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1 **Incorporating animal agency into research design could improve behavioral and**  
2 **neuroscience research**

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13

14

15 **Abstract**

16 Despite increasing numbers of publications showing that many animals possess the neural  
17 substrates involved in emotions and consciousness, and exhibit agency in their behavior,  
18 many animals are still restrained and forced to take part in applied or fundamental research.  
19 However, these restraints and procedures, because they stress animals and because they  
20 limit the expression of adaptive behavior, may result in compromised findings. Researchers  
21 should alter their research paradigms to understand mechanisms and functions of the brain  
22 and behavior so that the paradigms incorporate animals' agency. This paper discusses how  
23 animal agency can not only be the key to more wide-ranging and improved research in  
24 existing domains, but can also lead to new research questions about behavior and brain  
25 evolution.

26

27 **Keywords:** 3Rs, animal research, ethology, ethics, animal welfare, scientific advance

28

29

30 **Introduction**

31 By definition, animal research requires the involvement of animals. Although researchers  
32 have made great progress and improved experimental conditions for animals through the  
33 application of the 3R (Replace, Reduce, Refine) rules, some behavioral experiments showed  
34 that animals are still restrained through different methods, such as the use of throw nets,  
35 primate restraint chairs (specifically-designed chairs that require non-human primates to 'sit'  
36 in place for sustained periods of time (NC3Rs, [https://www.nc3rs.org.uk/our-portfolio/chair-  
37 restraint-training-non-human-primates](https://www.nc3rs.org.uk/our-portfolio/chair-restraint-training-non-human-primates))), rat restrainer, cages, or by food deprivation (Ben-Ami  
38 Bartal et al., 2011; Chang et al., 2017; He et al., 2020; McMillan et al., 2017; Prescott &  
39 Buchanan-Smith, 2003; Slater et al., 2016). According to McMillan et al. (2017), too many  
40 researchers continue to use methods that entail negative reinforcement (when the  
41 individual has to perform an action to remove a stressor), whilst procedures using restraint  
42 chairs in primates or similar restrainers in other species could comprise positive  
43 reinforcement methods (when the individual receives a reward after entering in the chair

44 and then getting its head out from the chair) (McMillan et al., 2017). These protocols are  
45 used to obtain results in behavioral or neuroscience research but are problematic for several  
46 reasons. Beyond the ethical issues of such restraints for animals, these examples of  
47 experimental setups lead us to consider which possibilities and results have yet to be  
48 investigated and more importantly, whether such compulsory protocols could lead to false  
49 negatives or false positives (Chang et al., 2017; Huttunen et al., 2017; Liu et al., 2017). False  
50 negatives or false positives mean that studies show respectively negative (not expected, H<sub>0</sub>)  
51 or positive results (expected, H<sub>1</sub>) but these results are not due to the tested condition (e.g. a  
52 drug, a gene, an environmental condition) but to uncontrolled factors (e.g. stress,  
53 personality). Indeed, stress and coercion (i.e., the animal is immobilized and restrained in an  
54 apparatus, such as a chair for primate or a box or a system of collars for rats or dogs) can not  
55 only modify some behaviors but also entirely prevent others from being displayed (Lecorps  
56 et al., 2021; Mason et al., 2019; Prescott, 2016). Some authors, such as Van Patter, Blattner,  
57 Matsuzawa, King and McMillan consider that the current 3R framework is not sufficient to  
58 ensure that animals are meaningful participants in experiments, which is crucial to  
59 guarantee that scientific results are not altered by stress or personality of animals (King,  
60 2021; Matsuzawa, 2016a; McMillan et al., 2014; Van Patter & Blattner, 2020). Studies carried  
61 out on animals under restraints offer few meaningful opportunities for them to show their  
62 full behavioral and cognitive capacities, and in this way to exercise agency with their  
63 environment and in their relationships, both with each other and with humans (*Homo*  
64 *sapiens*) (Blattner et al., 2020). Gillespie (2019) wrote that ‘there is a long tradition of  
65 studying nonhuman animals in spaces of animal use and exploitation, where researchers and  
66 teachers in effect become complicit through passive participation in violence against  
67 nonhuman animals...’ (p. 19). According to Blattner et al. (2020), who worked on animal  
68 agency in rehomed farm animals and from which this paper is inspired, ‘longstanding  
69 ideological blinders and anthropocentric bias frame animals as limited beings whose lives  
70 unfold according to fixed genetic or species-specific scripts, rather than as complex subjects  
71 who act with intention and purpose, both individually and collectively’ (p. 1).

72 Culture, ontology, political leaning, as well as university courses influence how a person  
73 considers animals as objects (Bègue & Vezirian, 2021; Furnham & Heyes, 1993; Miele et al.,  
74 1993). It would be interesting to look at the textbooks of comparative cognition to find

75 evidence that students are being taught to think of animals as objects; that is the method  
76 (Andrews, 2020b) used to defend the claim that comparative cognition eschews the study of  
77 consciousness. This view of animals as objects is not limited to research but is also found in  
78 different aspects of everyday life (food, work, clothing, etc.). In this way, the consideration of  
79 animals as agents could be extended from research to other domains: a new ontology  
80 considering non-human animals as agents can have political, ethical, and legal  
81 consequences.

82 We argue that restraint-based experiments are severely limited in terms of what researchers  
83 can learn from animals, in individual and group contexts. In contrast, letting animals express  
84 their will or intentions in behavior could bring new advances in research and human-animal  
85 cooperation. Incorporating animal agency should be considered a central feature of research  
86 and husbandry protocols, particularly when applying for funding. In this article we seek to  
87 provide researchers with arguments in favor of this practice.

## 88 **Animal agency**

89 Agency is the capacity of an individual to act in a given environment. In the broadest sense,  
90 agency is the ability to have an influence or an effect on something. However, agency is  
91 considered here as the expression or manifestation of a subjective existence; agency implies  
92 affecting the world in ways that reflect a subject's desires or will (Krause, 2013). It refers to  
93 an individual pursuing its own good in its own way (Taylor, 2011). Gergely & Jacob (2012)  
94 described that from birth on, human infants are exposed to two basic kinds of agency:  
95 instrumental action and communicative action. When researchers allow too little room for  
96 the animals' own forms of agency, the true abilities of these individuals are obscured  
97 (McFarland & Hediger, 2009).

98 Blattner et al. (2020) investigate animal agency in a sanctuary for rehomed farm animals,  
99 considering how a careful exploration of dimensions of agency in this setting might inform  
100 ideas of interspecies interactions (work, research, politics, etc.) and ethics. Their study  
101 focused on animals of many species living in this sanctuary. For the owners of the sanctuary  
102 and the researchers, the sanctuary is an 'integrated multispecies community or society  
103 whose members shape spaces and practices together, take on recognized social roles, and  
104 create and transmit social norms across species lines'. Blattner et al. (2020), De Waal (2016),

105 Le Neindre et al. (2017, 2018), and Meijer (2019) affirm that researchers need to spend time  
106 in community with animals, learn from them, and be prepared to respond and adjust  
107 scientific learning process through relationships with them. This means that animals should  
108 no longer be considered as the subjects of scientific experiments, but rather as participants –  
109 that is, as agents (Haraway, 1989). For example, when it comes to assessing cognitive  
110 abilities, the researchers' focus should encompass goals that are meaningful, useful, and of  
111 interest to animals instead of focusing on goals that are only relevant to the human scientist  
112 (Pepperberg, 2006).

113 It is also important to recognize animals as agents by forming relationship with them. As  
114 Andrews (2020) notes, it is important to treat animals as sentient research participants who  
115 exist within their own context and with whom researchers will be in a relationship. She  
116 defends a range of scientific benefits that come from forming relationships with animal  
117 research subjects and that we develop below. Interaction and communication have to go in  
118 both directions. Researchers need to make themselves understandable to animals as many  
119 species are able to understand our facial expressions and emotions (Bhattacharjee et al.,  
120 2019; Good et al., 2018; Hoffman et al., 2018; Patterson & Cohn, 1990; Pedersen, 2020;  
121 Savage-Rumbaugh & Lewin, 1994). For instance, applying the same agency and research  
122 protocols in horses (*Equus caballus*) as were applied in primates led to advances in our  
123 understanding of equine cognition (Matsuzawa, 2017). The first study with horses using  
124 computer touch panels was realized recently (Tomonaga et al., 2015). The primary  
125 motivation to study horses comes from the idea of understanding humans not just from a  
126 primate perspective, but from a broader mammalian (*Mammalia*) perspective. Tomonaga et  
127 al. (2015) used a computer-controlled touchscreen system to show differences in  
128 discrimination abilities between horses, chimpanzees (*Pan troglodytes*) and humans.

129 Animals may act in different dimensions as space and time and different situations as  
130 socializing, foraging, parenting, etc. Blattner et al. (2020) analyzed in their paper what  
131 freedoms of actions may result in the expression of agency in animals as well as how humans  
132 take up these freedoms, meaning how they use these dimensions to enhance animals'  
133 agency or the behavioral repertoire. Their observational analysis, using multispecies  
134 ethnography (i.e., the study of the interconnectedness and inseparability of humans and  
135 other life forms; Kirksey & Helmreich, 2010; Ogden et al., 2013) and directed toward a

136 number of methodological and ethical questions on animal-human and animal-animal  
137 relationships, led them to divide animal agency into four domains (Figure 1):

138 *1. Agency through space and time:*

139 Animals are mobile and explore/exploit their environments. Their exploration and  
140 exploitation can be used to better understand animals' preferences in terms of habitats,  
141 sleeping areas, and social relationships. Studies on these issues contribute to the emergence  
142 of new disciplines such as animal geographies (Buller, 2014) or animal mobilities (Hodgetts &  
143 Lorimer, 2020). Whilst this form of agency seems obvious to many researchers and the  
144 criteria are often applied to livestock and farmed animals (Bouissou et al., 2001; Scanes,  
145 2018; Sosa et al., 2019), it is less often applied in comparative psychology or neuroscience,  
146 despite well-known works on exploration and curiosity in animals published more than half a  
147 century ago (Berlyne, 1966; Glickman & Sroges, 1966). In neurophysiological studies of  
148 nonhuman primates, restraint chairs are widely used (McMillan et al., 2017) as boxes or  
149 other systems in rats (Bartal et al., 2011; Galichanin et al., 2011).

150 Modifications of the environment can be used to shape animals' decisions and can remove  
151 some of the negative reinforcement that is still applied to animals. For example, animals  
152 could experience less stress in some parts of their environment than others, and carrying out  
153 experiments in these places could increase their motivation to participate and increase the  
154 power of the study to detect experimental effects (Coe & Hoy, 2020; Matsuzawa, 2020). Of  
155 course, this statement implies that the housing of animals should be designed to take  
156 advantage of animals' preferences and adjustments to features of their environment. For  
157 example, boundaries and fences cannot be only considered as barriers and limitations of  
158 freedoms but also as security and communication touchstones as suggested by Blattner et  
159 al. (2020) or Grandin (1987, 1989). Humans should create barriers and fence placements  
160 according to the behavior of animals. Similarly, for behavioral experimental apparatus,  
161 animals should not be forcibly brought to where researchers want to test them but  
162 researchers should observe animals to determine the best position to place the devices.

163 Good urban design is adapted to human behavior in order to increase health, decrease  
164 stress, and the costs of urban refurbishment (Park & Evans, 2016; Pereira et al., 2019). A  
165 similar way of thinking could be applied to designing housing and testing spaces for

166 nonhuman animals. For example, in “modern” zoos animals of different species are housed  
167 together in larger enclosures, while retaining the possibility for each species to be isolated  
168 from the others if needed. This is a way to apply the concept of nudge (i.e. any aspect of the  
169 choice architecture that alters behavior in a predictable way without forbidding any options,  
170 Thaler, 2008) to some captive animals studies, as has already been done for species  
171 conservation (Czap et al., 2015; Eberle, 2021; Reddy et al., 2017). Kyoto University applied  
172 this concept with the WISH cages, a set of enclosures connecting habitats and equipped with  
173 a computer-controlled touch panel system for cognitive tests. This framework increases the  
174 fission-fusion dynamics of chimpanzees, i.e. their social agency, and their cognitive agency  
175 (Matsuzawa, 2020). Other labs provide similar voluntary participation testing stations  
176 associated with group-living such as the Goffin laboratory in Vienna with cockatoos (*Cacatua*  
177 *goffini*) (O’Hara et al., 2021) or the Living Links station with nonhuman primates at  
178 Edinburgh zoo (Jordan et al., 2022). This principle is not restricted to vertebrates as ants for  
179 instance showed their abilities to escape their captive nest when it was not well designed,  
180 thanks to behaviors as raft, bridge, jump or even tool use (Dussutour & Wystrach, 2022).

## 181 *2. Agency through practice and routine:*

182 Animals have habits. Social animals collectively organize their day in order to meet their  
183 requirements and maintain the advantages of living in groups (Sueur, 2011). Allowing  
184 animals to accept or refuse to participate in a research activity according to their routine  
185 would increase the robustness and reliability of the results. For example, some studies allow  
186 an animal to use a digital tablet or workstation or to open boxes to obtain food inside (Aplin  
187 et al., 2015, Whiten et al., 1996). In domains such as visual cognition testing could be  
188 conducted in a naturalistic environment with an integrated touchscreen workstation,  
189 favoring animal exploration (Jacob et al., 2021). Specific protocols for individuals in a group  
190 can be based on technologies like RFID (Radio Frequency IDentification) (Claidière et al.  
191 2017; Matsuzawa, 2013); these tools allow individuals to participate in the testing at the  
192 time and for the duration of their choosing. Health checks or medical procedures that  
193 require restraints, should also be based on these routines in order to decrease animal stress  
194 and injuries, as already shown in their use by zoos (e.g., the Great Ape Heart Project,  
195 Murphy et al., 2018). Knowing routines of animals or observing why the routine of an animal  
196 is different from others or for a day allows us to better understand their behavior without



197 the need to disturb them by subjecting them to experiments or health checks. Moreover,  
198 modifying the routines of animals is a way to measure their behavioral flexibility,  
199 personality, and group cohesiveness.

200 Whilst many researchers working with captive nonhuman primates already invoke a form of  
201 consent to work with animals (Fenton, 2014), this protocol could be applied to many other  
202 orders and classes, such as rodents. To our knowledge, there are no testing devices that can  
203 be used in the cages of rats with which they can play when they want and for the duration  
204 they want (although some housing includes different kinds of objects and surfaces for  
205 voluntary activity; Bailoo et al., 2018; Crawford et al., 2020). This kind of system should be  
206 extended to all species involved in research.

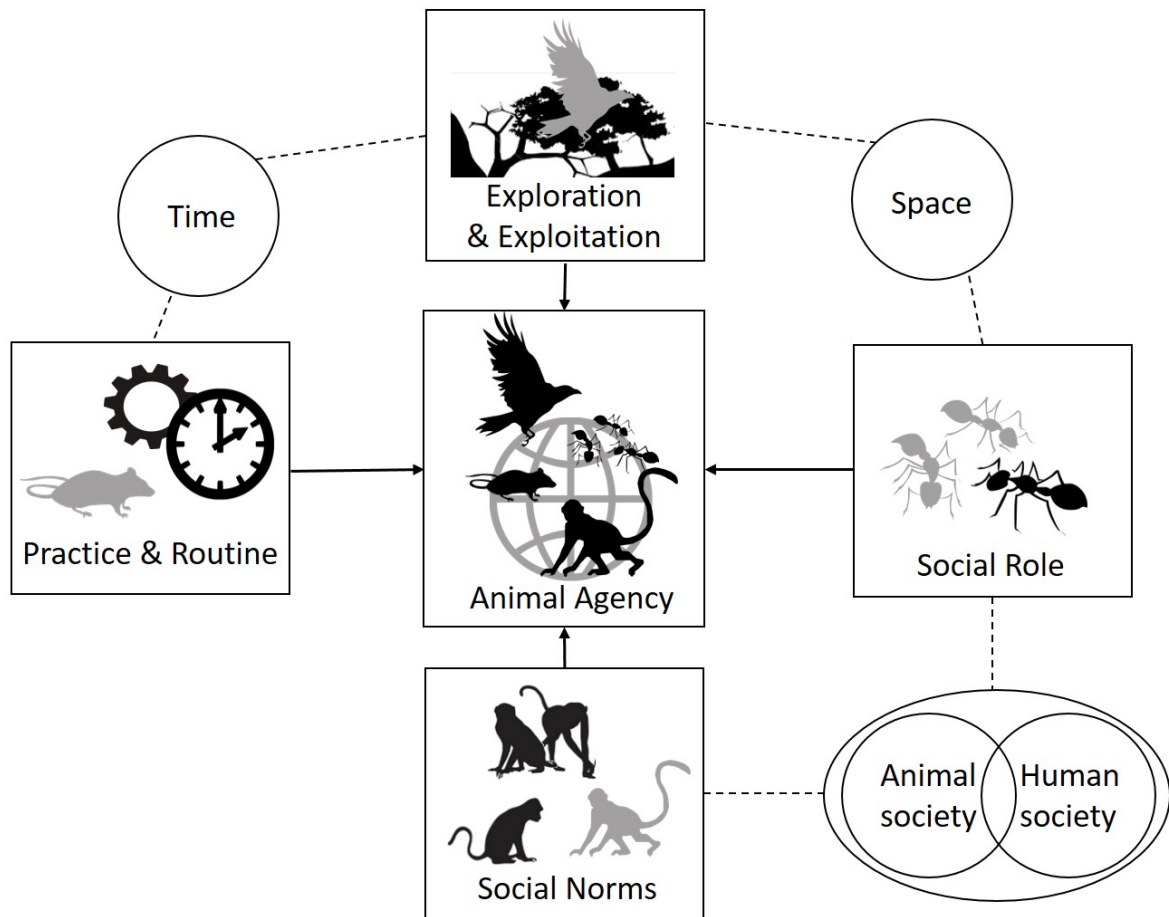
### 207 *3. Agency in the social environment:*

208 A social role is the behavior expected of an individual who occupies a given social position or  
209 status. Individuals understand the place that conspecifics hold in their society (Borgeaud et  
210 al., 2016; Bret et al., 2013; Levé et al., 2016). The adoption of roles that are recognized and  
211 acknowledged by others, and indeed mutually constructed with conspecifics, is an important  
212 dimension of relational agency and a means by which researchers can effectively affirm their  
213 subjective existence within a community. This role can be intraspecific or interspecific. Roles  
214 of individuals inside their group have been amply described in terms of dominance (policing  
215 behaviors, protecting groups), kinship, and maternal relationships (Krause & Ruxton, 2002).  
216 Individuals also develop strong relationships when they share similar attributes, such as sex  
217 or age (Abeyesinghe et al., 2013; Massen & Koski, 2014; Rault, 2012; Silk, 2002; Tsuji et al.,  
218 2007). These affiliative but interspecific relationships are used in the case of animal  
219 mediation and zootherapy where dogs, cats, and horses respond to the pain of patients, not  
220 only passively but also proactively by initiating for instance play sessions (Chouinard, 2021;  
221 Muschel, 1984). With time, these mediation animals developed strong relationships with  
222 certain patients. When doing tests, researchers also know which pairs of individuals can  
223 easily be tested together or not. Group members influence each other (Duboscq et al., 2016)  
224 and can transmit important information to others (Grampp et al., 2019). Social learning can  
225 aid animals learning to use experimental apparatus or spaces (Biro et al., 2006; Whiten,  
226 2011). This works in many vertebrate species and even in invertebrates: fruitflies (*Drosophila*  
227 *sp.*) are able to learn from their conspecifics where to lay eggs and bumblebees (*Bombus*

228 *terrestris*) learn to pull a string to obtain food when interacting with another bumblebee that  
229 does so (Alem et al., 2016; Battesti et al., 2015; Pasquaretta et al., 2016). Biased attention of  
230 group members towards dominant or older individuals in some species (Grampp et al., 2019)  
231 might be used by researchers to make animals more rapidly or more efficiently learn a new  
232 behavior. By influencing the leaders, researchers can manage the movements of an entire  
233 group (Ramos et al., 2018, 2021).

#### 234 4. Agency through social norms:

235 Social norms are the customary rules that govern behavior in groups and societies (Bicchieri  
236 & Muldoon, 2011). Behavioral rules and social systems are partly genetic in animals but are  
237 also transmitted through learning (Brent et al., 2013; Krause & Ruxton, 2002; Sinha, 2005;  
238 Sueur, 2015; Ward & Webster, 2016). There is a debate as to whether animals have social  
239 norms, but all theorists agree that social norms require a social maintenance constraint,  
240 such that other group members care whether an individual follows the pattern or not  
241 (Andrews, 2020a; Fitzpatrick, 2020). This might be the case in animal collective decisions  
242 (Sueur et al., 2021). Although collective decision processes are species-specific, variations  
243 are observed between groups and individuals of the same species. The roles played by  
244 individuals can lead to a strong leadership or the development of a more democratic  
245 process, such as voting (King & Sueur, 2011). Voting systems (Pennisi & Giallongo, 2018) are  
246 described in many species, reinforcing the idea of agency. A sense of community (Blattner et  
247 al., 2020) seems to exist in chimpanzees and cetaceans (*Cetacea*), and indeed animals of  
248 many species know exactly who belongs or does not belong to their group.



249

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

252

253 These different instances show that animals have agency over their spatial, temporal, and  
 254 social environment. Animals can therefore be viewed as *agents*; their choice to act has direct  
 255 consequences on their environment, or they can also resist conditions that do not please  
 256 them and act accordingly to change them (Carter & Charles, 2013). The behavior that  
 257 animals show, the facial expressions they display, and the places they occupy are cues to  
 258 indicate their intentions as well as their stress. By observing these intentions and/or stress,  
 259 researchers could use animals' agency to improve their welfare and to obtain more robust  
 260 experimental results whilst extending the scope of behavioral and neuroscience research to  
 261 more natural conditions. Indeed, a major challenge facing behavioral neuroscientists today is  
 262 to measure the behaviors and the neuronal activities of sentient animals in natural  
 263 conditions. We have to keep in mind that in the research process, some of the limitations

264 shown by the animals are actually the limitations of the scientific methods, rather than the  
265 animals themselves (Savage-Rumbaugh et al., 2006). This is particularly the case with visual  
266 cognition (Hopper et al., 2021; Jacob et al., 2021) and auditory cognition (Calapai et al.,  
267 2022) with new systems allowing significant advances in testing animals. Similarly, De Waal  
268 (2006) argues, about studies with apes (*Hominidae*) aiming to examine their theory of mind:  
269 'All that most experiments have done thus far is test the ape's theory of the human mind.  
270 We would do better to focus on the ape's theory of the ape mind', (p. 70). Following the  
271 concept of animal agency, this paper proposes a future research framework to work with  
272 animals and progress in research.

273

#### 274 **Evidence that animals have agency**

275 Many animals (mammals, birds, and other classes) possess the neural substrates involved in  
276 emotions and consciousness (Ben-Haim et al., 2021; Low et al., 2012). Authors have argued  
277 that nonhuman animals may evidence several aspects of cognition that until recently were  
278 attributed to humans but not other animals. For example, rats, apes, macaques (*Macaca*  
279 *sp.*), and pigeons (*Columba livia*) may be capable of metacognition, i.e., knowing if they are  
280 wrong or right in a test (Le Neindre et al., 2017, 2018). Cetaceans and apes may be conscious  
281 of their own existence, and that of others (Gallup et al., 2002). Cleaner fish may have some  
282 elements of self-awareness (Kohda et al., 2019). Apes may know what their conspecifics  
283 know (Kaminski, Call, & Tomasello, 2008) and believe (Krupenye et al., 2016). Apes (De Waal,  
284 2012) and rats (Ben-Ami Bartal et al., 2011) may experience empathy. Finally, some apes  
285 may have a sense of morality (De Waal, 2006; Jensen et al., 2007; Tomasello & Vaish, 2013).

286 Of course, there remains debate on how to interpret behavioral studies when it comes to  
287 the cognitive capacities we listed above (Bekoff & Allen, 1997; Buckner, 2011; Sober, 2009),  
288 and we need to be careful about how to interpret these results (Janson & Byrne, 2007;  
289 Péron, 2012). Whilst some individuals show the particular capacities in some experiments,  
290 other members of the same species fail in other studies or replications (Boyle, 2021; Voelkl  
291 et al., 2020, 2021), thus proving the importance of comparative methods to investigate  
292 these phenomena (Krasheninnikova et al., 2019; Schmitt et al., 2012). Moreover, there is no  
293 need to have these specific cognitive capacities to be an agent according to some views of

294 agency (Carter & Charles, 2013). Methods used by ants to find resources are used as an  
295 algorithm for the traveling salesman problem (Dorigo & Gambardella, 1997a, 1997b). In both  
296 illustrations, the organisms are not only an inspiration for researchers to resolve a problem,  
297 they resolved it with their own capacities in their own world. In that sense, both can be  
298 considered as co-creators of the new knowledge, even if they are not aware of it. Accepting  
299 this paradigm of co-creation of knowledge can create new research questions that are  
300 different from those made under an anthropocentric view.

301 More and more, researchers showed that animals may have previously unrecognized  
302 cognitive capacities by changing their way of thinking from an anthropocentric approach,  
303 looking for human-like cognition to hypothesizing that animals can think in a way different  
304 from how humans do (Andrews, 2020b; Birch et al., 2020; De Waal, 2016). For instance,  
305 some species do not respond to mark on themselves when looking in a mirror (Gallup et al.,  
306 2002) but do respond in a self-directed manner, suggesting a sense of self, when researchers  
307 presented stimuli in a sensory modality relied upon by the particular animal, such as the  
308 sense of smell for dogs (Cazzolla Gatti, 2016) or hearing in gibbons (*Nomascus leucogenys*)  
309 (D'Agostino et al., 2017). As the same way for mirror and face recognition, researchers  
310 presented to gibbons and dogs respectively vocalizations and odors of themselves and  
311 observed how they reacted compared to vocalizations and odors of conspecifics. Merleau-  
312 Ponty had already noted this problem in his *Causeries* back in 1948: researchers usually do  
313 not try to understand animals in their singularity, *as they are*, but rather in comparison with  
314 human beings, projecting what are essentially human characteristics onto animals (Merleau-  
315 Ponty, 2017). However, this is a means to measure the distance between human beings and  
316 other animals rather than a tool allowing a real understanding of how animals live and  
317 express a subjective existence (Sueur et al., 2020; Sueur & Pelé, 2017; Tokuyama et al.,  
318 2012). Studied in the light of human normative references, animals always lack something  
319 (Merleau-Ponty, 2017). For as long as animals are studied from a human perspective and are  
320 tested in terms of human problems (capacity to count, to draw, to speak a human language)  
321 instead of their own questions and problems, they will always respond 'as they can'  
322 (Canguilhem, 1992), without ever being able to fully express their agency. However, there  
323 have been philosophical and anthropological attempts to blur the boundaries between  
324 humans and other animals (Andrews, 2020b; Böhnert & Hilbert, 2018; Daly Bezerra de Melo,

325 2012, 2018; De Waal, 2016; Langlitz, 2020; Wendler, 2020). As Jacques Derrida wrote in *The*  
326 *Animal That Therefore I Am* (2008), the traditional scientific and philosophical discourse on  
327 animals observes and speaks of non-human animals but never really engages with,  
328 experiments *with*, or gains experience with the latter (Derrida, 2008): this type of discourse  
329 can therefore only position animals as mere passive objects of the theoretical knowledge  
330 these disciplines build. Such methods are completely blind to the animals' own processes of  
331 interacting with their world (Derrida, 2008), and are completely blind to their agency.  
332 Animals interact with the world in their own ways and these ways, i.e. their agency, are  
333 precisely the view that researchers need to adopt to perform better research and develop a  
334 better understanding of how the brain and behavior evolve.

335

## 336 **Future research framework**

337

### 338 1. *Testing agency from the laboratory*

339 Some studies, especially in the biomedical or physiological/cellular domains, cannot be  
340 performed outside the laboratory. It is important for these experiments to respect the 3Rs  
341 (Replace, Reduce, Refine) but also to think about the Bateson cube (Bout et al., 2014),  
342 meaning that scientists need to evaluate the ethical acceptability of their research for  
343 society as a whole, including animals. Bateson's cube is a model of the cost–benefit analysis  
344 for animal research in which research protocols are evaluated through three criteria: the  
345 degree of animal suffering, the quality of the research and the potential applied or  
346 fundamental benefit. The principles can be extended by testing animals in correct  
347 conditions, meaning in conditions not leading to strong false negatives or strong false  
348 positives. Overly standardized laboratory conditions, for instance, decrease the replicability  
349 of studies by decreasing behavioral variability; this is commonly known as the  
350 standardization fallacy (Voelkl et al., 2021; Würbel, 2000).

351 Indeed, laboratory conditions for nonhuman primates and rodents were standardized for  
352 many years in terms of husbandry and diet, in order to support comparisons across  
353 experiments and laboratories. However, this way of conducting research is criticized today  
354 because the conditions in which animals live have a strong effect on them, and thus on the

355 scientific results, so studies of animals in narrow conditions provide results relevant only to  
356 those narrow conditions. Moreover, it is difficult to replicate conditions across laboratories,  
357 specifically in studies about comparative cognition because of a large variance of  
358 physiological, behavioral or cognitive traits between individuals (Boyle, 2021). Indeed, it is  
359 first difficult to replicate same group living conditions in terms of animal density, group  
360 composition, conditions which have an impact on cognitive capabilities (Meguerditchian et  
361 al., 2021), but even when it is possible, animals that are genetically similar and live in similar  
362 environments develop different personalities (Bierbach et al., 2017). Lastly, poor husbandry  
363 conditions stress individuals (Cait et al., 2022; Pomerantz et al., 2022) and do not allow them  
364 to express their full agency. Indeed, sociality has an important impact on the health of  
365 animals, and a large number of publications highlight the link between sociality and health  
366 aging (Boyer et al., 2019; Lacreuse et al., 2020; Rosati et al., 2020). Enabling animals' social  
367 agency can even reverse cognitive decline and extend longevity (Baker et al., 2012;  
368 Richardson et al., 2020; Wild et al., 2021). Sociality is an important part of animal agency and  
369 social life of animals has to be respected even in laboratory conditions, for their welfare as  
370 well as for the robustness of scientific results.

## 371 2. ... To the wild or at least in more natural conditions

372 Traditional approaches to studying for instance visual cognition or decision-making involve  
373 bringing animals into a laboratory and restraining them while they perform tasks in order to  
374 ensure accurate measurements, for example, of gaze-tracking and neural activity (see for  
375 instance D'Souza et al., 2021; Honda et al., 2021). However, this unnatural setting does not  
376 permit the study of brain activity during natural, social, and complex behaviors (Testard et  
377 al., 2021). Many discoveries about ants' behavior could not be made if not in natural  
378 conditions (Dussutour & Wystrach, 2022) as the one showing that the termite-hunting ant  
379 (*Megaponera analis*) is capable of saving injured individuals by taking them back to the nest  
380 (Frank et al., 2017). Ideally, experimental settings will permit animals to move normally and  
381 to engage in natural activities, such as foraging and in social interactions, but this requires  
382 that animals accept to wear some devices, not tear off some cables or even just come at the  
383 right place at the right time. Culture of animals also have to be considered and for instance,  
384 study of percussive tools by nonhuman primates, known from field observations, has been  
385 difficult to achieve in the laboratory. Laboratory studies of this phenomenon (e.g., Bril et al.,

386 2009) have been less numerous than field experiments, that have been very productive (e.g.,  
387 Biro et al., 2006; Leca et al., 2007; Visalberghi et al., 2009). In the same way, field  
388 experiments or experiments close to natural conditions led to important results in  
389 understanding foraging strategies in bees (*Apidae*) (Pasquaretta et al., 2017) and  
390 hummingbirds (*Trochilidae*) (Bateson et al., 2002). Several authors highlight that studying  
391 animals in nature instead of in the laboratory provides more easily interpretable findings  
392 (Cauchoix et al., 2017; Kumpan et al., 2020; Verhaeghen et al., 2012). Specific ethical  
393 guidelines exist now for behavioral or psychological research in the wild (Costello et al.,  
394 2016; Soulsbury et al., 2020). The likely benefits and possible negative effects of researchers'  
395 presence and field methods on study subjects, their environment, and the local human  
396 community should, of course, be considered (MacKinnon & Riley, 2010).

397 Progress has to be made first to avoid restraining animals in a captive environment and  
398 second, to conduct tests on animals in more natural conditions. Such processes are applied  
399 today to not only different primate species (Huebner et al., 2018; Schofield et al., 2019; Van  
400 de Waal et al., 2013) but also to horses (Maeda et al., 2021; Matsuzawa, 2017), birds (Aplin  
401 et al., 2015; Shaw, 2017), and even bees (Muth et al., 2018). These studies, conducted on  
402 different species all showed that testing in the wild is more productive than testing in the  
403 labs in terms of ecological and social cognition (Pritchard et al., 2016). An intermediate  
404 method would be research in zoos. Zoos provide more adequate living conditions than many  
405 laboratories. This seems to allow animals to express their agency (McEwen et al., 2022).  
406 Testing these same species in more natural and more complex captive habitats or even in  
407 natural settings could enhance the possibility of them expressing their agency.

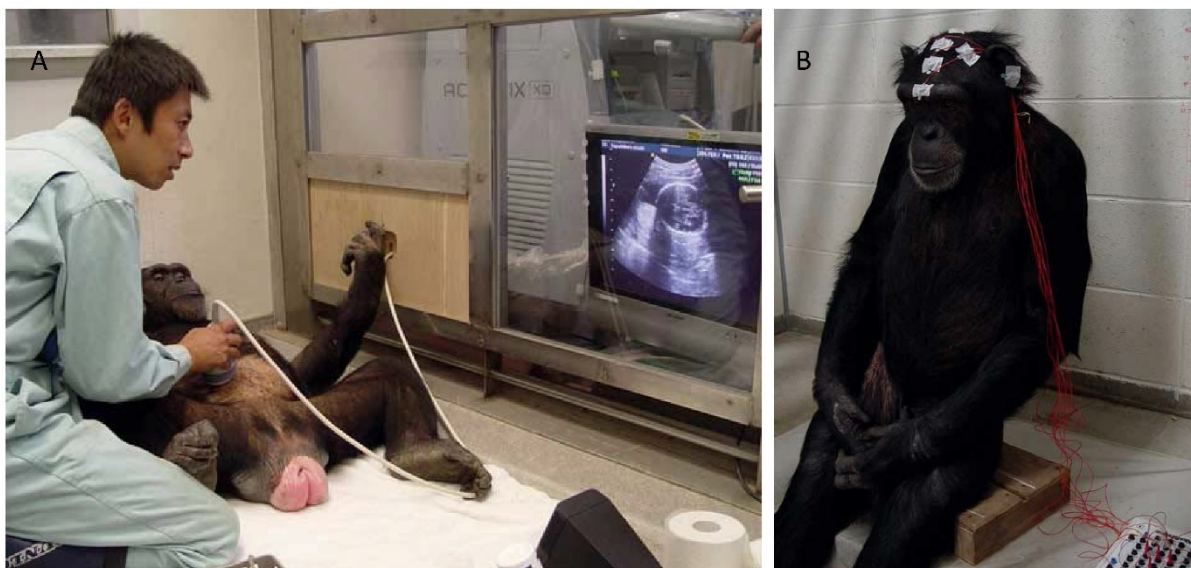
### 408 *3. Agency promotes the use of new technologies and vice-versa*

409 Researchers need to change their way of thinking to a perspective of working *with* animals  
410 rather than *on* animals. Researchers need to trust their capabilities (Nielsen, 2018; Nielsen,  
411 2020) in order to increase research possibilities. Experimental setups, such as restraint chairs  
412 or food privation, cause stress to animals and prevent them (both physically and mentally)  
413 from fully expressing their agency. This challenge of giving animals more freedoms may  
414 certainly takes time but would be hugely beneficial. Van Patter and Blattner (2020) suggest  
415 core principles to follow with animals: non-maleficence, beneficence, and voluntary  
416 participation (Webb et al., 2019). Positive methods exist and have proved to be efficient



417 (Laule et al., 2003; Prescott et al., 2010; Prescott, 2016; Prescott & Buchanan-Smith, 2003;  
418 Prescott & Buchanan-Smith, 2007; Schapiro et al., 2003). Use of cooperation handling in  
419 macaques instead of chair restraint leads to a diminution of stress, decreases the use of  
420 sedation and increases behavioral acquisition (Graham et al., 2012). The readiness of  
421 chimpanzees (which are no longer used for invasive experiments – Matsuzawa, 2016b) to  
422 voluntarily participate in interactions or allow humans to observe them can facilitate the  
423 measurement of embryo development and brain activities in unanesthetized and  
424 unrestrained individuals (Figure 2 - Matsuzawa, 2013; Sakai et al., 2011, 2012; Ueno et al.,  
425 2010). Unrestrained or minimally restrained and voluntary animals can be trained to put  
426 their head in a mask voluntarily (Slater et al., 2016) and be tested whilst receiving fruit juice.  
427 This allows the measurement of different metrics with eye tracking (apes: Kano &  
428 Tomonaga, 2009; Krupenye et al., 2016; monkeys: Machado & Nelson, 2011; Ryan et al.,  
429 2019) and non-invasive neuroimaging (Basso et al., 2021) (Figure 3.A). Magnetic resonance  
430 imaging (MRI) requires the subject to remain still during the scan. Dogs can be trained to  
431 remain still during fMRIs without any restriction (Berns & Cook, 2016). Surely, this  
432 cooperation can be achieved with other species, allowing testing emotions and cognitive  
433 capacities as done with humans (Cheng et al., 2010; Eisenberger et al., 2003; Yang et al.,  
434 2022; Yates et al., 2021).

435



436  
437 Figure 2: (A) Developmental neuroscience. Fetal brain development in chimpanzees was  
438 measured by a non-invasive ultrasound technique. (B) EEG recordings in a chimpanzee. The

439 chimpanzee quietly sat on the chair and allowed the experimenter to put electrode patches  
440 on the skin of her forehead and the top of her head. Photos provided courtesy of Satoshi  
441 Hirata.

442

443 Touchscreens are useful tools that demonstrate agency in nonhuman animals. Individuals  
444 have to learn by themselves how to solve visual problems. Software running the displays and  
445 data collection systems are easy to adapt to individuals' cognitive capacities and perception.  
446 Researchers can measure different parameters (time of answering the test, success, type of  
447 answers) for each individual and species. The possibility of more freedoms of action can  
448 produce individual and group specificity. For instance, Claidière et al. (2014) gave a task to  
449 baboons (*Papio papio*) where they have to click on red squares on a 4\*4 squares matrix.  
450 Instead of forcing animals to answer specific patterns, the authors took into account how  
451 baboons succeed to click on some patterns to transmit these patterns to other baboons and  
452 showed evidence of cultural transmission in baboons as in humans. Some years ago,  
453 applying the use of touchscreens with nonhuman animals, or studying mouse personality  
454 was almost unimaginable in neuroscience. Yet today, these projects have become reality. For  
455 instance, the use of a touchscreen was initially difficult but eventually, use of this testing  
456 method led to tests of new concepts more quickly than tests without touchscreens in  
457 chimpanzees (Gao et al., 2018; Inoue & Matsuzawa, 2007; Martinet et al., 2021) and  
458 macaques (Ballesta et al., 2021; Ferrucci et al., 2019; Huskisson et al., 2021). In the same  
459 vein, it took time for naïve capuchins (*Sapajus sp.*), macaques (*Macaca sp.*), and apes (*Pan*  
460 *troglydytes*, *Pongo pygmaeus abelii*) to understand a food – for - food exchange task (Dufour  
461 et al., 2007; Pelé et al., 2009; Pelé et al., 2010; Ramseyer et al., 2006), but once the behavior  
462 was acquired, it was easily transmitted from adults to their young (Pelé, personal  
463 observation). Touchscreens or joysticks are now used to understand cognition (Kaneko &  
464 Tomonaga, 2011) in a wide range of species (pigs – *Sus scrofa*, macaques, baboons – *Papio*  
465 *papio*, marmosets - *Callithrix jacchus*, goats, horses, rats, mice – *mus musculus*, etc.) (Belsey  
466 et al., 2020; Calapai et al., 2022; Claidière et al., 2017; Croney & Boysen (2021); Jacobson et  
467 al., 2019; Tomonaga et al., 2015; Washburn et al., 2004; Yang et al. 2022; Zeagler et al.,  
468 2014). Researchers trained archerfish (*Toxotes chatareus*) to spit on a touchscreen and  
469 showed that they are able to differentiate human faces (Newport et al., 2016). However,

470 touchscreen technology is still limited despite its potential and even if more and more  
471 neuroscience studies have been using it in mice or rats (Bussey et al., 1997, 2008; Delotterie  
472 et al., 2015; Slutzky et al., 2010). So, touchscreens and joystick apparatuses promote animal  
473 agency, even though it is in a limited artificial environment. However, these devices can be  
474 extended to the wild and the principle of touchscreen (touching for a visual choice) should  
475 be extended to other senses as it was done for testing auditory capabilities in common  
476 marmosets (Calapai et al., 2022).

477 Other new technologies allow us to bring devices into natural settings to test unrestrained  
478 animals in their natural (including social) environment, thus removing experimental sources  
479 of stress and allowing them agency and expression of their entire behavioral repertoire.  
480 Field experiments of this type are possible in many species including rodents (Evans et al.  
481 2020; Lopes & König, 2020; Raulo et al., 2021). The animals can be identified individually by  
482 observation or by using RFID techniques (Fehlmann & King, 2016) or via artificial intelligence  
483 with the recognition of individuals by video tracking (Charpentier et al., 2020; Ferreira et al.,  
484 2020; Schofield et al., 2019). The latter removes the need to capture animals. RFID  
485 techniques allowed demonstration, for example, that bats (*Myotis bechsteinii*) form long-  
486 term social relationships (Kerth et al., 2011) and that tits (*Parus major*) learned according to  
487 their social networks (Aplin et al., 2015). Face and behavioral recognition using artificial  
488 intelligence gave some indices about social networks in chimpanzees (Schofield et al., 2019)  
489 and signaling kinship in mandrills (*Mandrillus sphinx*) (Charpentier et al., 2020). It could also  
490 be extended to theory of mind and intentionality as gaze-following (Horschler et al., 2020) or  
491 false belief attribution (Krupenye et al., 2016).

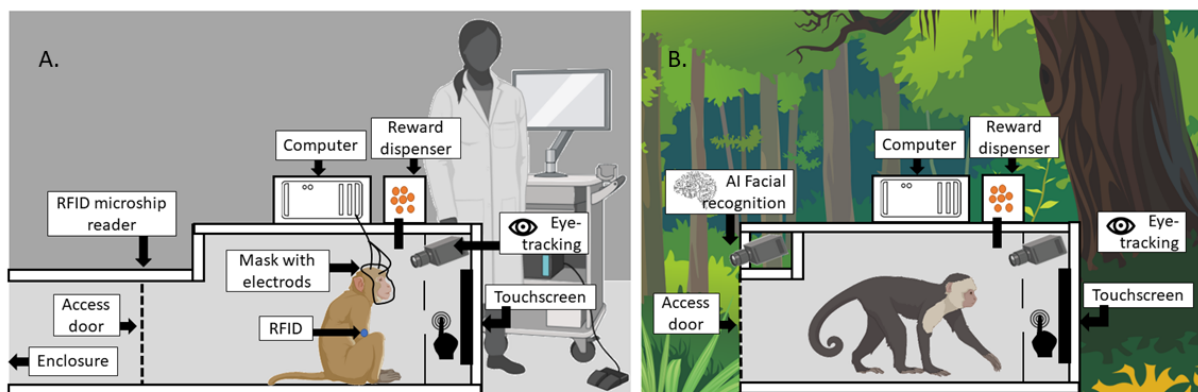
492 A general idea of how a laboratory- bound experimental method could be adapted for use  
493 in a field experiment is given in Figure 3.B. A location is defined where different operable  
494 devices can be installed, such as touchscreens, to deliver food or another valuable  
495 commodity, with activation only for certain species and individuals. Researchers can imagine  
496 implementing eye tracking and other apparatus in the wild when technology permits. This  
497 could open up new research avenues in species that cannot be maintained in captivity.

498 Some automatic devices already exist to make some playback experiments as BoomBox: An  
499 Automated Behavioral Response (ABR) camera trap module for wildlife experiments (Palmer  
500 et al., 2022). Food containers of various kinds, have been used in field experiments (De la

501 Fuente et al., 2022; Van de Waal et al., 2013) and robots are increasingly used with wild  
502 animals (Grémillet et al., 2012; Le Maho et al., 2014). Research possibilities in this domain  
503 are huge.

504 Although there are logistical challenges attendant on any new methodology, we should  
505 consider how to take advantage of technological advances to bring our science to animals in  
506 natural settings, while ensuring the health and security of the animal participants. As  
507 Schaefer and Claridge-Chang (2012) wrote, ‘the new automation is not just faster: it is also  
508 allowing new kinds of experiments, many of which erase the boundaries of the traditional  
509 neuroscience disciplines (psychology, ethology, and physiology) while producing insight into  
510 problems that were otherwise opaque’ (p. 170). Figure 3 illustrates a hypothetical system for  
511 conducting eye tracking while an individual voluntarily operates a touchscreen apparatus, in  
512 the laboratory and in field settings.

513



514

515 Figure 3: (A) Hypothetical non-invasive neuroimaging and eye-tracking system with  
516 touchscreen interactive component and voluntary participation in the laboratory. (B)  
517 Hypothetical touchscreen system with voluntary engagement and individual identification in  
518 the field. In setup A, the subject would show better agency than if it was restrained in a  
519 chair. However, the same subject in setup B would show greater agency than in setup A, as it  
520 is free to express its entire behavioral repertoire in natural conditions. The box is needed to  
521 assure the isolation of the tested individual and the resistance of the materials to outside  
522 conditions. This figure was realized using FAVPNG.com and Biorender.

523

524 **Conclusion**

525 Great efforts have been made toward enabling the agency of animals in behavioral research  
526 but there is still much progress to be made to obtain a more compassionate, less stressful,  
527 and more robust animal research model. This requires training and teaching researchers to  
528 adopt new methods including animal agency and to change their view of the role animals  
529 play in research (see for instance the book “Handbook of Primate Behavioral Management”  
530 Schapiro, 2017, for methods to achieve voluntary participation of primates in various health-  
531 related and husbandry procedures). Animals are agents in scientific research. They are active  
532 in the research process and agency may promote the use of new technologies. This  
533 recognition of animals as agents rather than objects is not approved by some researchers,  
534 who consider that this position is tantamount to committing over-anthropomorphism, and  
535 overstepping the will of animals to cooperate. However, acknowledging animal agency could  
536 facilitate broader social acceptance of research with nonhuman animals (Webb et al., 2019)  
537 and be of benefit to the animals concerned (supporting well-being through learning,  
538 creating, and participating – Franks et al., 2020).

539 Considering the agency of the animals we work with is clearly a time investment that  
540 ultimately pays off for more time-efficient data collection in the long term. This time  
541 investment in animal agency should be highlighted and recognized as promoting animal  
542 welfare (in the same way as plans for adoption research animals, for instance) when  
543 readying a proposal for financial support. This new way of viewing animal agency can  
544 therefore raise critical ethical questions in regard to the treatment of animals in research  
545 and to the place humans grant them in the human social world.

546

547 **Author Contributions Statement**

548 Conceptualization: CS and MP; Project administration: CS and MP; Writing original draft: CS;  
549 Review and editions: all authors.

550

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554

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