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Review

Adaptation by learning: Its significance for farm animal husbandry

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Abstract

Farm animals are confronted with major changes in their environment as they go through different phases of the production system. Examples include introduction to a new housing system, provision of a new type of feed, mixing with unfamiliar conspecifics or being exposed to new human handlers. Learning processes that reduce uncertainty in such situations are likely to be very important both for animal welfare and for performance.

The aim of this paper is to describe, from the animal's point of view, situations typical of learning in farm animal husbandry and to provide a framework for assessing the significance of learning processes for farm animal husbandry and welfare. The literature reviewed covers experimental studies into the learning abilities of ruminants, pigs and poultry as well as evidence stemming from applied studies showing problems farm animals may face in situations of change. We argue that knowledge of species-specific learning abilities may help in the design of housing systems and the establishment of management routines that facilitate learning by the animals.

Having searched the literature, we conclude that there is a lack of studies focusing on the initial phase after the introduction of farm animals into a new housing system and on the way they learn to use new housing equipment. Moreover, we suggest that studies into: (a) learning of farm animals during transport and in the slaughterhouse, (b) their motivation to explore the environment and (c) the development of enrichment tasks taking into account their learning abilities may provide solutions to some animal welfare problems.

Keywords: Ruminants; Pigs; Poultry; Learning; Behaviour; Adaptation; Animal welfare

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1. Introduction

When adaptation of farm animals to a given housing system is addressed in papers on animal welfare, it is typically emphasised that the behavioural organisation of domestic animals has been shaped by evolution, resulting in species-specific behavioural needs that have to be considered in the design and management of the housing system. For example, studies into the behaviour of domestic pigs kept in semi-natural enclosures showed that nest-building behaviour is still performed by sows of domestic breeds (Stolba and Wood-Gush, 1984; Jensen, 1989), thus calling into question the housing of sows due to farrow in crates and without provision of straw. Furthermore, experimental studies analysing the behavioural organisation of farrowing sows provided evidence that the sows are highly motivated to have access to nest-building material on the day before farrowing (Arey, 1992) and are stressed if kept in crates and without straw during that period (Lawrence et al., 1994). As a consequence of these results, loose-house systems for farrowing sows have been developed (e.g. Cronin et al., 2000; Weber, 2000). In line with this example, it is generally agreed that farm animal welfare is at a high level when the animals can behave naturally, i.e. in the way their behaviour has been shaped by evolution in adaptation to the habitat of their ancestors, and thereby satisfy their behavioural needs (Fraser et al., 1997; Wechsler, 2007).

The concept of adaptation refers, however, not only to evolutionary adaptation but also to changes in behaviour brought about during the lifetime of an individual animal by processes of learning. Consequently, learning processes should also be considered to assess the animals' ability to adapt to and cope with a given housing system. Wechsler (1995) defined coping as ''behavioural responses that aim at reducing the effect of aversive stimuli on fitness or physiological measures related to fitness''. If the aversive situation can be attenuated or removed by the coping response, this will also lead to a change in the animal's assessment of the situation in terms of emotional states, and alter its future behaviour. As a consequence, successful coping responses will result in learning. The first few hours or days after introduction of a farm animal into a given housing system are thus likely to lead to significant alterations in behaviour due to information that is acquired and processed by the animal. The animal will learn about specific characteristics of its housing environment, and the resulting behavioural modifications can be interpreted as an attempt to optimise its behaviour, both in terms of improving survival and fitness and in terms of trying to achieve positive emotional states and to avoid suffering.

Astonishingly, adaptation by learning has not been paid much attention in the applied animal behaviour literature on farm animals. In the literature search we did in the preparation of this review article, we found only a few studies focussing on the first hours or days the animals spent in a new housing system. Typically, studies assessing the welfare of farm animals in a given housing system begin when the animals are already accustomed to the housing conditions, and this is usually mentioned in the ‘‘Methods section’’ to give assurance that the situation investigated was stable and that the behaviour observed was typical for animals kept in such a housing system. However, this approach neglects processes of learning that take place when animals become familiar with a new environment, and it may even fail to recognise welfare problems that arise specifically during that period. The lack of interest in the initial phase after the introduction of farm animals into a new housing system also contrasts with the scientific interest that has been paid to farm animals that have been released into semi-natural environments in experimental studies on the natural behaviour of domestic animals in the late 1970s. Both with the study on laying hens (Wood-Gush and Duncan, 1976) and the study on pigs (Wood-Gush et al., 1990) a report on the initial phase of the experiment was published, probably because this phase was thought to be critical with regard to the animals' success to fare well in the wild on the one hand, and very informative concerning the animals' ability to cope with a new environment on the other. But why should these aspects not be of special interest when animals are confronted with a new indoor environment?

The aim of this review article is to provide a framework for assessing the significance of learning processes for farm animal husbandry, focussing on ruminants, pigs and poultry. We will first address different aspects that usually have to be learned by farm animals. Secondly, we will discuss possibilities for facilitating learning in order to enhance the animals' ability to adapt to housing conditions. Finally, we set out a number of fields that, in our opinion, are of interest for future research into learning in farm animals.

2. What a farm animal needs to learn

2.1. Learning about sites

Unless animals are tethered or crated, they can move around and use different sites of their housing system for different activities. Current housing systems typically provide different resources in different sites, so the animals are expected to use different areas for resting, feeding, drinking, and comfort behaviour. With poultry, the third dimension may also be important when nest sites and perches are provided at different levels above the ground in aviary systems.

When animals are introduced into such a housing system, they have to learn how the resources are distributed within it. This is probably not a demanding task in the case of weaned pigs moved to a fully slatted fattening pen. However, if the floor of the pen is only partly slatted, it is of much advantage both to the pigs and the farmer if the animals learn to use the slatted part of the pen as a dunging area and the solid floor as a lying area, thus avoiding pen fouling, animal dirtiness, and increased ammonia concentrations (Aarnink et al., 1997). Similarly, it is important that sows due to farrow in loose-house systems choose the place near the heated piglet nest as their nest-site to ensure that the piglets start to use the piglet nest soon after birth, and dairy cows housed in cubicle systems should not lie down in the alleys but choose the cubicles for lying to avoid dirtiness of the udder which may lead to problems with udder health and milk quality.

At first sight, such a differentiation in the use of different areas of a housing system for different activities seems to be trivial. After all, the housing systems were designed to be used in a particular way, and activity and resting areas are labelled on the plans drawn by the architects. Animals, however, do not read architects' plans. There is evidence that there are problems with fattening pigs fouling the pen floor (Randall et al., 1983; Aarnink et al., 1996), dairy cows lying down outside the cubicles (Kjaestad and Myren, 2001), and hens laying eggs outside the nest boxes (floor eggs) (Appleby et al., 1988; Cooper and Appleby, 1996). Consequently, it is worth having a closer look at the learning processes leading to appropriate use of the housing systems as well as at possible constraints on learning responsible for any difficulty animals may find in selecting the right place for a given activity.

Experimental investigations with farm species have shown that they are good at solving tasks requiring spatial memory. For example, Mendl et al. (1997) reported that pigs could remember the location of food across a 2-h retention interval. Edwards et al. (1996) and Dumont and Petit (1998) showed that sheep remembered the spatial location of patches in which they had found food 12 and 24 h previously, and Edwards et al. found that the sheep's performance did not decline when the time between successive visits was increased to 72 h. Similarly, chicks accurately return to the geometric location of food 24 h after training (Tommasi and Vallortigara, 2000). Both chicks and grazing cattle may use long-term spatial memory to return to food locations (Zimmerman et al., 2003; Laca, 1998), and cattle can remember food locations accurately for at least 48 days (Ksiksi and Laca, 2002). Given this evidence, when farm animals do not use a given area of a housing system adequately, it is unlikely that this is because of any difficulty in remembering which site they had used previously to perform a given behaviour. Rather, we have to suppose that the area where a given behaviour has been made possible by the design of the living quarters is, from the animal's point of view, unsuitable in some way.

Firstly, it is possible that the perceptual cues available are inadequate to elicit the required behaviour in a given area. For example, pigs prefer to show eliminative behaviour at sites that are wet and where they can have contact with pigs in a neighbouring pen (Mollet and Wechsler, 1991; Hacker et al., 1994). However, if these environmental characteristics are not limited to a specific area of a pen but can be found at different sites within the pen the pigs will find it difficult to choose a specific site where all members of the group defecate. Similarly, sows due to farrow typically select as a nest site an area with straw bedding and solid walls separating it from neighbouring pens (Arey et al., 1992; Schmid, 1992). In pens where these cues are provided in a specific area supposed to be the nest site they will show eliminative behaviour away from that site. Schmid (1992, 1997) followed the process of selection of a dunging area both in sows due to farrow and in fattening pigs after introduction into new pens and observed that eliminative behaviour is more scattered over the whole pen floor on the 1st day than thereafter, showing that learning does take place.

Secondly, animals may be reluctant to use a specific site within their housing system for a given behaviour because of negative experiences they made on previous use of that site. For example, dairy cows need ample space in front of the lying area in cubicles to make a head swing when standing up (Lidfors, 1989). If large cows are housed in stables with cubicles that are too short, the difficulty of standing up in these cubicles may result in cows lying in the alleys rather than in the foreseen lying place. With pigs, pens may not be used in the way they were designed if there is draught in the lying area; the animals will then tend to lie elsewhere in their housing system (Geers et al., 1986). Finally, sites near to the door of a shed may generally be unattractive to farm animals, as there is a risk of being disturbed every time a human enters the building.

Thirdly, animals may be unable to visit sites intended for a given behaviour. With laying hens, it has been found that rearing chicks without early access to perches impairs the spatial skills they need to reach perches (Fröhlich, 1991; Gunnarsson et al., 2000). This may result in an increased prevalence of floor eggs in adult hens, as they have difficulty in reaching elevated nest boxes (Appleby et al., 1988; Gunnarsson et al., 1999). Similarly, Bircher et al. (1996) reported that turkeys had more and more difficulty in using elevated perches for resting during the fattening period, and this was paralleled by an increase in leg problems.

2.2. *Learning about what to eat*

It is not surprising that farm animal species have innate preferences for food over non-food items, a phenomenon that has been investigated extensively in poultry (Dawkins, 1968). Nevertheless, they do have to learn what they can eat in the environment in which they actually grow up (Hogan, 1973), and there is much experimental evidence in various species that food avoidance learning occurs when animals are given the experience of harmful feed (e.g. cattle: Kronberg et al., 1993; sheep: Burritt and Provenza, 1989; goats: Zahorik et al., 1990; poultry: Hale and Green, 1988); conversely, goats and sheep may learn to eat foods that have a medicinal effect (Rogosic et al., 2006; Villalba et al., 2006).

Several studies with farm animals have shown that social learning may be important for feed acceptance. For example, Fukasawa et al. (1999) reported that calves who could eat a novel food in early ontogeny when housed together with their dam, who was familiar with that food, were more likely to feed on it 12 weeks later than calves without such a social experience. With weaned piglets, the presence of a piglet that is already experienced with eating solid food stimulates food intake of an inexperienced piglet (Morgan et al., 2001). It has also been found that an experimentally induced feed aversion my be overcome by social learning. For example, Ralphs and Olsen (1990) observed that averted heifers started to sample of the formerly avoided feed when paired with non-averted conspecifics, and the aversion was even extinguished in some animals. Similar results were obtained in a study with sheep (Thorhallsdottir et al., 1990).

With fattening ruminants in intensive housing, it is typical that they have to learn to accept food they would not eat in their natural environment. For example, Chapple et al. (1987a) observed how sheep learned to eat wheat and reported that it took up to 14 days until a sheep began eating this feed. In this case too, sheep learned the new type of feed faster if they were grouped with conspecifics who were experienced in eating wheat (Chapple et al., 1987b).

Another problem farm animals may face is that the food they are offered changes suddenly; this is often the case when animals are weaned or translated from rangeland to intensive housing for finishing, for example. Experimental evidence shows that there are several ways of promoting intake of a novel food. Launchbaugh et al. (1997) found that addition of a familiar flavour to a novel food may increase its acceptance. Lambs that were used to eating onion-flavoured barley ate more onion-flavoured rice than lambs that had previously eaten only unflavoured barley. Moreover, it may help animals to accept a novel food if it is provided in a familiar environment. Burritt and Provenza (1997) reported that lambs ate less of the novel feeds at an unfamiliar than at a familiar location suggesting that feed neophobia is greater in unfamiliar environments. Therefore, a simultaneous change of the environment and the feed should be avoided, and the new feed should be presented to the animals for some time in the familiar environment before they are moved to the new environment. With pigs, the change from milk to solid food at weaning is critical, resulting in a temporary decrease in daily weight gain, which is more pronounced in piglets weaned early (Worobec et al., 1999). This may reflect the piglets' difficulty in learning about solid food at an early age, though it may simple be a consequence of problems they face in digesting solid food at that age.

2.3. Learning about housing equipment

Because of the development of the technology used in farm animal husbandry, animals have to learn more and more about housing equipment. For example, sows learn to feed from electronic feeding stations and dairy cows may have to get used to be milked in an automatic milking system. There are, however, only a few studies in which the process of adaptation to housing equipment has been monitored extensively. For example, Pojtner et al. (1984) described the adaptation of dairy cows to automatic feeders and Kashiwamura et al. (2001) reported how habituation was used to encourage dairy cows to enter the milking boxes of an automatic milking system.

Evidence from experimental studies suggests that social learning may help animals to learn about housing equipment. In a study with heifers, Veissier (1993) found that the activity of a demonstrator would draw the attention of observers to stimuli involved in a task (pushing a panel to get food into a box) and hence enhance the learning of the task. Veissier and Stefanova (1993) showed that newborn lambs learned to suck milk from a bucket provided with teats in 3 days rather than 9 if they had an older, experienced lamb in their group. With pigs, individuals who had observed a trained sibling demonstrator press one of two panels for food reward directed more non-rewarded presses at the operant panels in a subsequent test (Nicol and Pope, 1994a). Similarly, Nicol and Pope (1994b) reported that small flocks of laying hens exposed to a demonstrator trained to peck a key for a food reward made more keypecks after demonstration sessions than controls without such a social cue, especially if the demonstrator was a dominant individual.

2.4. Learning about characteristics of group members

It is typical of farm animal husbandry that animals are moved from the group in which they were raised to other groups for breeding or fattening. Thus, they are confronted with the situation of meeting strange conspecifics, and there must therefore be a process of learning about the characteristics of the group members and finding its place in the social organisation of the group. Quite often, this process involves aggressive interactions resulting in knowledge about asymmetries in dyadic relationships concerning access to resources (Addison and Baker, 1982; Bolhuis et al., 2005). Interestingly, the process of group formation may vary with group size. Andersen et al. (2004) found that the number of fights per individual decreased with increasing group size in newly mixed groups of weaned piglets, indicating that the pigs are able to alter the way groups are settled according to the number of individuals involved. Similarly, D'Eath and Keeling (2003) reported that laying hens kept in small groups performed more aggressive behaviour towards conspecifics presented in test cages with vertical bars than hens kept in large groups, suggesting a shift from a peck order to social tolerance as group size increases.

Learning about other group members may, however, include characteristics other than fighting ability, and positive social relationships are also likely to be the result of a learning process. It is thus not surprising that farm animals are able to discriminate between individual familiar group members, as has been shown for cattle (Hagen and Broom, 2003), sheep (Ligout and Porter, 2003), pigs (McLeman et al., 2005) and hens (Bradshaw, 1991).

2.5. Learning about characteristics of humans

Unlike wild animals, farm animals are regularly in close contact with humans, and in many cases those humans interact with them, thus becoming a significant aspect of their environment. Experimental studies have shown that farm animals are able to discriminate between humans based on previous experience with them. For example, Miura et al. (1996) reported that weaning pigs that had been handled regularly by an experimenter for 2 weeks approached the handler rather than a stranger. Dairy cows were found to keep a longer distance from an aversive than a gentle handler (Munksgaard et al., 2001), and calves that were treated repeatedly either positively or adversely in their home pen contacted the positive handler significantly more than the aversive handler in their home pen, but did not discriminate between the two handlers when retested outside their home pens (de Passillé et al., 1996). Similarly, Koba and Tanida (1999) observed that miniature pigs could differentiate between a handler who touched and fed them on approach and a non-handler in a familiar environment, though they had difficulty discriminating the two people in a new place. Sheep that were rewarded in the presence of a handler but not in the presence of a second handler also showed the ability to differentiate between individual humans (Davis et al., 1998). Rybarczyk et al. (2001) showed in formal experiments that cattle used both face and height information to discriminate between people, while Peirce et al. (2001) found in maze experiments that sheep could discriminate between human faces.

Several studies have provided evidence that animals' initial fear of humans can be overcome by regular handling. For example, Miura et al. (1996) observed that regularly handled weanling pigs showed significantly less aversion to a non-familiar human than did non-handled pigs. With chicks, Jones (1994) reported that regular gentle handling in early ontogeny reliably reduces the animals' fear of humans. Moreover, he found that chicks habituated to one person through regular handling also exhibited reduced fear of other people wearing either similar or different types of clothing, thus showing stimulus generalisation. Similarly, Hemsworth et al. (1996) observed that pigs fed by an experimenter were subsequently less fearful both of the handler and of other humans.

With farm animals, it is inevitable that they sometimes have negative experiences with humans, for example when they are caught for marking or veterinary treatment, or subjected to mutilations, such as dehorning, tail-docking or castration. Experimental studies suggest that such situations are perceived as less aversive by the animals if they have been regularly handled by humans before. With sheep, it has been shown that gentle handling reduces the flight distance and the heart rate response to humans during subsequent aversive treatment (Hargreaves and Hutson, 1990) and improves the ease of handling during weighing procedures (Uetake et al., 2000). Similarly, Tanida et al. (1994) found that piglets receiving regular handling showed less aversion and even tried to make frequent physical contact with an experimenter in spite of repeated chasing and catching events. Interestingly, Jones and Waddington (1992) reported that early environmental enrichment also attenuated the tonic immobility reaction of chicks to manual restraint, suggesting that enrichment may have modified general, non-specific fearfulness.

There is growing evidence that farm animals' fear of humans does not only impair their welfare but may also markedly affect their performance (Rushen et al., 1999). As a consequence, it is worth investing in the establishment of positive human–animal relationships through regular gentle handling, which seems to be most effective if it occurs in early ontogeny. Given that the experiences an animal has with one person may also affect its behaviour towards other people, such an investment will have a positive impact on a wide range of situations the animal will face during its life.

3. Facilitating learning in farm animal husbandry

Inglis (2000) emphasised the role of uncertainty reduction in determining animal behaviour, and this aspect of behavioural organisation is not only important in the wild, but also for farm animals. The process includes information gathering as well as information processing resulting in a cognitive model of the environment, from which rules of behavioural responses to specific environmental situations are derived and further selected based on the feedback the animal gets when performing the response. If learning in farm animals is viewed in this way, it is possible to deduce general principles from learning theories that may be applied to enhance farm animals' adaptation to housing conditions and hence their welfare.

3.1. Innate preferences regarding relevant cues

For an animal, not all aspects of its environment are equally relevant. For example, for newborn piglets, cues of the sow, such as udder shape and temperature, are probably of much importance in terms of survival. It is thus not surprising that behavioural organisation is characterised by innate preferences regarding cues to which they will react, as exemplified by the preference of newborn piglets to approach and lie down close to soft and warm tissue (Welch and Baxter, 1986). Similarly, specific cues in the environment of newly hatched chicks are important for the development of sufficient eating behaviour to ensure their survival (Shreck et al., 1963).

Such preferences can be used to facilitate farm animals' learning about the housing system. For example, cows have a preference for a soft surface of the floor in the place they lie down (Herlin, 1997). Such information can be used to design cubicles that are well accepted as lying places. With poultry, Appleby and McRae (1986) showed that enclosure is an important stimulus in nest-site selection by laying hens, and Duncan and Kite (1989) found that hens opt for nests containing loose material that can be moulded by body and feet movements. As noted above, knowledge of such preferences is important for the design of aviary systems to ensure that the hens will learn to lay their eggs in the available nest boxes and not elsewhere in the housing system. Moreover, chicks of both broiler and layer strains preferentially show active behaviour in bright light and resting and perching in dim light (Davis et al., 1999). Consequently, it may be useful to structure the housing system according to this preference with feeding and drinking equipment provided in brighter areas than perches. Dairy cows have a clear preference for lighted over unlighted passageways (Phillips and Morris, 2001) and it is important to take this into account in order to ensure that cows return willingly to the different resources of their housing system, such as the concentrate feeder or the milking parlour.

3.2. Previous experiences of animals

Given that the behaviour of animals is modified by previous experience, taking such experience into account and, where possible, actively providing possibilities for new experiences is an important way of facilitating animals' ability to adapt to new situations. As discussed above, animals learn from interactions with humans, and they tend to use the response rules they develop when in contact with a given person also in interactions with other people. Similarly, it is likely that the animals get used to other cues present on a farm, such as noises, smells and daily management routines which will influence the way they react to future changes in their environment. In an experimental study with laying hens, Dawkins (1977) found that animals that had been kept in battery cages preferred cages over an outdoor run in the initial trials of a preference test and only gradually changed their preference towards the outdoor run, whereas hens that were already familiar with an outdoor run chose this option preferentially right from the beginning of the testing.

Consequently, if it is known that the animals will be moved to a certain type of housing system or will have to be handled in a certain way, it may be useful to give them opportunities to learn about features that will be important in the future. With fattening pigs, for example, it can be foreseen that they will have to be moved outside their pen at loading for the transport to the slaughterhouse, and Abbott et al. (1997) showed experimentally that their willingness to move is increased if they are moved outside the building and back to the pen three times during the month before slaughter. Laying hens that will be kept in aviary systems during the laying period should preferentially also be raised in aviary systems that allow them to use different vertical levels, thus enhancing their ability to cope with this housing system (Häne et al., 2000).

Rearing farm animals in enriched rather than barren environments seems to be another promising approach for enhancing their learning ability and thus their ability to cope with challenges they will meet later in life. For example, Sneddon et al. (2000) found that growing pigs performed better in both an operant task which involved learning to push a panel for a reward and a maze test which involved spatial learning if they had been reared in an enriched environment, incorporating extra space and areas which contained peat and straw in a rack, compared to pigs from barren, intensive housing. Similarly, the possibility of building up social relationships in early ontogeny may have a significant influence on the animals' future learning ability, as it does in non-farm animals, such as rats (e.g. Morgan, 1973). The effects of environmental enrichment on brain development and cognitive abilities have been studied extensively in laboratory animals (e.g. Rosenzweig and Bennett, 1996; van Praag et al., 2000; Würbel, 2001) and results achieved in these studies may also be relevant for farm animals.

3.3. Information transfer through social learning

The behavioural organisation of animals that ancestrally lived in groups, such as our farm animals, has probably been shaped by evolution to use information stemming from conspecifics reacting to a given event and interacting with a given environmental feature to form rules of response to similar events and features. As discussed above, social learning occurs in farm animal species in a variety of situations, probably mainly in the form of local or stimulus enhancement. If possible, it may thus be preferable to introduce naïve animals to groups that are already familiar with a given housing system or equipment instead of composing groups in which all individuals lack experience. In line with this, Nicol (1995) suggested that few trained demonstrators could be added to newly established groups to facilitate habituation and correct use of equipment by naïve animals.

3.4. Eliciting interest and appropriate timing of reinforcements

If farm animals have to learn about the distribution of resources in their housing systems or how to manipulate equipment, such as feeders or drinking fountains, it is essential that first they pay attention to the site or equipment and then that, if they start exploring it, they receive a reinforcing feedback without much delay. In order to encourage correct manipulation of feeders or drinkers it is usually helpful to spread some feed or sprinkle water in the vicinity of the equipment. Studies of natural foraging have shown that, when hungry or thirsty, animals will look for cues for food and water and, once they have found small quantities, typically modify their behaviour so that they stay in the vicinity (Smith, 1974), so long as the source is not experienced as being exhausted (Kamil, 1978). Of course, food may also be used to draw the attention of animals to a site for other reasons than feeding. Prescott et al. (1998) showed experimentally that food is significantly more rewarding than milking and likely to be a necessary incentive to attract cows to an automatic milking system.

If an operant response is required to produce more food or water, for example, pressing on a bar to induce the delivery of food pellets or squeezing a nipple drinker to start a continuous flow of water, it is always recommended that the interval between the behaviour of the animal about to learn and the delivery of the resource should be as short as possible. Experiments in tightly controlled situations show that even the briefest delay between response and reinforcement can greatly slow learning (Grice, 1948). However, in simple operant situations of the sort likely to be encountered in agricultural practice, learning can still occur even with quite substantial response-reinforcer delays (Lattal and Gleeson, 1990; Wilkenfeld et al., 1992), and in any case the effects of response-reinforcer delay can usually be overcome by providing an immediate stimulus which has been pre-associated with food (Schlinger and Blakely, 1994). This ‘‘bridging’’ effect of a stimulus, which becomes a conditioned reinforcer, has been well understood from the time of Grice’s work, and one of the purposes of procedures such as clicker training is to provide it.

With farm animal equipment, there is pressure to make learning to operate equipment correctly as easy for the animals as possible. Extensive training involving human assistance will increase labour costs. Furthermore, the length of the period the animals need to learn the task tends to be negatively related to their performance. As a consequence, the equipment in use has to be simple if it is to be successful on the market. Nevertheless, there is room for further improvement, for example in providing apparatus to promote water intake of newborn piglets (Deligeorgis et al., 2006) and dairy cows (Teixeira et al., 2006) or feed intake in weaned piglets (O’Connell et al., 2002). Furthermore, new technology, such as distance sensors and electronic tags used for individual recognition of animals may offer new opportunities to shape the behaviour of farm animals using operant conditioning techniques without human intervention.

4. Topics of interest for future research

4.1. Observing farm animals in situations of novelty

Given the importance of learning for the animals’ ability to adapt to a housing system, it would be desirable to give more attention to the process of information gathering and processing in novel situations, both to describe the mechanisms of learning involved, and also to identify problems in learning in farm animals. Methodologically, this would probably be best achieved by recording the behaviour of individuals chosen as focal animals and analysing the behavioural changes occurring after introduction to the new housing conditions. Such studies would contrast sharply with the usual current approach, i.e. using behaviour to measure the outcome of an adaptation process some time after introduction to a housing system, and using these data to judge whether the animals are able to cope with it.

In experimental psychology, a number of standard tests exists in which animals are confronted with defined experimental situations to measure their response to novel environments, from the traditional open field test introduced by Hall (1934) to more recently introduced procedures, such as the "strange situation" adapted from experiments with human children (Topal et al., 1998). The ways animals approach spatial or manipulative tasks and the cues they use have been investigated extensively (e.g. Jacobs and Schenk, 2003; Osthaus et al., 2005). Thus, the methods for such recording and analysis of behaviour can be found in the publications of this field of research. In applied animal behaviour science, standardised test situations, such as open field tests or novel object tests have also been used as a measure of fear or personality traits (e.g. Andersen et al., 2000; Thodberg et al., 1999). What is missing, however, are studies that focus in similar detail on the behaviour of individuals when they are confronted with a novel situation typical for farm animal husbandry, such as being introduced to a new housing system or having to learn to use a new housing equipment.

Such studies would be of interest for both practical and theoretical reasons. They could make a contribution to the design of housing systems and development of equipment that do not cause problems to the animals in terms of learning. Furthermore, they could provide insight into the basic mechanisms by which animals, other than traditional laboratory animals, form response rules to reduce uncertainty. Carrying out such experiments with farm animals in an animal husbandry context has a number of possible benefits. It is possible to investigate more complex situations than those typically studied in laboratory experiments, e.g. in a Skinner box, without facing the problems of doing such studies with wild animals in a natural environment. With farm animals there should be no problem with sample size, their behaviour can be observed for 24 h a day, they are very suitable for experimental manipulations, and they are already adapted or habituated to tolerate interactions with humans.

4.2. Learning during animal transport and in the slaughterhouse

Transport is a situation that a farm animal usually experiences only rarely, and the last few hours spent in the slaughterhouse are experienced only once. Nevertheless, as reduction of uncertainty is a major issue of behavioural organisation, animals will gather information and use their learning ability to cope as well as possible with these new situations. It is thus likely that they will be very attentive to stimuli allowing them to make predictions about coming events and that they will immediately incorporate experiences they make on these journeys into their response rules. Furthermore both these situations are of great concern from the point of view of animal welfare, so it is particularly important to consider what animals may learn about them (see also Lea, 2001).

We suggest that animals' attentiveness and readiness to learn in these situations should be investigated in detail, with the aim of identifying cues that help them take stress-reducing responses. For example, the cues provided by races should be considered as an essential element in their design. Furthermore, the visual and vocal signals given by humans (often humans with whom the animals are unfamiliar) to move or guide the animals could be tested and screened for their effect on animal learning. It would also be relevant to analyse how experiences the animals have at the beginning of the journey, when leaving their housing system and during loading, affect their behaviour at unloading and in the slaughterhouse. Animals that are given time and clear signals to learn to cope with uncertainty at loading may be better able to adjust their response rules to their experiences at the slaughterhouse, thus reducing stress and there increasing welfare and also, very probably, meat quality.

4.3. Motivation to show exploratory behaviour

Exploratory behaviour is an important part of animal learning, and there is a theoretical discussion whether information gathering may be motivated per se or only in the context of other needs (Inglis, 2000). For example, animals will work for food even though identical food is easily accessible in a trough, a phenomenon called contrafreeloading. Inglis et al. (1997) argue that this may be based upon the advantage of gathering information for animals living in changing environments. Wood-Gush and Vestergaard (1991) investigated the reaction of piglets to novel objects and concluded that they seem to possess a high level of curiosity and show inquisitive exploration, defined as an animal acting so as to initiate a change in its environment rather than responding to a stimulus. Hagen and Broom (2004) reported that heifers subjected to a learning task had higher heart rates and tended to move more vigorously along the race on the way to their food reward if they had made clear improvements in learning, indicating that cattle may react emotionally to their own learning improvement. Thus, farm animals seem to be interesting species in which to investigate motivational aspects of the process of information gathering and formation of response rules.

With regard to animal welfare, studies into the exploratory behaviour of farm animals may also result in hypotheses concerning the development of redirected behaviour, such as feather pecking in laying hens (Huber-Eicher and Wechsler, 1998) or tail-biting in fattening pigs (Day et al., 2002). In the process of redirecting foraging behaviour from environmental structures to the body of a conspecific, i.e. learning to use an alternative substrate to perform such behaviour, exploration and emotionally rewarding aspects of learning are likely to be crucial (Wood-Gush and Vestergaard, 1989).

4.4. Learning abilities and enrichment tasks

In recent years, farm animals have been increasingly used in experiments on animal cognition, such as discrimination learning (e.g. cattle: Rehkämper and Gorlach, 1997; pigs: Moustgaard et al., 2004; poultry: Lea et al., 2006), spatial learning (e.g. cattle: Bailey et al., 1989; pigs: Held et al., 2005; poultry: Regolin et al., 2005) and use of environmental cues for spatial learning (e.g. cattle: Howery et al., 2000; pigs: Croney et al., 2003; poultry: Ueda et al., 2005). Furthermore, there have been many studies using operant conditioning techniques to measure farm animals' motivation to work for a given resource (e.g. pigs: Matthews and Ladewig, 1994; poultry: Cooper and Appleby, 2003; cattle: Jensen et al., 2004), and a range of apparatus has been designed with farm species particularly in mind (Kilgour et al., 1991). In summary, these studies show that farm animals are able to learn difficult experimental tasks. It might therefore be of interest to use their ability to learn and to work for rewards to overcome boredom in animal husbandry, an idea first put forward by Kiley-Worthington (1983).

Interestingly, three studies taking advantage of operant conditioning to determine the animals' use of feeders have been published recently. Wredle et al. (2004) showed that heifers are able to learn to approach a feeder in response to an auditory signal, and Wredle et al. (2006) used an acoustic signal to train dairy cows to visit the milking unit of an automatic milking system where they received a food reward. With pigs, Ernst et al. (2005) trained group housed fatteners to discriminate and recognise an individual acoustic signal and approach a feeder to receive a food reward whenever they were called at several, unpredictable times each day. In our opinion, the cognitive skills of farm animals would allow them to solve even more sophisticated tasks to attain a given resource. To be used on practical farms, however, the tasks should ideally be designed such that there is no need for human assisted training, and laboratory experiments have shown that animals will learn simple operant tasks without human intervention (Lattal and Gleeson, 1990). Tasks should be based on the animals' motivation to explore their housing system and to derive rules of behavioural responses to redundant patterns in their environment upon reinforcement. Given the fact that farm animals usually have plenty of time to explore and manipulate their environment, it is likely that they will sooner or later solve enrichment tasks by trial and error learning. For example, Smith et al. (1990) reported that caged laying hens developed three different methods of opening a door in order to lay in a dust bath and spent on average 34 min attempting to open the door before access was finally achieved.

5. Conclusion

The ability of farm animals to adapt to and cope with their housing conditions is likely to be much influenced by learning processes. We therefore suggest that studies focusing on the initial phase after changes in the housing environment would be promising for both identifying and solving problems animals may face when exposed to such changes. Knowledge of species-specific learning abilities may help in the design of housing systems and in establishing management routines which facilitate learning and, assuming that uncertainty reduction is an important goal to the animals, are favourable regarding animal welfare.

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