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Incorporating animal agency into research design could improve behavioral 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, and exhibit agency in their behavior, many animals are still restrained and forced to take part in applied or fundamental research. However, these restraints and procedures, because they stress animals and because they limit the expression of adaptive behavior, may result in compromised findings. Researchers should alter their research paradigms to understand mechanisms and functions of the brain and behavior so that the paradigms incorporate animals' agency. 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 about behavior and brain evolution.

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

Introduction

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

and then getting its head out from the chair) (McMillan et al., 2017). These protocols are used to obtain results in behavioral or neuroscience research but are problematic for several reasons. Beyond the ethical issues of such restraints for animals, these examples of experimental setups lead us to consider which possibilities and results have yet to be investigated and more importantly, whether such compulsory protocols could lead to false negatives or false positives (Chang et al., 2017; Huttunen et al., 2017; Liu et al., 2017). False negatives or false positives mean that studies show respectively negative (not expected, H0) or positive results (expected, H1) but these results are not due to the tested condition (e.g. a drug, a gene, an environmental condition) but to uncontrolled factors (e.g. stress, personality). Indeed, stress and coercion (i.e., the animal is immobilized and restrained in an apparatus, such as a chair for primate or a box or a system of collars for rats or dogs) can not only modify some behaviors but also entirely prevent others from being displayed (Lecorps et al., 2021; Mason et al., 2019; Prescott, 2016). Some authors, such as Van Patter, Blattner, Matsuzawa, King and McMillan consider that the current 3R framework is not sufficient to ensure that animals are meaningful participants in experiments, which is crucial to guarantee that scientific results are not altered by stress or personality of animals (King, 2021; Matsuzawa, 2016a; McMillan et al., 2014; Van Patter & Blattner, 2020). Studies carried out on animals under restraints offer few meaningful opportunities for them to show their full behavioral and cognitive capacities, and in this way to exercise agency with their environment and in their relationships, both with each other and with humans (*Homo sapiens*) (Blattner et al., 2020). Gillespie (2019) 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...’ (p. 19). According to Blattner et al. (2020), 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’ (p. 1).

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

evidence that students are being taught to think of animals as objects; that is the method (Andrews, 2020b) used to defend the claim that comparative cognition eschews the study of consciousness. 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.). In this way, 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.

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

Animal agency

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

Blattner et al. (2020) investigate animal agency in a sanctuary for rehomed farm 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 animals of many species living in this sanctuary. For the owners of the sanctuary and the researchers, the sanctuary is an 'integrated multispecies community or society whose members shape spaces and practices together, take on recognized social roles, and create and transmit social norms across species lines'. Blattner et al. (2020), De Waal (2016),

Le Neindre et al. (2017, 2018), and Meijer (2019) affirm that researchers need to spend time in community with animals, learn from them, and be prepared to respond and adjust scientific learning process through relationships with them. This means that animals should no longer be considered as the subjects of scientific experiments, but rather as participants – that is, as agents (Haraway, 1989). For example, when it comes to assessing cognitive abilities, 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 scientist (Pepperberg, 2006).

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

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

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

1. Agency through space and time:

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

Modifications of the environment can be used to shape animals' decisions and can remove some of the negative reinforcement that is still applied to animals. For example, 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 increase the power of the study to detect experimental effects (Coe & Hoy, 2020; Matsuzawa, 2020). Of course, this statement implies that the housing of animals should be designed to take advantage of animals' preferences and adjustments to features of their environment. For example, boundaries and fences cannot be only considered as barriers and limitations of freedoms but also as security and communication touchstones as suggested by Blattner et al. (2020) or Grandin (1987, 1989). Humans should create barriers and fence placements according to the behavior of animals. Similarly, for behavioral experimental apparatus, animals should not be forcibly brought to where researchers want to test them but researchers should observe animals to determine the best position to place the devices.

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

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

2. Agency through practice and routine:

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

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

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

3. Agency in the social environment:

A social role is the behavior expected of an individual who occupies a given social position or status. Individuals understand the place that conspecifics hold in their society (Borgeaud et al., 2016; Bret et al., 2013; Levé et al., 2016). The adoption of roles that are recognized and acknowledged by others, and indeed mutually constructed with conspecifics, is an important dimension of relational agency and a means by which researchers can effectively affirm their 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 behaviors, protecting groups), kinship, and maternal relationships (Krause & Ruxton, 2002). Individuals also develop strong relationships when they share similar attributes, such as sex or age (Abeyesinghe et al., 2013; Massen & Koski, 2014; Rault, 2012; Silk, 2002; Tsuji et al., 2007). These affiliative but interspecific relationships are used in the case of animal mediation and zootherapy where dogs, cats, and horses respond to the pain of patients, not only passively but also proactively by initiating for instance play sessions (Chouinard, 2021; Muschel, 1984). With time, these mediation animals developed strong relationships with certain patients. When doing tests, researchers also know which pairs of individuals can easily be tested together or not. Group members influence each other (Duboscq et al., 2016) and can transmit important information to others (Grampp et al., 2019). Social learning can aid animals learning to use experimental apparatus or spaces (Biro et al., 2006; Whiten, 2011). This works in many vertebrate species and even in invertebrates: fruitflies (*Drosophila* 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.

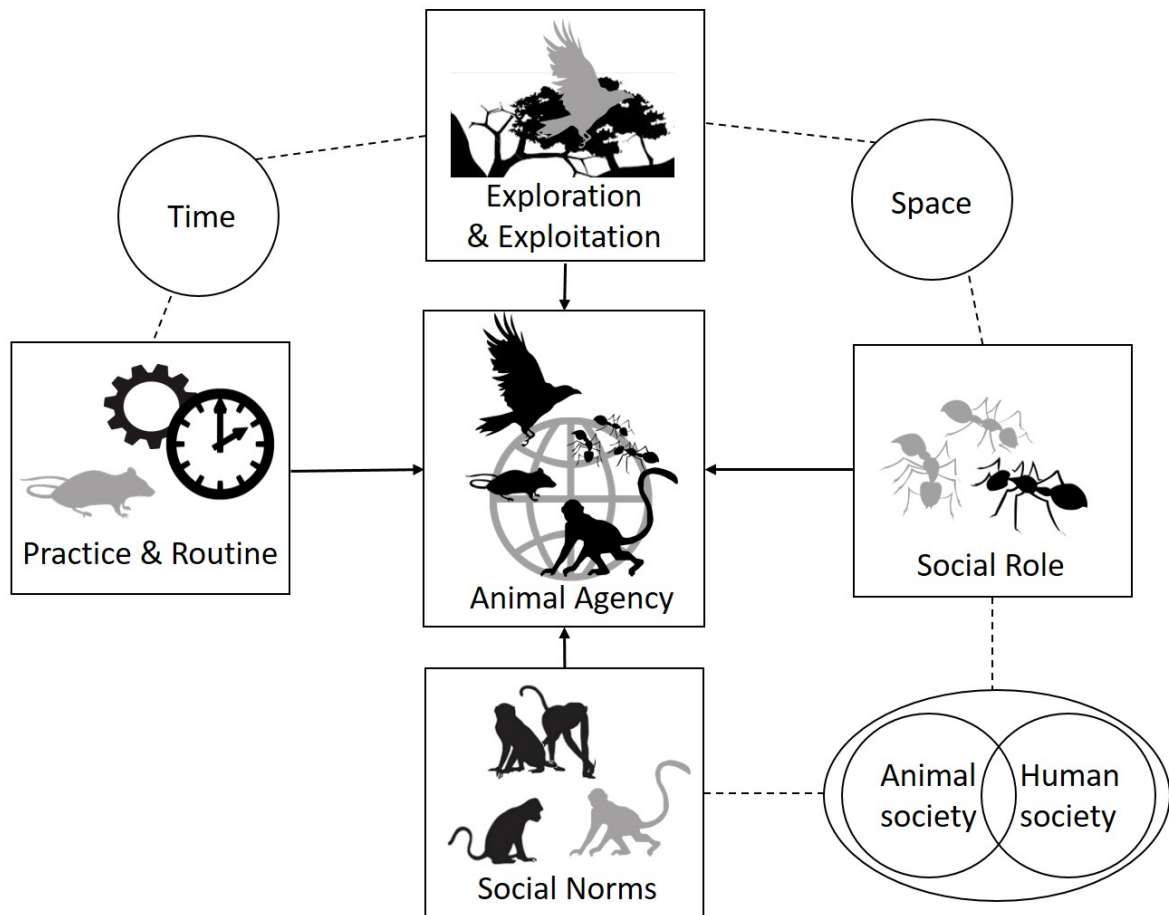


Figure 1: The four schemes of animal agency (squares) and the environmental factors affecting them (circles).

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 them (Carter & Charles, 2013). The behavior that animals show, the facial expressions they display, and the places they occupy are cues to indicate their intentions as well as their stress. By observing these intentions and/or stress, researchers could use animals' agency to improve their welfare and to obtain more robust experimental results whilst extending the scope of behavioral and neuroscience research to more natural conditions. Indeed, a major challenge facing behavioral neuroscientists today is to measure the behaviors and the neuronal activities of sentient animals in natural conditions. We have to keep in mind that in the research process, some of the limitations

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

Evidence that animals have agency

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

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

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

More and more, researchers showed that animals may have previously unrecognized cognitive capacities by changing their way of thinking from an anthropocentric approach, looking for human-like cognition to hypothesizing that animals can think in a way different from how humans do (Andrews, 2020b; Birch et al., 2020; De Waal, 2016). For instance, some species do not respond to mark on themselves when looking in a mirror (Gallup et al., 2002) but do respond in a self-directed manner, suggesting a sense of self, when researchers presented stimuli in a sensory modality relied upon by the particular animal, such as the sense of smell for dogs (Cazzolla Gatti, 2016) or hearing in gibbons (*Nomascus leucogenys*) (D'Agostino et al., 2017). As the same way for mirror and face recognition, researchers presented to gibbons and dogs respectively vocalizations and odors of themselves and observed how they reacted compared to vocalizations and odors of conspecifics. 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 what are essentially human characteristics onto animals (Merleau-Ponty, 2017). 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 (Sueur et al., 2020; Sueur & Pelé, 2017; Tokuyama et al., 2012). Studied in the light of human normative references, animals always lack something (Merleau-Ponty, 2017). 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' (Canguilhem, 1992), without ever being able to fully express their agency. However, there have been philosophical and anthropological attempts to blur the boundaries between humans and other animals (Andrews, 2020b; Böhnert & Hilbert, 2018; Daly Bezerra de Melo,

2012, 2018; De Waal, 2016; Langlitz, 2020; Wendler, 2020). As Jacques Derrida wrote in *The Animal That Therefore I Am* (2008), 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 latter (Derrida, 2008): 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 world (Derrida, 2008), and are completely blind to their agency. Animals interact with the world in their own ways and these ways, i.e. their agency, are precisely the view that researchers need to adopt to perform better research and develop a better understanding of how the brain and behavior evolve.

Future research framework

1. Testing agency from the laboratory

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

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

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

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

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

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

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

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

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

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



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 courtesy of Satoshi Hirata.

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

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

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

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

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

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

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

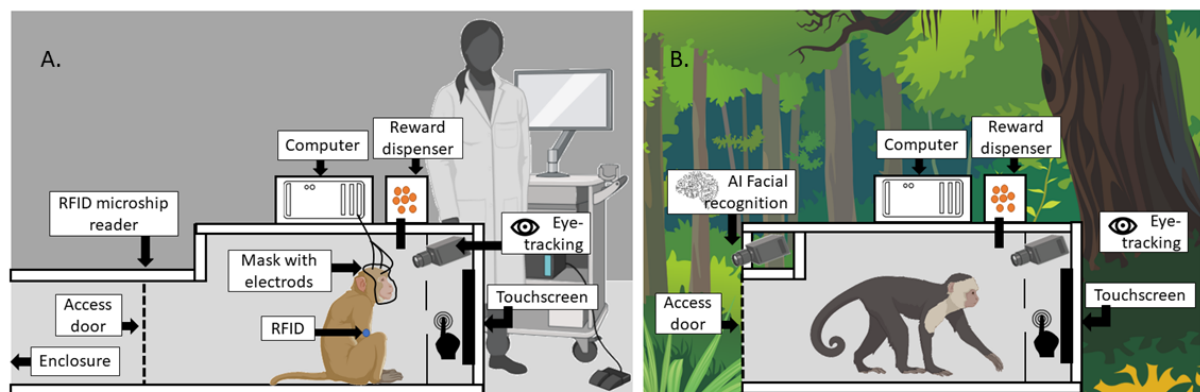


Figure 3: (A) Hypothetical non-invasive neuroimaging and eye-tracking system with touchscreen interactive component and voluntary participation in the laboratory. (B) Hypothetical touchscreen system with voluntary engagement and individual identification in the field. In setup A, the subject would show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

Conclusion

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

Considering the agency of the animals we work with is clearly a time investment that ultimately pays off for more time-efficient data collection in the long term. This time investment in animal agency should be highlighted and recognized as promoting animal welfare (in the same way as plans for adoption research animals, for instance) when readying a proposal for financial support. 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 humans grant them in the human social world.

Author Contributions Statement

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

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