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Animal agency can accelerate behavioural and neuroscience research

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Abstract

Despite increasing numbers of publications showing that many animals possess the neural substrates involved in emotions and consciousness, animals are still constrained and forced to take part in applied or fundamental research. However, these constraints stress animals and may result in false negatives or false positives. A change is needed in our work paradigm with animals to progress in behavioural and neuroscience research and thus gain access to hitherto inaccessible yet important scientific results. Animals interact in their own ways with the world and we need to adopt these ways, i.e. their agency, to perform better research and develop a better understanding of how the brain and behaviour evolve. This paper discusses how animal agency can not only be the key to more wide-ranging and improved research in existing domains, but can also lead to new research questions resulting from our anthropocentric view.

Keywords: 3Rs, animal research, ethology, ethics, sentience

Introduction

By definition, animal research requires the involvement of animals. Although researchers have made great progress and improved experimental conditions for animals through application of the 3R rules (replace, reduce, refine), some behavioural experiments showed that animals are still forced to enter experimental apparatus through different processes such as throw nets, restraint chairs, cages or food privation. Thirty percent of researchers still continue to use methods that entail negative reinforcement, whilst 70% of procedures using restraint chairs could comprise positive reinforcement methods¹. Beyond the ethical issues of such constraints for animals, these examples of experimental set-ups lead us to consider which possibilities and results have yet to be investigated and more importantly, whether such invasive protocols could lead to false negatives or false positives²⁻⁵. Indeed, stress and contention can not only modify some animal behaviours but also entirely prevent others from being displayed⁶⁻⁸. Some authors consider that the current 3R framework is not sufficient to ensure that animals are meaningful participants, which is crucial to guarantee that scientific results are not altered. These contexts offer few meaningful opportunities for animals to exercise agency in their relationships, both between each other and with humans⁹. Gillepsie wrote that 'there is a long tradition of studying nonhuman animals in spaces of animal use and exploitation, where researchers and teachers in effect become complicit through passive participation in violence against nonhuman animals...' ¹⁰. According to Blattner et al. (2020)⁹ who worked on animal agency in rehomed farm animals and from which this paper is inspired, 'longstanding ideological blinders and anthropocentric bias frame animals as limited beings whose lives unfold according to fixed genetic or species-specific scripts, rather than as complex subjects who act with intention and purpose, both individually and collectively'. We believe that constraint-based experiments are severely limited in terms of what we can learn from animals, in individual and group contexts.

Indeed, increasing numbers of publications show that many animals (mammals, birds and other creatures including octopuses) possess the neural substrates involved in emotions and consciousness^{11,12}. Rats, primates and pigeons are capable of metacognition, i.e. knowing if they are wrong or right in a test^{13,14}. Cetaceans and apes are conscious of their own existence, and that of others¹⁵. Self-awareness was also found in cleaner fishes^{16,17}. Apes know what their conspecifics know¹⁸ and believe¹⁹. Empathy has been observed in apes²⁰

and in rats ²¹. Finally, some apes have a sense of morality ^{22–24}. Researchers obtained these results by changing their way of thinking from an anthropocentric approach ²⁵ to an acceptance of anthropomorphism ²⁶. For instance, self-awareness was not found in some species when the mirror test was used, but it was found when researchers used the senses of animals, such as the sense of smell for dogs ²⁷ or vocalisations in gibbons ²⁸. Merleau-Ponty had already noted this problem in his *Causeries* back in 1948: researchers usually do not try to understand animals in their singularity, *as they are*, but rather in comparison with human beings, projecting essentially human characteristics on to animals ²⁹. However, this is a means to measure the distance between human beings and other animals rather than a tool allowing a real understanding of how animals live and express a subjective existence ^{30,31}. Studied in the light of properly human normative references, animals always lack something ²⁹. For as long as animals are studied from a human perspective and are tested in terms of human problems (capacity to count, to draw, to speak a human language) instead of their own questions and problems, they will always respond “as they can”³², without ever being able to fully express their agency. Animals interact with the world in their own ways and these ways, i.e. their agency, are precisely what we need to adopt to perform better research and develop a better understanding of how the brain and behaviour evolve.

Animal agency

Agency is the capacity of an actor to act in a given environment. In the broadest sense, agency is the ability to have an influence or an effect on something. In this sense, the agency is owned by all humans and animals, but also by viruses, stones or tornadoes as explained by Blattner et al. (2020) ⁹. However, its focus might be narrower when agency is considered as the expression or manifestation of a subjective existence; agency implies affecting the world in ways that reflect a subject’s desires or will ³³. It refers to an individual pursuing its own good in its own way ³⁴. Blattner et al. ⁹ investigate animal agency in a sanctuary for formerly farmed animals, considering how a careful exploration of dimensions of agency in this setting might inform ideas of interspecies interactions (work, research, politics, etc.) and ethics. Their study focused on multispecific animals living in a sanctuary. For the owners of the sanctuary and for the study researchers, the sanctuary is an ‘integrated multispecies community or society whose members shape spaces and practices together, take on recognised social roles, and create and transmit social norms across species lines’. The

authors affirmed that we need to spend time in community with animals, to learn from them, and to be prepared to respond and adjust our learning process through relationships with them. This can be extended to scientific research, and means that animals should no longer be considered as the subjects of our experiments, but rather as participants. For example, when it comes to assessing animal intelligence, the researchers' focus should encompass goals that are meaningful, useful and of interest to animals instead of focusing on goals that are only relevant to the human scientist³⁵. Animals should no longer be seen as objects of knowledge, or mere matter for the act of the human knower, but should rather be granted a status as an *agent* in the production of knowledge³⁶. Interaction and communication have to go in both directions. We need to make ourselves understandable to animals. Of course, this communication would only be possible for some species, such as apes and some monkeys, cetaceans, certain birds including parrots or corvids, social carnivores and cephalopods. However, we need to extend this circle as some other species are surely able to understand our intentions as behavioural or even neuroscientific experiments. When researchers allow too little room for the animals' own forms of agency, the true abilities of these individuals are obscured³⁷.

The study of agencies in animals can be divided into four schemes according to Blattner et al. (2020)⁹ (Figure 1):

1. Agency through space and time: animals are mobile and explore/exploit their environments. This exploration and exploitation can be used to better understand the behaviours of animals but also their preferences in terms of habitats, sleeping areas and social relationships. Whilst this agency seems obvious for many researchers and is often applied for livestock and farmed animals^{38–40}, it is rarely applied in comparative psychology or neuroscience. Specifically, modifications of the environment can be used to shape animal decisions and can remove some of the negative reinforcement that is still applied to animals. Animals could experience less stress in some parts of their environment than others, and carrying out experiments in these places could increase their motivation to participate and decrease the risk of false negatives^{41,42}.
2. Agency through practice and routine: Animals have habits, even in the wild. Social animals collectively organise their day in order to meet their requirements and

maintain the advantages of living in groups⁴³. Rather than forcing animals to participate in experiments, accepting that animals can accept or refuse to participate according to their routine would increase the robustness and viability of results. Any animals that want to be tested seek to use tablets or other interactive apparatus that are based on technologies such as RFID^{44,45}; these tools respect their habits and routines. Medical aspects such as health checks or medical procedures that require constraints and restraints should also be based on these routines to decrease animal stress and injuries, as already shown in their use by zoos.

3. Agency through social roles: A social role is the behaviour expected of an individual who occupies a given social position or status. Individuals understand the place that conspecifics hold in their society. The adoption of roles that are recognised and acknowledged by others, and indeed mutually constructed with conspecifics, is an important dimension of relational agency and a means by which we can effectively affirm our subjective existence within a community. This role can be intraspecific or interspecific. Roles of individuals inside their group 'have been amply described in terms of dominance (policing behaviours, protecting groups), kinship and maternal relationships⁴⁶. Individuals also develop strong relationships when they share similar attributes as sex or age. Group members influence each other, and particularly share knowledge⁴⁷. Dominant or old individuals can transmit important information to others, and this social transmission can be used to make animals learn how to use experimental apparatus or spaces. These individuals can consequently become leaders. Multispecific and positive interactions or associations are also found naturally in the wild in situations such as multispecies group protection, interspecies grooming and predator alerts, even if negative interactions (cheating, predating, competition) are also observed. Blattner et al.⁹ described multispecies interactions in the sanctuary for formerly farmed animals. Individuals of specific species adopt different roles with geese, cows or dogs acting as guardians and policers, cows teaching sheep and multispecies friendship and parenting. Multispecific leadership is also described in different reports with geese leading ducks and chickens, and goats leading sheep⁴⁸⁻⁵⁰.

4. Agency through social norms: Social norms are the customary rules that govern behaviour in groups and societies⁵¹. The previous example of learners and teachers

brings us to the subject of social norms. Behavioural rules and social systems are partly genetic in animals but are also transmitted by cultures. In macaques, for instance, species are divided into grades ranging from despotic and aggressive to tolerant and democratic⁵². However, if an individual from one specific grade is transferred into a group of another grade, it will adopt their behaviours. Many traditions of tool use and social habits have been described in chimpanzees or macaques⁵³. Although collective decision processes are species-specific, variations are observed between groups of the same species. The roles played by individuals can lead to a strong leadership or the development of a more democratic process such as votes⁵⁴. Voting systems⁵⁵ are described in many species, with intentional behaviours and perceptions of the mental states of conspecifics indicating some theory of mind and reinforcing the idea of agency. A sense of community⁹ seems to exist in chimpanzees and in cetaceans, and indeed many other animals know exactly who belongs or does not belong to their group by recognising the faces or voices of group members.

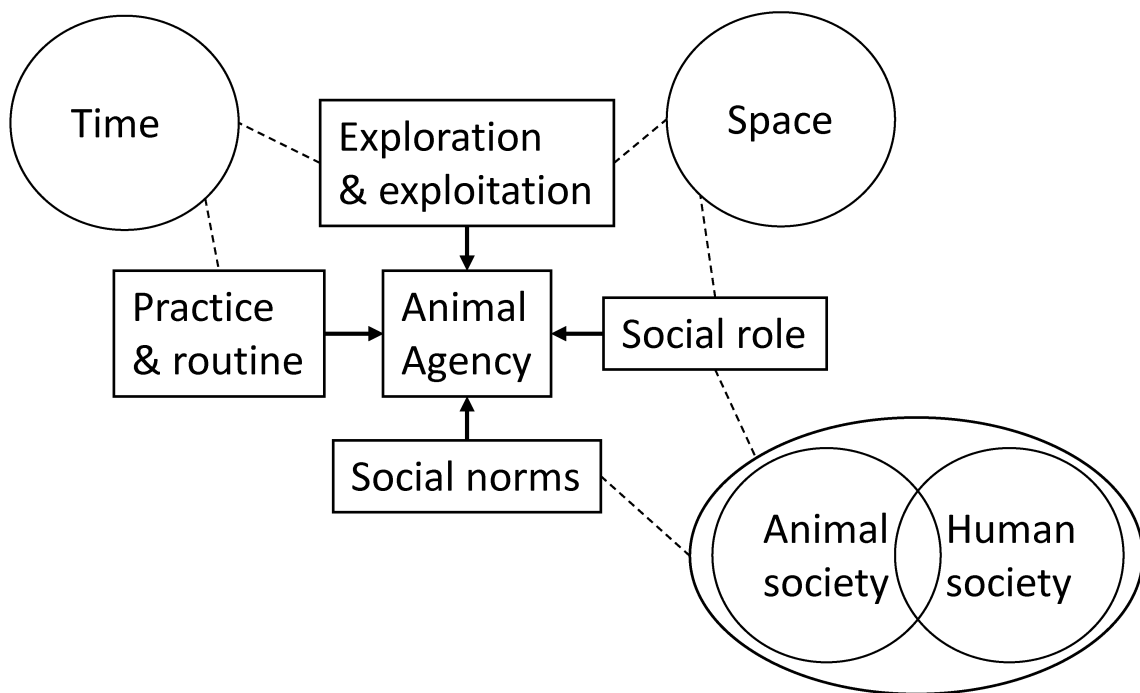


Figure 1: The four schemes of animal agency (squares) and the environmental factors affecting them (circles)

These different instances show that animals have agency over their spatial, temporal and social environment. Animals can therefore be viewed as *agents*; their choice to act has direct consequences on their environment, or they can also resist conditions that do not please them, and act accordingly to change them⁵⁶. Researchers could use this agency to increase animal welfare and obtain more viable and robust results, whilst extending the scope of behavioural and neuroscience research. Indeed, the great difficulty today is to measure the behaviours or the neuronal activities of aware animals whilst seeking to do so in natural conditions: the results of many experiments have been criticised, as the associated captivity, animal microbiota, genetic or behavioural variance of animals made it impossible to allow to reproduce or generalise any results that were unaffected by false negatives or false positives^{57–59}. Often, in the research process, many of the limitations shown by the animals to date are actually the limitations of the scientific methods, rather than the animals themselves⁶⁰. Similarly, Frans De Waal argues: ‘All that most experiments have done thus far is testing the ape’s theory of the human mind. We would do better to focus on the ape’s theory of the ape mind’²². Following the concept of animal agency, we propose a future research framework to work with animals and progress in research.

Future research framework

We remember some years ago, talking with colleagues in neuroscience or medical research about applying the use of touchscreens in macaques, or suggesting to doctors that studying mouse personality could help to avoid false negatives or false positives. Our interlocutors laughed, saying that our suggestions were either unnecessary or impossible. Yet today, these projects have become reality. Touchscreens or joysticks are used to understand cognition and self-agency⁶¹ in a wide range of species (pigs, macaques, baboons, goats, horses, etc.^{45,62–65}). However, this use is still limited to behavioural studies and should now be extended to neuroscience¹. There is a huge amount of literature describing how animal personality and microbiota can influence results. This success demonstrates the importance of not limiting our imagination about how we could work with animals to obtain new results in biological sciences.

First we need to change our way of thinking to a perspective of working *with* animals rather than *on* animals. Animals are agents endowed with intentions which transcend traditional subject-object relations. We need to trust their capabilities in order to increase our research

possibilities. Experimental set-ups that restrain animals, such as restraint chairs or food privation, stress animals and prevent them both physically and mentally from fully expressing their agency. This challenge may certainly take time, but would be hugely beneficial. Patter and Blattner⁶⁶ suggest core principles to follow with animals: non-maleficence, beneficence and voluntary participation⁶⁷. Economic or convenience euthanasia of animals should not be an option^{68,69}. Euthanasia also has a strong impact on the emotions of caretakers⁷⁰. Positive methods exist and have proved to be efficient^{6,71-75}. The readiness of chimpanzees to voluntarily participate in interactions or allow humans to observe them can facilitate the measurement of embryo development and brain activities in unanesthetized and unrestrained individuals (Figure 2⁴⁴). Unrestrained and voluntary animals can be trained to put their head in a mask⁷⁶ and be tested whilst receiving fruit juice. This allows the measurement of different metrics with eye tracking^{19,77,78} and non-invasive neuroimaging⁷⁹ (Figure 3.A).



Figure 2: (A) Developmental neuroscience. Fetal brain development in chimpanzees was measured by a non-invasive ultrasound technique. (B) EEG recordings in a chimpanzee. The chimpanzee quietly sat on the chair and allowed the experimenter to put electrode patches on the skin of her forehead and the top of her head. Photos provided with the courtesy of Satoshi Hirata.

Traditional approaches involve bringing animals into a lab and restraining them while they perform tasks in order to ensure stable gaze-tracking and neural recordings (in the case of neuroscience). However, this unnatural setting does not permit the study of brain activity during natural, social and complex behaviours. Specific ethical guidelines exist now for research in the wild^{80,81}. The likely benefits and possible negative effects of our presence and field methods on study subjects, their environment and the local human community should, of course, be considered⁸². New technologies allow us to bring science into the wild and test animals in a free condition in their natural environment, thus removing any experimental source of stress and measuring their entire behavioural repertoire. The animals studied can be identified using RFID techniques⁸³ but also via artificial intelligence with the recognition of individuals by videotracking^{84–86}. The latter removes the need to catch animals. A location can then be defined where different touchscreens deliver food, with activation only for certain species and individuals. We can imagine going beyond the use of touchscreens with the implementation of eye-tracking and neuroimaging apparatus in the wild (Figure 3.B). This could open up new research avenues in species that are in danger of extinction or cannot be easily maintained in captivity.

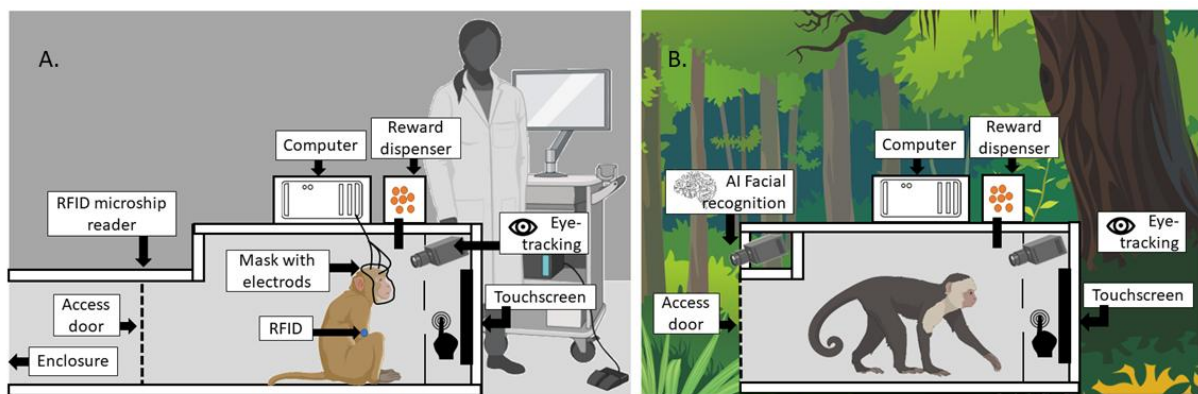


Figure 3: (A) Non-invasive neuroimaging and eye-tracking system with voluntary experience in the lab. (B) Non-invasive touchscreen system with voluntary engagement and individual identification in the wild. This figure was realized using FAVPNG.com and Biorender.

Some research, and especially the biomedical or physiological/cellular domains, cannot be performed outside the research structure. It is important for these experiments to respect the 3Rs but also to think about the Bateson cube⁸⁷, meaning that scientists need to evaluate

the ethical acceptability of their research for society as a whole, including animals. The 3Rs can be extended by testing animals in viable conditions. Indeed, lab conditions were standardised for many years in terms of animal genetics, husbandry, food for study comparison and repeatability. However, this way of doing research is criticised today as animals are agents interacting with their world, and the lab conditions in which they live have a strong effect on them and thus on scientific results. Moreover, it is difficult to replicate similar conditions in the laboratory, as even animals that are genetically similar and live in similar environments develop different personalities⁸⁸. Moreover, even if animals are living in similar conditions, similar food and litter sources affect their microbiota^{89–91} and their behaviours differently⁹². Animal sociality was long forgotten in neuroscience or biomedical research, but it is an important part of animal agency⁹. Indeed, sociality has an important impact on the health of animals, and a great number of publications highlight the link between sociality and health ageing^{93–95}. Making use of the sociality of animals, i.e. their agency, can even reverse cognitive decline and extend longevity^{96–98}.

Conclusion

There is still much progress to be made to attain a more compassionate, less stressful and more robust animal research model. This requires training and teaching researchers to adopt new methods including animal agency and change their view of the role animals play in research. As Jacques Derrida wrote in *The Animal That Therefore I Am*, the traditional scientific and philosophical discourse on animals observes and speaks of non-human animals but never really engages with, experiments *with* or gains experience with the latter⁹⁹: this type of discourse can therefore only position animals as mere passive objects of the theoretical knowledge these disciplines build. Such methods are completely blind to the animals' own processes of interacting with their world⁹⁹, and are completely blind to their agency. This view of animals as objects is not limited to research but is also found in different aspects of everyday life (food, work, clothing, etc.). Researchers worldwide must have the conviction that ethical animal research must consider individuals as subjects of their own life and of their own world, and as co-creators of knowledge. Accepting this co-creation of knowledge can create new research questions from our anthropocentric view, as animal cognition dimensions are different from ours²⁵. Animals are agents in our research. They are active in the research process and some researchers have even gone so far as to

add them in the acknowledgments or even list them as co-authors^{66,100}. This recognition of animals as agents rather than objects is not approved of by some researchers, who consider that this is tantamount to removing animal agency, committing over-anthropomorphism and overstepping the will of animals to cooperate. Acknowledging animal agency could facilitate social acceptance of animal research⁶⁷ and be of benefit to the animals concerned (well-being through learning, creating and participating¹⁰¹). The consideration of animals as agents could be extended from research to other domains: a new ontology considering non-human animals as agents can have political, ethical and legal consequences. The concept of capital applied to animals needs to be extended to social capital, ecological capital and cultural capital¹⁰²: we can learn from animals and they can be part of our societies¹⁰³. This new way of viewing animal agency can therefore raise critical ethical questions in regard to the treatment of animals in research and to the place we grant them politically in our social world.

References

1. McMillan, J. L., Bloomsmith, M. A. & Prescott, M. J. An International Survey of Approaches to Chair Restraint of Nonhuman Primates. *Comp. Med.* **67**, 442–451 (2017).
2. Chang, L., Zhang, S., Poo, M. & Gong, N. Spontaneous expression of mirror self-recognition in monkeys after learning precise visual-proprioceptive association for mirror images. *Proc. Natl. Acad. Sci.* **114**, 3258–3263 (2017).
3. Huttunen, A. W., Adams, G. K. & Platt, M. L. Can self-awareness be taught? Monkeys pass the mirror test—again. *Proc. Natl. Acad. Sci.* **114**, 3281–3283 (2017).
4. Liu, X., Liu, T. & Huang, X. Commentary: Spontaneous expression of mirror self-recognition in monkeys after learning precise visual-proprioceptive association for mirror images. *Front. Psychol.* **8**, 1151 (2017).
5. Ueno, H. *et al.* Behavioural Changes in Mice after Getting Accustomed to the Mirror. *Behav. Neurol.* **2020**, (2020).

- 302 6. Prescott, M. J. Online resources for improving the care and use of non-human primates in
303 research. *Primate Biol.* **3**, 33 (2016).
- 304 7. Mason, S. *et al.* Effective chair training methods for neuroscience research involving rhesus
305 macaques (*Macaca mulatta*). *J. Neurosci. Methods* **317**, 82–93 (2019).
- 306 8. Lecorps, B., Weary, D. M. & von Keyserlingk, M. A. G. Captivity-Induced Depression in Animals.
307 *Trends Cogn. Sci.* (2021) doi:10.1016/j.tics.2021.03.010.
- 308 9. Blattner, C. E., Donaldson, S. & Wilcox, R. Animal Agency in Community. *Polit. Anim.* **6**, 1–22
309 (2020).
- 310 10. Gillespie, K. A. For a politicized multispecies ethnography. *Polit. Anim.* **5**, 17–32 (2019).
- 311 11. Low, P. *et al.* The Cambridge declaration on consciousness. in 1–2 (2012).
- 312 12. Ben-Haim, M. S. *et al.* Disentangling perceptual awareness from nonconscious processing in
313 rhesus monkeys (*Macaca mulatta*). *Proc. Natl. Acad. Sci.* **118**, (2021).
- 314 13. Le Neindre, P. *et al.* Animal consciousness. Summary of the multidisciplinary assesment. (2017).
- 315 14. Le Neindre, P., Dunier, M., Larrère, R. & Prunet, P. *La conscience des animaux*. (Quae, 2018).
- 316 15. Gallup Jr, G. G., Anderson, J. R. & Shillito, D. J. The mirror test. *Cogn. Anim. Empir. Theor.*
317 *Perspect. Anim. Cogn.* 325–333 (2002).
- 318 16. de Waal, F. B. Fish, mirrors, and a gradualist perspective on self-awareness. *PLoS Biol.* **17**,
319 e3000112 (2019).
- 320 17. Kohda, M. *et al.* If a fish can pass the mark test, what are the implications for consciousness and
321 self-awareness testing in animals? *PLoS Biol.* **17**, e3000021 (2019).
- 322 18. Kaminski, J., Call, J. & Tomasello, M. Chimpanzees know what others know, but not what they
323 believe. *Cognition* **109**, 224–234 (2008).
- 324 19. Krupenye, C., Kano, F., Hirata, S., Call, J. & Tomasello, M. Great apes anticipate that other
325 individuals will act according to false beliefs. *Science* **354**, 110–114 (2016).
- 326 20. De Waal, F. B. The antiquity of empathy. *Science* **336**, 874–876 (2012).

- 327 21. Bartal, I. B.-A., Decety, J. & Mason, P. Empathy and pro-social behavior in rats. *Science* **334**,
328 1427–1430 (2011).
- 329 22. De Waal, F. „Morally Evolved.“. *Primates Philos. Moral. Evolved* 1–80 (2006).
- 330 23. Jensen, K., Call, J. & Tomasello, M. Chimpanzees are vengeful but not spiteful. *Proc. Natl. Acad.*
331 *Sci.* **104**, 13046–13050 (2007).
- 332 24. Tomasello, M. & Vaish, A. Origins of human cooperation and morality. *Annu. Rev. Psychol.* **64**,
333 231–255 (2013).
- 334 25. Birch, J., Schnell, A. K. & Clayton, N. S. Dimensions of animal consciousness. *Trends Cogn. Sci.*
335 (2020).
- 336 26. Griffin, D. R. *Animal minds: Beyond cognition to consciousness*. (University of Chicago Press,
337 2013).
- 338 27. Cazzolla Gatti, R. Self-consciousness: Beyond the looking-glass and what dogs found there.
339 *Ethol. Ecol. Evol.* **28**, 232–240 (2016).
- 340 28. D’Agostino, J., Pasetta, C. & Reichard, U. Preliminary results of a vocal self-recognition test in
341 northern white-cheeked gibbons (*Nomascus leucogenys*). in vol. 162 157–157 (WILEY 111
342 RIVER ST, HOBOKEN 07030-5774, NJ USA, 2017).
- 343 29. Merleau-Ponty, M. *Causeries 1948*. (Média Diffusion, 2017).
- 344 30. Sueur, C. & Pelé, M. Editorial: Anthropomorphism, between merits and demerits. *Lett. CEERE*
345 *Cent. Eur. Enseign. Rech. En Ethique* **107**, 1 (2017).
- 346 31. Sueur, C., Forin-Wiart, M.-A. & Pelé, M. Do They Really Try to Save Their Buddy?
347 Anthropomorphism about Animal Epimeletic Behaviours. (2020)
348 doi:10.20944/preprints202008.0711.v1.
- 349 32. Canguilhem, G. *La connaissance de la vie*. (Vrin, 1992).
- 350 33. Krause, S. R. Beyond non-domination: Agency, inequality and the meaning of freedom. *Philos.*
351 *Soc. Crit.* **39**, 187–208 (2013).

- 352 34. Taylor, P. W. *Respect for nature: A theory of environmental ethics*. (Princeton University Press,
353 2011).
- 354 35. Pepperberg, I. M. Intelligence and rationality in parrots. (2006).
- 355 36. Haraway, D. J. *Primate visions: Gender, race, and nature in the world of modern science*.
356 (Psychology Press, 1989).
- 357 37. McFarland, S. E. & Hediger, R. *Animals and agency: An interdisciplinary exploration*. vol. 8 (Brill,
358 2009).
- 359 38. Bouissou, M.-F., Boissy, A., Le Neindre, P. & Veissier, I. The social behaviour of cattle. *Soc.*
360 *Behav. Farm Anim.* 113–145 (2001).
- 361 39. Scanes, C. G. *Animal Agriculture: Livestock, Poultry, and Fish Aquaculture*. *Animals and Human*
362 *Society* 179 (Elsevier Inc., 2018). doi:10.1016/b978-0-12-805247-1.00007-1.
- 363 40. Sosa, S. O. *et al.* Impact of Group Management and Transfer on Individual Sociality in Highland
364 Cattle (*Bos taurus*). *Front. Vet. Sci.* **6**, 183 (2019).
- 365 41. Coe, J. & Hoy, J. Choice, control and computers: Empowering wildlife in human care.
366 *Multimodal Technol. Interact.* **4**, 92 (2020).
- 367 42. Matsuzawa, T. WISH cages: constructing multiple habitats for captive chimpanzees. (2020).
- 368 43. Sueur, C. A Non-Lévy Random Walk in Chacma Baboons: What Does It Mean? *PLoS ONE* **6**,
369 e16131 (2011).
- 370 44. Matsuzawa, T. Evolution of the brain and social behavior in chimpanzees. *Curr. Opin. Neurobiol.*
371 **23**, 443–449 (2013).
- 372 45. Claidière, N., Gullstrand, J., Latouche, A. & Fagot, J. Using Automated Learning Devices for
373 Monkeys (ALDM) to study social networks. *Behav. Res. Methods* **49**, 24–34 (2017).
- 374 46. Krause, J. & Ruxton, G. D. *Living in groups*. (Oxford University Press, 2002).
- 375 47. Duboscq, J., Romano, V., MacIntosh, A. & Sueur, C. Social Information Transmission in Animals:
376 Lessons from Studies of Diffusion. *Front. Psychol.* **7**, (2016).
- 377 48. Baratay, E. *Bêtes de somme-Des animaux au service des hommes*. (Points, 2011).

- 378 49. Baratay, É. Pour une histoire éthologique et une éthologie historique. *Etudes Rural.* **189**, 91–
379 106 (2012).
- 380 50. Baratay, E. *Biographies animales. Des vies retrouvées.* (Le Seuil, 2017).
- 381 51. Bicchieri, C. & Muldoon, R. Social norms. (2011).
- 382 52. Thierry, B. Unity in diversity: Lessons from macaque societies. *Evol. Anthropol. Issues News Rev.*
383 **16**, 224–238 (2007).
- 384 53. Laland, K. N. & Hoppitt, W. Do animals have culture? *Evol. Anthropol. Issues News Rev.* **12**, 150–
385 159 (2003).
- 386 54. King, A. J. & Sueur, C. Where Next? Group Coordination and Collective Decision Making by
387 Primates. *Int. J. Primatol.* **32**, 1245–1267 (2011).
- 388 55. Pennisi, A. & Giallongo, L. Animal Biopolitics: How Animals Vote. *Int. J. Semiot. Law-Rev. Int.*
389 *Sémiot. Jurid.* **31**, 491–499 (2018).
- 390 56. Carter, B. & Charles, N. Animals, agency and resistance. *J. Theory Soc. Behav.* **43**, 322–340
391 (2013).
- 392 57. Rader, K. *Making Mice: Standardizing Animals for American Biomedical Research, 1900-1955.*
393 (Princeton University Press, 2004).
- 394 58. Barbee, R. W. & Turner, P. V. Incorporating Laboratory Animal Science into Responsible
395 Biomedical Research. *ILAR J.* **60**, 9–16 (2019).
- 396 59. Voelkl, B. *et al.* Reproducibility of animal research in light of biological variation. *Nat. Rev.*
397 *Neurosci.* **21**, 384–393 (2020).
- 398 60. Savage-Rumbaugh, E. S., Rumbaugh, D. M. & Fields, W. M. Language as a window on rationality.
399 (2006).
- 400 61. Kaneko, T. & Tomonaga, M. The perception of self-agency in chimpanzees (*Pan troglodytes*).
401 *Proc. R. Soc. B Biol. Sci.* **278**, 3694–3702 (2011).
- 402 62. Zeagler, C., Gilliland, S., Freil, L., Starner, T. & Jackson, M. Going to the dogs: towards an
403 interactive touchscreen interface for working dogs. in 497–507 (2014).

- 404 63. Tomonaga, M. *et al.* A horse's eye view: size and shape discrimination compared with other
405 mammals. *Biol. Lett.* **11**, 20150701 (2015).
- 406 64. Jacobson, S. L., Kwiatt, A. C., Ross, S. R. & Cronin, K. A. The effects of cognitive testing on the
407 welfare of zoo-housed Japanese macaques (*Macaca fuscata*). *Appl. Anim. Behav. Sci.* **212**, 90–
408 97 (2019).
- 409 65. Croney, C. C. & Boysen, S. T. Acquisition of a Joystick-Operated Video Task by Pigs (*Sus scrofa*).
410 *Front. Psychol.* **12**, (2021).
- 411 66. Patter, L. E. V. & Blattner, C. Advancing Ethical Principles for Non-Invasive, Respectful Research
412 with Nonhuman Animal Participants. *Soc. Anim.* **28**, 171–190 (2020).
- 413 67. Webb, C. E., Woodford, P. & Huchard, E. Animal ethics and behavioral science: An overdue
414 discussion. *BioScience* **69**, 778–788 (2019).
- 415 68. Hayashi, M., Sakuraba, Y., Watanabe, S., Kaneko, A. & Matsuzawa, T. Behavioral recovery from
416 tetraparesis in a captive chimpanzee. *Primates* **54**, 237–243 (2013).
- 417 69. Matsuzawa, T. Euthanasia is not an option: 10 years' care of a chimpanzee with acute
418 tetraparesis. (2016).
- 419 70. Coleman, K. Caring for non-human primates in biomedical research facilities: scientific, moral
420 and emotional considerations. *Am. J. Primatol.* **73**, 220–225 (2011).
- 421 71. Laule, G. E., Bloomsith, M. A. & Schapiro, S. J. The Use of Positive Reinforcement Training
422 Techniques to Enhance the Care, Management, and Welfare of Primates in the Laboratory. *J.*
423 *Appl. Anim. Welf. Sci.* **6**, 163 (2003).
- 424 72. Prescott, M. J. & Buchanan-Smith, H. M. Training nonhuman primates using positive
425 reinforcement techniques. *J. Appl. Anim. Welf. Sci.* **6**, 157–161 (2003).
- 426 73. Prescott, M. & Buchanan-Smith, H. Training laboratory-housed non-human primates, part I: a
427 UK survey. *Anim. Welf.-POTTERS BAR THEN WHEATHAMPSTEAD-* **16**, 21 (2007).

- 428 74. Schapiro, S. J., Bloomsmith, M. A. & Laule, G. E. Positive Reinforcement Training As a Technique
429 to Alter Nonhuman Primate Behavior: Quantitative Assessments of Effectiveness. *J. Appl. Anim.*
430 *Welf. Sci.* **6**, 175 (2003).
- 431 75. Prescott, M. J. *et al.* Refinement of the use of food and fluid control as motivational tools for
432 macaques used in behavioural neuroscience research: report of a Working Group of the NC3Rs.
433 *J. Neurosci. Methods* **193**, 167–188 (2010).
- 434 76. Slater, H. *et al.* Individually customisable non-invasive head immobilisation system for non-
435 human primates with an option for voluntary engagement. *J. Neurosci. Methods* **269**, 46–60
436 (2016).
- 437 77. Machado, C. J. & Nelson, E. E. Eye-tracking with nonhuman primates is now more accessible
438 than ever before. *Am. J. Primatol.* **73**, 562–569 (2011).
- 439 78. Ryan, A. M. *et al.* Non-invasive Eye Tracking Methods for New World and Old World Monkeys.
440 *Front. Behav. Neurosci.* **13**, (2019).
- 441 79. Basso, M. A. *et al.* Using non-invasive neuroimaging to enhance the care, well-being and
442 experimental outcomes of laboratory non-human primates (monkeys). *NeuroImage* **228**,
443 117667 (2021).
- 444 80. Costello, M. *et al.* Field work ethics in biological research. (2016).
- 445 81. Soulsbury, C. D. *et al.* The welfare and ethics of research involving wild animals: A primer.
446 *Methods Ecol. Evol.* **11**, 1164–1181 (2020).
- 447 82. MacKinnon, K. C. & Riley, E. P. Field primatology of today: current ethical issues. (2010).
- 448 83. Fehlmann, G. & King, A. J. Bio-logging. *Curr. Biol.* **26**, R830–R831 (2016).
- 449 84. Schofield, D. *et al.* Chimpanzee face recognition from videos in the wild using deep learning. *Sci.*
450 *Adv.* **5**, eaaw0736 (2019).
- 451 85. Ferreira, A. C. *et al.* Deep learning-based methods for individual recognition in small birds.
452 *Methods Ecol. Evol.* **11**, 1072–1085 (2020).

- 453 86. Poirotte, C. & Charpentier, M. J. E. Unconditional care from close maternal kin in the face of
454 parasites. *Biol. Lett.* **16**, 20190869 (2020).
- 455 87. Bout, H. J., van Vlissingen, J. M. F. & Karssing, E. D. Evaluating the ethical acceptability of animal
456 research. *Lab Anim.* **43**, 411–414 (2014).
- 457 88. Bierbach, D., Laskowski, K. L. & Wolf, M. Behavioural individuality in clonal fish arises despite
458 near-identical rearing conditions. *Nat. Commun.* **8**, 15361 (2017).
- 459 89. Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H. & Newington, J. E. Microbiota, fauna,
460 and mesh size interactions in litter decomposition. *Oikos* **99**, 317–323 (2002).
- 461 90. McCoy, K. D., Geuking, M. B. & Ronchi, F. Gut Microbiome Standardization in Control and
462 Experimental Mice. *Curr. Protoc. Immunol.* **117**, 23.1.1–23.1.13 (2017).
- 463 91. Xiang, Q. *et al.* Effects of diet on gut microbiota of soil collembolans. *Sci. Total Environ.* **676**,
464 197–205 (2019).
- 465 92. Montiel-Castro, A. J., González-Cervantes, R. M., Bravo-Ruiseco, G. & Pacheco-López, G. The
466 microbiota-gut-brain axis: neurobehavioral correlates, health and sociality. *Front. Integr.*
467 *Neurosci.* **7**, 70 (2013).
- 468 93. Boyer, F., Jaouen, F. & El Chérif Ibrahim, E. G. Deficits in social behavior precede cognitive
469 decline in middle-aged mice. *Front. Behav. Neurosci.* **13**, (2019).
- 470 94. Rosati, A. G. *et al.* Social selectivity in aging wild chimpanzees. *Science* **370**, 473–476 (2020).
- 471 95. Lacreuse, A., Raz, N., Schmidtke, D., Hopkins, W. D. & Herndon, J. G. Age-related decline in
472 executive function as a hallmark of cognitive ageing in primates: an overview of cognitive and
473 neurobiological studies. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190618 (2020).
- 474 96. Baker, N., Wolschin, F. & Amdam, G. V. Age-related learning deficits can be reversible in
475 honeybees *Apis mellifera*. *Exp. Gerontol.* **47**, 764–772 (2012).
- 476 97. Richardson, T. O. *et al.* Ant Behavioral Maturation Is Mediated by a Stochastic Transition
477 between Two Fundamental States. *Curr. Biol.* **30**, 1–8 (2020).

- 478 98. Wild, B. *et al.* Social networks predict the life and death of honey bees. *Nat. Commun.* **12**, 1–12
479 (2021).
- 480 99. Derrida, J. *The animal that therefore I am*. (Fordham Univ Press, 2008).
- 481 100. Savage-Rumbaugh, S., Wamba, K., Wamba, P. & Wamba, N. Welfare of Apes in Captive
482 Environments: Comments On, and By, a Specific Group of Apes. *J. Appl. Anim. Welf. Sci.* **10**, 7–
483 19 (2007).
- 484 101. Franks, B., Webb, C., Gagliano, M. & Smuts, B. Conventional science will not do justice to
485 nonhuman interests: A fresh approach is required. *Anim. Sentience* **4**, 17 (2020).
- 486 102. Pelé, M., Georges, J.-Y., Matsuzawa, T. & Sueur, C. Editorial: Perceptions of Human-Animal
487 Relationships and Their Impacts on Animal Ethics, Law and Research. *Front. Psychol.* **11**, (2021).
- 488 103. Donaldson, S. & Kymlicka, W. *Zoopolis: A political theory of animal rights*. (Oxford University
489 Press, 2011).
- 490
- 491

