

Review: Rethinking environmental enrichment as providing opportunities to acquire information

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Review: Rethinking environmental enrichment as providing opportunities to acquire information



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ABSTRACT

Environmental enrichment, that is making the environment of animals more complex, was first designed to enhance the welfare and cognitive abilities of captive animals, and was more recently applied to farm animals. Enrichments can be sensory, physical, social, occupational, feeding-based, or a mix of these, with a view to improve animals' welfare. We posit that enrichments share the common factor of providing information to animals so that enrichment is all about providing the animal with a way to acquire information by interacting with the environment. Animals enjoy acquiring information, and the process of acquiring information acts in a way that enables them to better adapt to future environments. This reframed view of enrichment has several implications including prolonging the duration of exposure to an enrichment does not necessarily increase the impact of that enrichment, neutral and even slightly negative stimuli may still be enriching, complex and variable environments are enriching, and the more intensively an animal can engage with the environment, the more it will benefit from enrichments. These implications should be further explored by comprehensive re-analyses of findings from the enrichment literature and/or by dedicated experiments.

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Implications

We posit that environmental enrichments act on animals by providing them with opportunities for active acquisition of information. Enrichment strategies should thus aim to provide captive animals (in zoos, labs, or farms) with complex environments that vary in time and that encourage voluntary engagement from the animal. Enrichments that are added to enclosures should therefore be changed regularly. There should also be regular checks that animals are interested in enrichments and interacting with them. If challenges are used as enrichments, they need to fit the animals' behavioural and cognitive skills.

Introduction

The benefit of enriching the environment of animals was acknowledged in laboratory rodents and captive primates from the early 20th century. After the finding from Hebb (1949, cited by Gardner et al., 1975) that rats reared as pets in homes performed better in a maze than rats reared in cages, environmental

enrichment was used as a model for studies in experimental psychology. In parallel, Yerkes (1925, cited by Shepherdson, 2003) recommended that captive animals are positively occupied with play and work. The concept of environmental enrichment was then applied to all animals whose welfare is compromised by the barrenness of their environment, whether zoo, laboratory or farmed animals (Dean, 1999; Grandin, 2023; Tavares et al., 2023).

Laboratory or farmed animals are generally fed according to their physiological and possibly their behavioural needs, and housed in secure environments where their health is closely monitored and managed. However, these animals can still suffer welfare deficits. Poor environments can lead to repetitive behaviours or 'stereotypies', boredom, and ultimately depression (Wemelsfelder, 1993; Mason et al., 2007), all of which points to the fact that their environment is lacking something.

The concept of environmental enrichment embraces adding features to the animal's 'home' environment, such as the company of other animals, structuring the environment into separate functional areas, or adding natural or artificial devices, all with the aim of providing sensory stimulations and opportunities to express behaviour (Shepherdson, 2003). Environmental enrichment can have observable benefits. In the short term, it reduces the occurrence of abnormal behaviours: it reduces jumping stereotypies in bank voles (Odberg, 1987) or non-nutritive oral activities in calves

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(Zhang et al., 2022a), promotes species-specific behaviours (Wiedenmayer, 1997), and can generate positive emotions that translate into optimistic cognitive bias (Brydges et al., 2011; Douglas et al., 2012). In the long term, environmental enrichment can help animals cope with their environment: animals reared in complex environments (housed in groups and with objects to interact with) are often more curious (more ready to explore novel items), quicker to acquire tasks in conditioning designs, and better able to memorise information than animals reared in socially or perceptually poor environments (Gardner et al., 1975; Zhang et al., 2022b).

Adding stimulations in the animal's environment and encouraging natural behaviours may not always improve animal welfare (discussed by Mason et al., 2007; Dawkins, 2023). For instance, adding predator cues to trigger flight is unlikely to improve the welfare of a prev animal. Several options to enrich the environment of animals often get tried before adequate solutions are found (reviewed by Shepherdson, 2003 for zoo animals; van de Weerd and Day, 2009 for farmed pigs). In this paper, we question what makes an enrichment enriching for an animal. The answer to this question should help further design of (effective) enrichments. We start with a rapid description of the various ways to enrich the environment and their effectiveness on animals. We then analyse the commonalities of enrichments. This leads us to propose that enrichment is all about the acquisition of information by the animal. We then go on to discuss the implications of this reframed view of enrichment.

Various ways to enrich the environment

There are several ways to enrich the environment of animals. They are traditionally described as (Bloomsmith et al., 1991; Mandel et al., 2016):

- sensory enrichments,
- physical enrichments,
- enrichments that encourage exercise,
- cognitive enrichments,
- feeding-based enrichments (Bloomsmith et al. (1991) and Mandel et al. (2016) use the term 'nutritional enrichment'. However, because it comprises both what food is provided and the way it is provided, we prefer to use 'feeding-based enrichment'),
- social enrichments (intra- or inter-specific).

One way of enrichment does not exclude others. For instance, new food items can provide both feeding-based enrichment and sensory enrichment, a new food delivery system can provide both feeding-based and exercise, the possibility of seeing conspecifics can provide both sensory and social enrichment, it is difficult to separate physical enrichment from other ways of enrichment, etc. In the next paragraphs, we address the various ways of enrichment in order to get a broad view of what is considered as an enrichment. Whether the modification of the environment proposed as enrichment is enrichment will be discussed later.

Sensory enrichments

Sensory enrichments are designed to stimulate one or more of the animal's senses (Bloomsmith et al., 1991; Wells, 2009). They may include visual, auditory, olfactory, tactile or taste stimulations, alone or in combination. Some sounds, odours or images (e.g. using mirrors) can have calming effects, reducing agitation and increasing sleeping. For instance, classical music reduces stress in dogs (Bowman et al., 2015) and increases sleeping and decreases stereo-

typic behaviours in horses (Huo et al., 2021) and lavender odour reduces motility in rats (reviewed by Wells, 2009). Other sounds, odours or images can have stimulatory effects, encouraging activity and seeking to approach the source of the stimulus. Examples include country music in cows (Uetake et al., 1997), moving a laser light pointed on the ground in poultry (Lourenço da Silva et al., 2023), and peppermint and rosemary odours or moving pictures in several species (primates, mice, dogs, chickens, reviewed by Wells, 2009). Finally, some sensory stimuli can be perceived as stressful. Examples include loud sounds such as human shouting or metallic sounds (Waynert et al., 1999; Pajor et al., 2000), or the odour of a predator for a prey animal (discussed in Wells, 2009).

Natural stimuli may not necessarily be more effective than artificial stimuli. Captive monkeys in zoos are more interested by the sound of music than the sound of rainforest (discussed in Wells, 2009). In her review on sensory enrichment, Wells (2009) concluded that the effectiveness of sensory enrichment varies with species and individuals. More specifically, Wells (2009) concluded that an enrichment should be more effective if it targets the dominant sense of the species, but it does not need to be linked to the species' natural habitat, and that the stimuli must not be harmful or stressful to animals. How long the animals show interest in stimuli should also be considered, because habituation to new stimuli often can occur within a few days (e.g. in 2 days in Waynert et al., 1999; Bowman et al., 2015), thus limiting the enrichment effect.

Physical enrichments

Physical enrichment corresponds to enlarging an animal enclosure or providing additional devices (objects or substrates) (Bloomsmith et al., 1991). Enlarging enclosures and adding partitions to segregate functional areas may encourage patrolling activities and allow subordinate animals to avoid dominant ones and in turn reduce aggression (discussed in Mandel et al., 2016). Indeed, low-ranked goats are less disturbed by dominant goats during feeding when they are housed in an enclosure containing partitions, platforms and niches than when housed in a conventional enclosure (Aschwanden et al., 2009). Adding items to an animal enclosure can stimulate exploration. For instance, piglets housed in pens containing straw, logs, branches, peat, and other items spend more time exploring the environment (and not only the items added) than piglets reared in barren pens and are less aggressive to each other (Petersen et al., 1995). Animals reared in such enriched environments appear to be more adaptable. For instance, piglets reared in an environment enriched with substrates are less neophobic, as they are more inclined to eat new foods (Oostindjer et al., 2011). Similarly, hamsters reared in complex cages (i.e. several interconnected cages containing objects) are able to use more cues to solve tasks than hamsters reared in standard cages: When having to discriminate between objects of different sizes, they use not only the width of objects but also their surface area to check which object is larger (Thinus-Blanc, 1981).

Enrichments that encourage exercise

Enrichments that encourage exercise make the animal walk, run, or do any other physical activity. Exercise can be enhanced by providing access to larger enclosures (which can also be considered as a physical enrichment) or, for aquatic species, by modifying water flow. For instance, horses housed in stalls and regularly released in a paddock where they can exercise freely are less prone to display abnormal repetitive behaviour (Lesimple et al., 2020), and farmed fish in which swimming activity has been stimulated

by increasing the water flow show decreased levels of blood cortisol, which suggests better welfare (Palstra and Planas, 2011).

Cognitive enrichments

Enrichment can be achieved by stimulating the cognitive abilities of animals. Animals are not just able to solve tasks to access a resource, they also appear to actively seek out such task challenges. For instance, goats that can obtain water by pressing a button after solving a discrimination task continue to perform the task even when it is no longer necessary (Langbein et al., 2004). Cognitive tasks have essentially been developed for non-human primates, e.g. using computers (reviewed by Clark, 2017), but training animals on simple cognitive tasks has nevertheless been proposed as a means of enrichment for various species (reviewed by Fernandez, 2022). For instance, shelter cats initially rated as frustrated received training that shaped their behaviour towards holding paw-hand contact with the researcher apparently enjoyed such training (jumping out of their enclosure and freely walking to the training room) and their mood changed towards less frustration and apathy and more contentment (Gourkow and Phillips, 2016).

Feeding-based enrichments

Feeding-based enrichments embrace the provision of new or varied foods or new feed delivery methods or devices that increase the diversity of foods or the means to obtain them (Bloomsmith et al., 1991). Allowing lambs to choose between foods or varying the foods they are given during the day increases food consumption and reduces the occurrence of repetitive abnormal behaviour compared to always providing the same food (Garrett et al., 2021). Similarly, horses provided two feeds instead of just one spend more time eating and display fewer abnormal behaviours (Thorne et al., 2005). However, some animals may prefer monotonous food to varying foods or varying tastes of their food. Heifers that choose a monotonous food over alternative foods are also more neophobic in a novel object test, suggesting that the benefit of varying the food may be individual-dependent (Meagher et al., 2017), probably depending on the genetic background and the previous experience of the animal. Slow feeders can be used to increase time spent eating, which is usually far longer in natural than captive conditions. Slow-feeders include devices like haynets, large tubes with holes from which hay can be grasped, cylinder delivering pellets when the animal moves it,... Hay-nets have been successfully used with horses to increase time spent eating and reduce abnormal behaviours (Correa et al., 2020).

Social enrichments

Social enrichment refers to contacts with conspecifics or partners from other species, including humans (Bloomsmith et al., 1991). Opportunity for social interaction is very important for social species like farmed animals (e.g. ruminants, pigs, poultry some fish species). However, such animals may be housed individually or with only limited social interactions, as is the case for many dairy calves in their 1st weeks of life. Young animals appear to be particularly sensitive to the social environment. Social interactions, first with their dam and then with other conspecifics, are important for the young animal to develop its social and cognitive skills. Isolation during infancy can make animals less able to recognise and understand social cues, resulting in more aggressivity and impaired maternal behaviour (Melo et al., 2006; Toth et al., 2011). Isolation also increases behavioural reactivity to stressful events and favours anxiety-like behaviours and reduces cognitive abilities, especially during reversal learning (reviewed in Costa et al.,

2016). Individually housed animals will be calmer and display fewer abnormal behaviours when they can have physical and visual contacts with close neighbours via open walls: for instance, horses that can see their neighbours display less abnormal repetitive behaviour (Cooper et al., 2000). Contacts with handlers may play a social enrichment role, especially when contacts with conspecific are absent. Goat kids and piglets that receive positive human contacts are not only more attracted by humans but also less reactive during an isolation test (goat kids and piglets) and more ready to explore novel objects (piglets), suggesting that the contacts with humans affected their general emotionality (Boivin and Braastad, 1996; Lucas et al., 2024).

Why is an enrichment enriching?

Environment improvement vs environment enrichment

In the previous section, we reviewed ways to enrich the environment of animals. There is no point to make an extensive catalogue of enrichments. Rather one should identify the very nature of enrichment to be able to design enriching strategies. According to Newberry (1995), any 'improvement in the biological functioning of captive animals resulting from modifications to their environment' is an enrichment. Building on this definition, Taylor et al. (2023b) considers three levels of environmental enrichment: 1- Enrichments to meet the basic needs of animals, 2- Enrichment to provide pleasure to animals, 3- Enrichment for a positive welfare balance on the long term, leading to improved animal resilience, whereby resilience implies increased flexibility and ability to adapt to challenge. These three levels correspond to increasing levels of welfare permitted by the enrichment, suggesting that any welfare improvement is an enrichment. There is then a risk of devaluing the concept of enrichment, i.e. some environments could be described as rich when they only meet the basic needs of animals, because they improve on a previous situation where basic needs were not met. We thus question what differentiate the concept of enrichment to that of other solutions to improve welfare. We assume that enrichment has specific properties linked to the complexity of the environment and the stimulation of individuals (Shepherdson, 2003; Pritchett-Corning, 2020), as initially introduced in the early 20th century as a way to improve animal's cognitive abilities (Gardner et al., 1975). We therefore focus on enrichments that Taylor et al. (2023b) described as environments leading to increased resilience.

The various ways to enrich the environment described in the previous section stimulate animals in different and apparently unrelated manners. The only common denominator seems that enrichments induce a change in the environment (something is added to the environment) perceived by the animal and thus provide information to animals. Information corresponds to 'knowledge about facts or ideas gained through investigation, experience, or practice' (American Psychological Association, 2018). For the purpose of this paper, we propose to define 'information' for animals as stimuli that the animal perceives and can somehow process.

All environmental enrichments provide animals some kind of new information:

- sensory information (in the case of sensory enrichment): animals can get to know the properties of new stimuli, e.g. that some sensorial stimuli are associated with certain positive or negative consequences (e.g. a brush with a pleasant tactile contact vs a loud noise associated with a hit (Pajor et al., 2000)), or are neutral (e.g. laser light pointed on the floor (Lourenço da Silva et al., 2023));

- information about the environment or feeds (in the case of physical or feeding-based enrichments): animals can acquire information about properties of new objects or new feeds by sniffing, manipulating, biting, and so on;
- information about consequences of the animal's behaviour: clearly the case with a cognitive enrichment based on learning a task to obtain a reward (or to avoid a negative situation) but probably also the case when young animals play (see below);
- information about other individuals (conspecifics or from other species) and the consequences of interactions with them can be acquired in the case of social enrichment.

Enrichments provide opportunities to acquire information

Animals seem to be interested in acquiring information so that enrichments encourage engagement with the environment to obtain information. Enrichment items prompt various behaviours in animals, most commonly exploration. Items added to the environment or structuring the environment (with partitions, platforms,...) generally induce inspective exploration, i.e. the animal explores changes in its environment. Inspective exploration fades when the situation loses its novelty. Enrichment can also stimulate inquisitive exploration, i.e. the animal acts to obtain information (see Wood-Gush and Vestergaard, 1991 for discussion on the various forms of exploration). Inquisitive exploration has been demonstrated in piglets that preferentially enter a pen where they know a novel object is hidden compared to a pen where a familiar object is hidden, and preferentially explore and spend more time in contact with the novel object (Wood-Gush and Vestergaard, 1991). Exploration can be stimulated by sensory enrichments that animals are not expected to respond to or act on. Signs of this tendency to interact with sensory stimuli can be found in cows that more readily approach a milking parlour when they hear country music (Uetake et al., 1997) or chicks that peck at a laser beam pointed on the floor (Lourenço da Silva et al., 2023) even though these stimuli have no apparent biological significance. In both these examples, the tendency to approach the stimuli does not seem to fade with time, which suggests inquisitive exploration. Evidence suggests that beyond the significance of what is being explored, exploration is itself intrinsically rewarding. This is corroborated by the fact that rats explore ambiguous arms of a radial maze despite knowing which arms unambiguously led to a food reward; in other words, they prefer exploring over obtaining a reward (Franks et al., 2013).

Animals may also interact intrusively with enrichments. This is evidenced by the type of objects that attract pigs. When objects are included in their environment, pigs are first more interested in odorous, deformable and chewable objects, then after a few days, they become more interested in ingestible and destructible objects (Van De Weerd et al., 2003). This suggests a transition from inspective exploration on the first day (sniffing, chewing) to actively seeking more information, i.e. inquisitive exploration, thereafter (looking for more information by e.g. ingesting or destroying the object). Animals will also interact with new social partners. Calves, for instance, exchange essentially gentle interactions such as sniffing, licking and rubbing as well as some aggressive interactions such as fighting and butting with other calves they have just been mixed with (Veissier et al., 1994). It is likely that these interactions allow the animal to get information on conspecifics: who they are (based on sensory cues such as odours or the sight of physical characteristics) and how they behave.

In the case of cognitive enrichment, animals interact with devices to solve tasks. They can press buttons, touch screens, or do whatever is needed to get the task solved. There is evidence that during this process, the animal is interested not only in obtaining a reward (food in general) but also in the task-solving process itself;

in other words, in knowing that they performed correctly. For instance, during medical training, a click sound is often associated with food and the animal is rewarded with the click sound and the food when it behaves 'correctly', such as accepting to be approached, then touched, then examined, etc. After a while, the click sound is often enough to tell the animal that it is behaving correctly, suggesting that the animal finds it rewarding to know that it is performing correctly. This interpretation should be tested by looking at the exact behavioural and emotional response when the animal hears the click and by disassociating the click from the food reward. A more striking example of this phenomenon is found in monkeys presented with puzzle-feeders of increasing difficulty to obtain tasty pellets: the monkeys will not always eat the pellets before moving on to the next task, appearing more interested in solving the task than in the reward (Watson et al., 1999). The rewardingness of getting information that tell the animal it is correctly performing a task is confirmed by signs of excitement in the event of success and continuing to work to obtain a reward even if they can get the reward freely without work. Contrafreeloading, i.e. the preference for a food that requires some effort to obtain, rather than a food that is freely available, is thought to allow the animal to check that performing the task still allows to get the reward (Inglis et al., 1997). Contrafreeloading has been observed in many species, including farm animals, such as goats working to obtain water (Langbein et al., 2009) or heifers working to obtain roughage (Van Os et al., 2018).

Enrichment of the environment encourages play behaviour, especially in young animals. For instance, calves given access to large enclosures show erratic locomotor movements, often with several calves jumping, kicking and galloping, then suddenly interrupting their movements and continuing in another direction (Jensen, 2000). Play can also be a way for the animal to acquire information. Spinka et al. (2001) assert that "animals actively seek and create unexpected situations in play through self-handicapping; that is, deliberately relaxing control over their movements or actively putting themselves into disadvantageous positions and situations". Animals may thus learn the consequences of such situations and find out how to resume balance and control of their movements.

Animals can thus engage with the environment in different ways to acquire information: they can move towards stimuli, approach, explore, interact, play, or solve tasks. There may be other ways of interaction that may be difficult to identify by simple observation, such as drawing attention to stimuli without moving.

Enrichments develop further processing of information

Third, acquiring information prepares animals for future life. By acquiring information, animals learn the properties of their environment. For instance, when they are reared with conspecifics they can learn the rules that govern social life. However, this learning of specific properties of the environment does not seem to be the most important effect of enrichment. Enrichment is known to stimulate behavioural flexibility. It reduces neophobia and thus stimulates further tendency to seek information. For instance, rats or hens reared in a physically and/or socially enriched environment explore maze arms more readily than their counterparts reared in barren environments (Franks et al., 2013; Taylor et al., 2023a). Similarly, piglets reared in an environment containing wood shavings, straw bedding, peat and branches are more ready to eat new foods than piglets reared in a barren environment (Oostindjer et al., 2011). Acquiring information is also likely to enhance an animal's cognitive abilities. Animals reared in enriched environments perform better at solving tasks. For instance, when reared in a cage where environmental complexity was increased by adding levels connected with ramps, a shelter, a running wheel

and various other objects, rats performed better in various maze paradigms (Leggio et al., 2005). The enriched rats showed greater memory capacity than rats reared in standard cages: in a radial maze, they better memorised the arms that they had already visited within a session and the arms where food has been provided during previous sessions. The enriched rats also adopted more efficient strategies to find their way in a maze: they made 45° turns more often in an 8-arm-radial maze and took more direct routes to find a platform in a Morris water maze. Finally, the enriched rats were quicker to change strategy in response to a change in maze configuration. These changes are not specific to rats. Calves reared in an environment enriched with several features (brushes, chains, teats, hay nets) are better-memorised objects than calves reared in a barren environment (Zhang et al., 2022b). The higher cognitive performances of animals reared in rich environments appear to be related to the stimulation of brain development, i.e. enhanced cell proliferation and connectivity in the cortex, nucleus accumbens, hippocampus, amygdala, and hypothalamus (Leggio et al., 2005; Malone et al., 2022). These modifications suggest that enrichment also acts on information processing later in life. The precise mechanism connecting environmental enrichment to brain development has not been fully elucidated, but we assume that by stimulating the acquisition and processing of information by the animal, enrichment drives changes in the brain that in turn go on to shape cognitive abilities.

Our thesis is that enrichment works by providing stimuli from which the animal acquires information. The acquisition of information, especially when active, provides pleasure (in the short term), and cognitive processing of this information acts on brain development to confer further behavioural adaptability (in the long term) (Fig. 1).

Implications of understanding enrichment as providing opportunities to acquire information

In the previous section, we formulated the heuristic hypothesis that enrichment is all about information acquisition. If this hypothesis is valid, then:

- An enrichment is effective even when limited in access-time
- Not only positive but also negative stimuli can be enriching
- More environment complexity will be more enriching
- Variable environments are enriching
- Engagement of the animal is essential
- Natural and artificial stimuli can be enriching
- The effectiveness of enrichments depends on the balance between curiosity and neophobia

We consider an enrichment to be enriching — i.e. effective — if it has an impact on the animals' further ability to adapt to their environment by increasing their tendency to explore and their ability to learn. (memorisation, efficient strategies, flexibility...).

We now turn to test our hypothesis, i.e. that enrichment is all about information acquisition, against evidence of the above implications.

Implication 1: an enrichment is effective even when limited in accesstime

If enrichment is about acquiring information, then we assume that animals do not need to be permanently exposed to an enrichment to benefit from it, i.e. they would only need sufficient time to explore and interact with the enrichment to get to know it. Indeed, rats that were placed for 30 days in an enriched environment containing various objects (ten objects among which three were chan-

ged each day) are more ready to explore novel objects than rats reared in a poor environment, and this effect was observed regardless of whether the rats were exposed to the enrichment all day long or only for 2 h per day (Widman and Rosellini, 1990). However, there is likely to be a minimum period of exposure required for enrichment to be effective and this may also depend on when the exposure occurs in relation to sensitive periods.

Implication 2: not only positive but also negative stimuli can be enriching

If it is the acquisition of information itself that is important to animals, then both positive and negative stimuli should be enriching. Most of the enrichment literature is based on providing animals with pleasant or neutral stimuli. We expect enrichment by a negative stimulation to be efficient if the individuals can easily cope with that stimulation, i.e. if mild stressors are used. To find evidence of this, we need to look at the literature on chronic stress, but it tends to be based more on repetitions of strong stressors rather than mild ones. However, there is an experiment run by colleagues from our group (Boissy, personal communication) who set out to design a chronic stress protocol that would not be very aversive. In this protocol, sheep were kept in groups on large enclosures covered with straw, and the 'stress' treatment applied repeated events where the sheep were moved to new pens, the litter of the pen was wetted, the delivery of food was delayed, and so on. The researchers expected the 'stressed' sheep to become hyperreactive to new situations. But what they actually observed was that the 'stressed' sheep approached the researcher in a reactivity test more readily than the control sheep did. Presumably, the control sheep had been more stressed - because the environment they were reared in was too poor - than the sheep exposed to the 'stress' treatment. We thus assume that the mild stress treatment acted as an enrichment. Evidence that stress is not necessarily bad can also be found in the literature on human psychology. Stress resulting from challenges at work can have a positive effect - if the individual overcomes the challenge - whereas stress resulting from obstacles at work has a negative effect (Boswell et al., 2004). The ability to cope with a situation seems to determine whether the situation can be enriching or not.

Implication 3: more environment complexity will be more enriching

The complexity of an enrichment depends on the number of features necessary to describe it (Sambrook and Buchanan-Smith, 1997), i.e. the number of objects or structures added to an enclosure, the complexity of these objects (e.g. a simple cube vs a complex object made up of different parts of different sizes and shapes), the variety of sensory stimuli, the number of social partners, and so on. We assume that the more complex an environment, the more enriching it will be. Indeed, complexity stimulates exploration. Calves showed more exploration behaviour in an environment that contained five objects together (brushes, ropes, strings, hay net, dry teats) than only one at a time (Zhang et al., 2022a). Another evidence comes from mink kits who have been offered enrichment objects (balls, rope, chain, pig's ear) in addition to standard objects (plastic rings). These 'extra-enriched' kits explored both the objects and other parts of their cage more than the standard-enriched kits (Clark et al., 2023). More work however is needed to analyse the long-term effects of enrichment complexity.

Implication 4: variable environments are enriching

An enrichment may be effective when the animals first get contact with it, but prolonged contact will have little effect on the

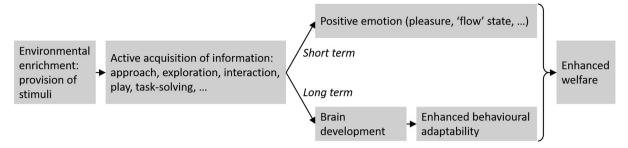


Fig. 1. Action of enrichment on the welfare of captive animals. We posit that enrichment works by providing stimuli from which the animal can acquire information. The acquisition of information, especially when active, provides pleasure (in the short term), and cognitive processing of this information acts on brain development to confer further behavioural adaptability (in the long term). Both are beneficial to animal welfare.

acquisition of further information. We therefore hypothesise that the variability of the environment is a key factor in enrichment because it assures a continuous flow of information acquisition. Evidence of this can be found in cognitive enrichment. As reported above, it appears necessary, at least in primates, to sustain cognitive stimulation by increasing task difficulty in order to keep animals interested (Watson et al., 1999). Another set of evidence can be found in social enrichment on pair-housed 1-year-old heifers: heifers that change partners regularly are less disturbed by and habituate more quickly to unusual events than heifers kept with the same partner (Raussi et al., 2006). This effect was probably obtained because cattle develop links between peers around puberty (Bouissou and Andrieu, 1977) whereas at other stages of the life and in other conditions (e.g. more than two animals mixed) changing partners is stressful and can negatively affect reactivity (e.g. calves that repeatedly get regrouped are hyper-reactive to unusual events (Boissy et al., 2001)). The animals themselves can make their surrounding variable, e.g. by exploring further their environment (discovering new items) or by using an object in a different way (discovering new properties, e.g. using a platform first to climb and then to watch over the surroundings).

Implication 5: engagement of the animal is essential

We expect that an enrichment that stimulates more engagement of the animal will have more impact. There are several levels of engagement: choice, control, challenge, and agency (Englund and Cronin, 2023). Choice refers to the possibility to select from alternatives. The act of choosing seems particularly rewarding: monkeys prefer to choose the order in which they perform tasks rather than be imposed a task order (Perdue et al., 2014). Choice is considered the basic step towards acquiring control, i.e. the ability to predictably and effectively produce a desired result. Animals perceive having control over the environment as positive. For instance, sheep that can control access to pellets by performing an operant task are more calm than sheep receiving the same pellets at the same time but without control (Greiveldinger et al., 2009). The acquisition of control appears especially rewarding (Sambrook and Buchanan-Smith, 1997), presumably because it corresponds to problem-solving, i.e. overcoming a challenge. As we saw earlier in examples from monkeys, cattle, and goats, solving challenges appears to be rewarding. Signs of excitement when animals succeed in a task, qualified as the 'eureka effect' or 'Aha! moment', confirm that getting information telling them they correctly performed a task is important to animals (in cattle and goats: Hagen and Broom, 2004; Langbein et al., 2004; discussed in Hintze and Yee, 2023). Finally, a sense of agency, i.e. the ability to consciously engage in goal-directed behaviours, appears to be important for the welfare of animals (Mellor and Beausoleil,

2015). There is still only scarce literature on agency in animals, but some findings point in this direction: horses, for instance, are much more motivated to freely exercise in a paddock than to be forced to exercise on a treadmill (Lee et al., 2011).

Implication 6: natural and artificial stimuli can be enriching

If it is the process of acquisition of information that is important in enrichment, then enrichments do not need to include or reproduce natural stimuli. Indeed, enrichments can be far divorced from what is found in wild conditions. Artificial objects can be attractive: a laser beam is more attractive to chicks than hay (Lourenço da Silva et al., 2023), a bicycle tyre, a silver-coloured plate, a pile of newspaper, and a rubber boot are all attractive to pigs (Wood-Gush and Vestergaard, 1991), and brushes, ropes, and springs are attractive to calves (Zhang et al., 2022a), but none of these objects are part of natural environments. Computer technology is increasingly being used to propose cognitive enrichment in the form of tasks or problems to solve (Clark, 2017), and again, these tasks are far from what is found in nature. Therefore, an enrichment does not need to be natural in order to be enriching.

However, there may still be connections between enrichments and natural behaviours. Indeed, carnivores and omnivores investigate their environment more than herbivores do (discussed in Sambrook and Buchanan-Smith, 1997), presumably due to the greater effort they have to invest in order to find their food. Consequently, carnivore and omnivore species might be more sensitive to variability and complexity of their environment than herbivore species. Furthermore, the way the animal interacts with an enrichment – e.g. with their hands, their nose, or any other part of their body – connects to their 'natural' way of exploration. For instance, we expect primates to interact with their hands but pigs to interact with their nose and mouth.

Implication 7: the effectiveness of enrichments depends on the balance between curiosity and neophobia

If enrichment is about acquiring information from the environment, then it is linked to curiosity, a trait that is an opposite of neophobia (Špinka and Wemelsfelder, 2011). Špinka and Wemelsfelder (2011) use 'agency' to refer to the actively seeking information; here, we use 'curiosity' to refer to this trait, so as to avoid confusion with other definitions of agency (as described above). Curiosity has a cost. When expressing curiosity, the animal expends energy and takes risks (e.g. eating the wrong food, being injured...). Conversely, neophobia is a mechanism that protects the animal against potential unknown harms. In the example reported earlier on heifers offered alternative foods in addition to their normal monotonous food during short periods, the heifers

that preferred varying food were also those that as calves were more ready to approach novel objects – in other words, those that were more curious than neophobic (Meagher et al., 2017). As discussed by Špinka and Wemelsfelder (2011), animals should express curiosity when the expected benefits are greater than the expected risks. They argue that young animals are likely to benefit more from interacting with their environment than older animals because the time remaining to benefit from the positive impacts of enrichment diminishes with age. Also, animals with higher nutritional needs should be less curious because they are less ready to take risks. For instance, when hay was offered simultaneously in the usual trough and in a new device (a hay net), pregnant ewes displayed neophobia in response to the new food delivery device whereas non-pregnant dry ewes started using the device from the first day (Goncalves-Casaco et al., 2023).

Further thoughts

Our thesis in this review is that environmental enrichment is all about providing animals with opportunities to acquire information from their environment. In our view, it is important to distinguish environmental enrichment from other forms of environment improvement. Environment improvement primarily aims to satisfy animals' needs and preferences, e.g. their preferences for certain foods or certain beddings, and their need to express specific behaviours. Although environmental enrichment and environment improvement appear to be separate concepts, it is likely that when a preferred item is introduced (e.g. a comfortable bedding, some substrate for pigs to root in, or a brush to rub on), it acts both as an improvement and an enrichment (because it is new). However, if the novelty fades once the animals get habituated with the item, only the improvement aspect will remain. The enrichment aspects of an item added to the environment will only remain if the item is not only used to satisfy a need or a preference but also to interact with (explore, play, etc.).

In the first section of this review, some modifications initially considered as enrichments may correspond to environment improvements without enrichment. For instance, adding sensory stimulations that calm animals – such as specific odours (lavender) or sounds (slow music) or pheromones - or that provide possibilities to satisfy behavioural needs - such as the need to walk in tethered cows or suckling in calves – or adding partitions or hiding places that allow subordinate animals to avoid dominant ones, are all cases that operate thanks to their specific biological properties (calming effects, satisfaction of a behavioural need, escape). They should therefore be classified as mere environment improvements. They may also constitute enrichments, especially when they are first introduced. For instance, when a brush is added to a pen, cows usually investigate it (smelling, touching,...) and eventually play with it before they use the brush for scratching on a regular basis, which is a behavioural need. Consequently, modifications of the environment should be considered either as improvements or enrichments depending on the balance between these effects.

Both environment improvement and enrichment contribute to animal welfare. Environment improvement may have direct impacts at the time it is provided to animals. The satisfaction of a behavioural need, e.g. suckling, gives the animal reward at the time as the behaviour is expressed (or soon after). Environmental enrichment, however, appears to have more indirect and delayed effects. Of course, animals appear to enjoy interacting with enrichments (see examples cited in this review about pigs looking for novel objects, calves expressing play in large enclosures, cats walking to a training room, monkeys solving tasks...). However, most of the effects of enrichments extend beyond the time spent in contact with the enrichment. Enrichment appears to equip animals with

skills that they can mobilise later in life to adapt to their environment.

The benefits of enrichment vary between animals. Young animals are likely to benefit more from an enriched environment than older ones, because they are generally more curious (see above) but also because they can gain more benefit from greater brain plasticity (Mora et al., 2007). In addition, when challenges are proposed to animals, the difficulty of the challenges must be adapted to the behavioural and cognitive skills of these animals. A task that is too easy given the animal's intrinsic set of skills will result in boredom, whereas a task that is too difficult may result in anxiety (Špinka and Wemelsfelder, 2011; Clark, 2017). The right balance between task difficulty and animal skills is likely to result in a state of flow. Flow refers to the engagement in an activity for that activity per se, and not the goal it may serve; flow results in a state where an individual animal is 'absorbed' in a rewarding activity (Hintze and Yee, 2023). There is some evidence that flow can be important for animals, but it has not been studied directly in non-humans (discussed by Hintze and Yee, 2023). We believe that enrichment can contribute to a state of flow. Moreover, as the animal gets more skilled after having overcome challenges, enrichment is likely to contribute to animal competence (Hintze and Yee, 2023).

Conclusion

In this review, we posit that enrichment is all about providing opportunities for the animal to acquire information. Enrichment strategies should thus be designed to stimulate the acquisition of information by the animal. These strategies should also be designed based on the animal's willingness and capacities to engage with the environment (through exploration, play, task-solving). Even though negative stimulations may have some enrichment properties, they are to be used with caution so as not to risk stressing the animals.

We identified the implications of our position that enrichment is about information acquisition: To be enriching, an environment must be complex and variable, not necessarily positive or natural, and should stimulate animal engagement. We are aware that each implication warrants its own comprehensive review of the literature – which was not possible in the space of the present review – and would also warrant empirical testing in different settings and species. More specifically further studies should be carried out to determine the minimum time exposure for an enrichment to be effective, the conditions in which negative situations can be enriching, the long-term impacts of environment complexity and variability, the possibilities for animals to make themselves their environment to vary, as well as the relation between animals' agency and temperament and the impacts of complex and variable environment.

Ethics approval

Not applicable.

Data and model availability statement

This article is a review. No data were collected or processed. Information can be made available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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