-1838
500
501 46 Alcock, J. (2009) *Animal behaviour: an evolutionary approach*. Sinauer Associates
502
503 47 McGregor, P.K. (ed.) (2005) *Animal Communication Networks*. Cambridge University
504 Press
505

506 48 Krause, J. *et al.* (2010) Personality in the context of social networks. *Philos. Trans. R. Soc.*
507 *B* 365: 4009-4016
508

509 49 Croft, D.P. *et al.* (2008) *Exploring Animal Social Networks*. Princeton University Press
510

511 50 Krause, J. *et al.* (2007) Social network theory in the behavioural sciences: potential
512 applications. *Behav. Ecol. Sociobiol.* 62, 15-27
513

514 51 Flack, J.C. *et al.* (2006) Policing stabilizes construction of social niches in primates.
515 *Nature* 439, 426-429
516

517 52 McDonald, D.B. (2007) Predicting fate from early connectivity in a social network. *Proc.*
518 *Natl. Acad. Sci. U. S. A* 104, 10910-10914
519

520 53 Mottley, K and Giraldeau, L.A. (2000) Experimental evidence that group foragers can
521 converge on predicted producer-scrounger equilibria. *Anim. Behav.* 60, 341-350
522

523 54 Grasmuck, V. and Desor, D. (2002) Behavioural differentiation of rats confronted to a
524 complex diving-for-food situation *Behav. Proc.* 58, 67-77
525

526 55 Nehaniv, C. and Dautenhahn, K. (eds) (2007). *Imitation and Social Learning in Robots,*
527 *Humans and Animals*. Cambridge University Press
528

529 56 Gribovskiy, A *et al.* (2010). Towards Mixed Societies of Chickens and Robots. In Proc. of
530 the 2010 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS) 4222-
531 4228.
532

533 57 Urbanek, R.P. *et al.* (2010) Winter release and management of reintroduced migratory
534 Whooping Cranes *Grus americana*. *Bird Cons. Inter.* 20, 43-54
535

536 58 Couzin, I.D. (2009) Collective cognition in animal groups. *Trends Cogn. Sci.* 13, 36-43
537
538

539 59 Krause, J. *et al.* (2010) Swarm intelligence in animals and humans. *Trends Ecol. Evol.* 25,
540 28-34
541
542 60 Reebs, S.G. (2000) Can a minority of informed leaders determine the foraging movements
543 of a fish shoal? *Anim. Behav.* 59, 403-409
544
545 61 Şahin, E. and Winfield, A.F.T. (2008) Special issue on swarm robotics. *Swarm Intelligence*
546 2, 69-72
547
548 62 Floreano, D. *et al.* (2007) Evolutionary conditions for the emergence of communication in
549 robots. *Curr. Biol.* 17, 514-519
550
551 63 Floreano, D. and Keller, L. (2010) Evolution of adaptive behaviour in robots by means of
552 Darwinian selection. *PLoS Biol.* 8, e1000292
553
554 64 Levi, P. and Kernbach S. (eds.) (2010) *Symbiotic Multi-Robot Organisms: Reliability,*
555 *Adaptability, Evolution.* Springer
556
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559 **Glossary**

560

561 **Animal personality:** individual consistency in behaviour across time and/or contexts.

562

563 **Autonomous robot:** a robot with sensory input, decision-making capabilities and behavioural
564 output.

565

566 **Cognitive ability:** information-processing ability in connection with problem solving.

567

568 **Collective behaviour:** the field of collective behaviour investigates the emergence of group-
569 level properties from interactions between individuals.

570

571 **Cyborg:** an organism with both biological and electronic parts.

572

573 **Consensus decision:** agreement among group members on one course of action.

574

575 **Quorum:** a threshold number of individuals that, once reached, will lead to a behaviour or
576 action for the whole group (see also consensus decision).

577

578 **Robot:** a machine that is able to physically interact with its environment and perform some
579 sequence of behaviours, either autonomously or by remote control.

580

581 **Self-organisation:** individuals follow local behavioural rules, resulting in organised
582 behaviour by the whole group without the need for global control.

583

584 **Swarm intelligence:** Collective behaviors, in both natural and artificial systems of multiple
585 agents, that exhibit group-level cognition.

586

587 **Swarm robotics:** the design and engineering of artificial robot swarms based on the
588 principles of swarm intelligence.

589

589 **Table 1. Overview of interactive technologies**

590

591 **Autonomous robot:** a robot with sensory input that is capable of determining its next action
592 (both what action to take and when to take it) without human intervention. It is autonomous in
593 the sense that it can make and execute decisions based on its own assessment of its
594 environment. Autonomous robots are capable of interaction with live animals without human
595 guidance. An example of this type of robot is the cockroach-robot (Fig. 1) which was used to
596 investigate communal shelter selection (see section on Robots in behavioural experiments).

597

598 **Cyborg:** an organism with both biological and electronic parts; the latter allow direct control
599 of an animal by manipulating its nervous system. This control can be used for manipulating
600 the animal's locomotion or social interaction with conspecifics. The control of flight
601 performance in beetles provides an example of this novel approach to controlling animal
602 behaviour (Box 1).

603

604 **Remote-controlled robot:** a robot whose behaviour is controlled externally (in contrast to an
605 autonomous robot whose control-centre is inside the robot itself) by a human observer or a
606 computer outside the robot. The robotic fish (Box 2) and the robotic bee [7] are recent
607 examples of this kind of approach.

608

609 **Smart collars:** a device that can be mounted on an animal (usually in the form of a collar
610 around the neck), which provides negative feedback if the animal enters an area where it is
611 not supposed to go. The negative feedback consists of weak electric shocks or repellent noises
612 and is triggered by a GPS-unit inside the collar that locates the animal's position, or an
613 underground wire. This approach is used to retain domestic animals within certain boundaries
614 without the use of fences (see section on Interactive technology).

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622 **Box 1. Cyborg insects**

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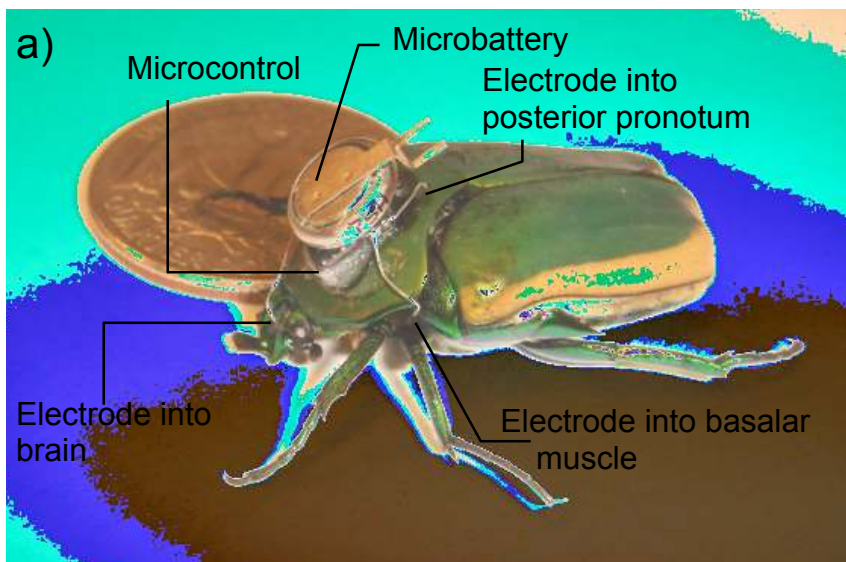
624 A novel way to control animal behaviour is to directly stimulate the neural system of an
625 organism. An impressive example of such a “cyborg-approach” is the remote-control of insect
626 flight [31-33]. A radio-equipped microcontroller emits pulses via electrodes to the brain and
627 selected muscle groups. Reliable control of flight initiation, cessation, elevation and direction
628 has been possible. Two different species of beetle (a) *Cotinis texana* and b) *Mecynorrhina*
629 *torquata*) were used, both of which are strong enough to carry the equipment during flight.

630

631 **Costs and benefits**

632 The Cyborg-approach opens up new ways of controlling locomotion in insects that could be
633 used in many different ways to manipulate interactions between con- or heterospecifics.
634 However, some inter-individual variation in responsiveness was observed and the approach is
635 restricted to species that are strong enough to carry the equipment. Both restrictions may be
636 overcome as smaller and more sophisticated technology becomes available. There are also
637 ethical considerations to be taken into account especially if this approach were to be applied
638 to vertebrates. Furthermore, in the case of more complex social behaviours it might be
639 necessary to show that the behaviour has not become artificial in any way. For example, a
640 behavioural response might be produced that is normally not observed in a given context.

641



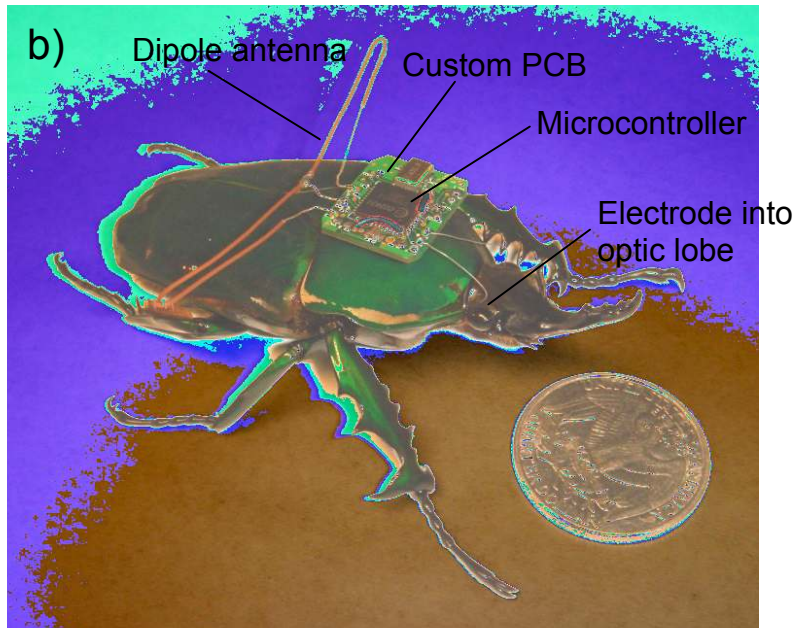
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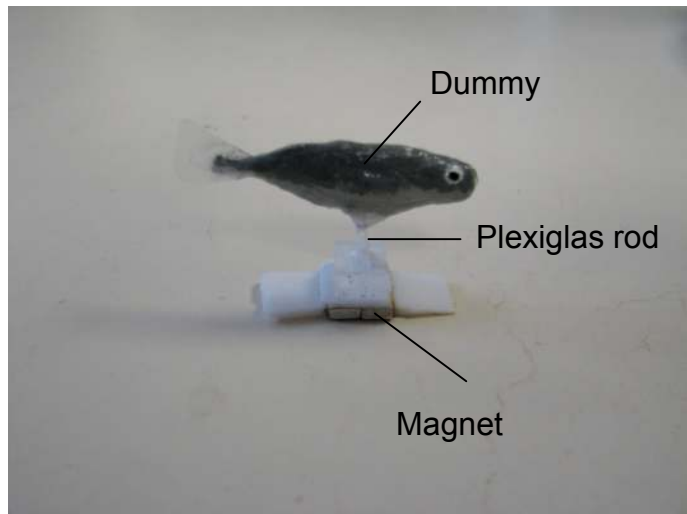


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648 **Box 2. Robofish**

649

650 Faria et al. [8] developed a robotic fish
651 where a dummy is mounted on a thin
652 Plexiglas rod fixed to a flat magnet and
653 guided by a robotic arm under the tank
654 that carries an electro-magnet. The
655 robotic arm is controlled via computer
656 so that the movements of the dummy
657 can be programmed. If a digital video
658 camera is positioned over the tank then
659 information on the relative position of



660 the dummy to live fish and their behaviour can be processed by a computer and behavioural
661 responses of the dummy can be initiated via the robotic arm. This would close the feedback
662 loop and allow interactions with live fish. If small remote-controlled devices are used under
663 the tank to carry electro-magnets instead of a robotic arm, then multiple dummies can be
664 controlled and moved at the same time.

665

666 **Costs and benefits**

667

668 The advantage of this system over autonomous robots lies in the fact that the control system is
669 separated from the dummy. This means that the same control system can now be used for all
670 kinds of dummies which can be produced in large number at low cost and quickly exchanged.
671 This approach is not limited to fish or aquatic systems but could be adopted for most
672 organisms that are small enough so that experiments can fit into an arena of a few square
673 metres. The system is relatively low cost because it only requires a standard PC, several
674 electro-motors and controllers. Potential costs are that this system can only be used in the
675 laboratory (outdoor use is, however, not necessarily straight forward with autonomous robots
676 either) and the dummies have a range that is restricted to that of the two-dimensional arena
677 which is monitored by the camera and serviced by the robotic arm.

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681 **Figure 1.** Interactive autonomous robot which can interact with cockroaches. It carries the
682 olfactory signature of a cockroach and is therefore treated as a conspecific by cockroaches.



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