

# Cognition studies with pigs: Livestock cognition and its implication for production<sup>1</sup>

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**ABSTRACT:** The purpose of this paper is twofold. First, it discusses in general terms how animal production can be affected by the animals' cognitive abilities; second, it aims to introduce our work on pig cognition. We suggest that livestock cognition does not only affect production indirectly through its effects on livestock welfare, but also that cognition can have direct effects. Direct effects are evident when cognitive abilities limit feed intake, for example, or in the recognition of groupmates or offspring. We illustrate such direct effects with two case studies from pig production: voluntary feed intake after weaning and production losses associated with aggression in groups. Voluntary feed intake after weaning is affected by preweaning experiences, weaning age, and postweaning practices. Some studies suggest a link between early environment and cognitive development in piglets, as has previously been demonstrated in other species. We suggest this as a possible contributing factor to low feed intake immediately after weaning. The other case study centers on

aggression in groups of pigs. Several studies indicate that some social assessment and recognition take place between individuals, allowing them to judge each other's aggressiveness and to avoid fighting once a dominance hierarchy has been established. However, the regrouping of previously familiar pigs can also lead to high aggression levels. This suggests that pigs may be able to form only short-term social memories, or that some aspects of their social memory are disrupted before regrouping. Our work shows that pigs have well-developed spatial memory abilities, which can be disrupted by common management procedures. If this were also the case for social memory, it could help explain increased aggression levels in previously familiar pigs after routine procedures. We also show that pigs are able to adjust their foraging behavior depending on the presence or absence of a subordinate, exploitable co-forager that knows where food is. This ability has potential implications for the way feed is best dispensed to pigs such that all group members can maximize their intake.

Key Words: Animal Behavior, Livestock Farming, Pigs

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## Introduction

In modern production systems, farm animals are constantly and inadvertently presented with many learning and memory challenges. Consider as an example chickens housed in large groups in free-range or barn systems. We rely on their learning and spatial memory abilities to locate important resources such as food, water, nesting areas, or familiar subgroups (Mendl et al.,

2001). Similarly, at weaning under commercial conditions without the provision of creep-feed, piglets have to learn instantly how to acquire food from unfamiliar sources. This is in stark contrast to natural conditions, in which the weaning process is prolonged and gradual, allowing the piglets to explore sources of solid food over many weeks before they have to rely exclusively on them (Held and Mendl, 2001). In single-space feeder systems, the learning challenge can be even greater. The weaners may have to work out how to operate the mechanism that releases the feed before they receive their first postweaning meal (e.g., Pluske and Williams, 1996). In addition to these spatial memory and operant conditioning abilities, the recognition of conspecifics as familiar or unfamiliar, as dominant or subordinate to oneself, or as own or other offspring (e.g., Kendrick et al., 1997) is also likely to be important if animals are to thrive in modern production systems.

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Our paper has two main aims. First, it discusses how livestock productivity can be affected by the animals' cognitive abilities. Postweaning growth-check in weaners and production losses linked to aggression in groups of pigs serve as case studies. Second, the paper briefly reviews some of our recent work on cognition in pigs.

### Livestock Cognition and Implications for Production

Until recently, the word *cognitive* was predominantly used to describe mental processes that require at least some form of mental representation of the processed information (Shettleworth, 1998). Or, put differently, it referred to mental abilities that involve information manipulation and storage beyond making simple stimulus-response connections. For example, considerable effort has been devoted to investigating whether animals, as humans, store information about the spatial layout of their environment as mental spatial representations or so-called cognitive maps (Tolman, 1948), or whether they attribute mental states to others (review on primates by Heyes, 1998).

We use a broader definition of *cognitive* here to include all mental processes animals use to acquire information about their environment, to store and recall it, and to use it in their decision making (cf. Shettleworth, 2001). This encompasses learning and memory abilities, but also what may be called "higher" cognitive abilities, such as forming cognitive maps, which are indicated by unlearned, complex, and flexible behavior patterns (e.g., finding new routes home from an unfamiliar release site).

How, then, can livestock cognition affect production? We suggest that it does so not only indirectly by the positive and negative effects it has on livestock welfare, and thus productivity, but that it can also have direct effects. In our distinction, "indirect" effects occur when cognition, or its failure, leads to some form of stress response, which may be associated with suffering and compromised welfare and may negatively affect productivity. "Direct" cognitive effects, on the other hand, result in the animals' not functioning appropriately with direct consequences for their productivity (e.g., failure to find food). They may also have welfare-related implications for productivity, but do not necessarily or always.

The relationship between the cognitive abilities of farm animals and welfare has already been discussed (see most recently Dantzer, 2001). We know that lack of predictability of and control over the variable aspects of the animals' environment increases the physiological symptoms of stress (Weiss, 1971; Wiepkema and Schouten, 1990) and associated loss of productivity such as decreased daily weight gains (e.g., de Jonge et al., 1996) or reproductive disorders (Varley and Stedman, 1994). For the environment to be predictable to an animal in the first place, not only must the environment have some predictable properties, but the animal must

also realize that it does. To have control over its environment, the animal must learn and understand how the environment works and how the environment can be changed to its benefit. And to this end, the animal must be able to perceive, store, and use appropriately the pertinent environmental information.

We want to emphasize again that in our view welfare is crucially linked to suffering, which implies at least some subjective awareness (see Dawkins, 1990), though the study of cognition as we refer to it here does not concern itself with the subjective emotional experiences of the animals. However, knowledge of how much farm animals understand about their surroundings, how they use information about their physical environment and about the behavior and intentions of their groupmates can help us understand how they are negatively or positively affected by their surroundings. For example, social stress induced by common husbandry procedures such as mixing of unfamiliar animals or social isolation from familiar individuals is one of the most potent sources of stress in farm animals (Zayan and Dantzer, 1990). The extent to which animals suffer in social environments is likely to be affected by their "social cognitive" abilities, that is, their ability to assess, monitor, and predict the behavior and intentions of their groupmates (Wiepkema and Schouten, 1990).

As another example, one might consider animals that are capable of forming only short-term memories. They would be unlikely to suffer from memories of negative experiences in the more distant past. Similarly, if animals were unable to form expectations based on events in the past in the absence of present external and internal (for example physiological) stimuli, it would be unlikely that they suffered because their expectations are not met (Nicol, 1996). The cognitive abilities of livestock can thus inform us about the sorts of environments, or situations, in which the animals might suffer and in which their welfare may be compromised.

Direct effects are evident where cognitive abilities limit feed intake, for example, or recognition of groupmates or own offspring. In the following, we illustrate such direct effects with two case studies from pig production.

#### *Postweaning Growth-Check in Piglets*

The first is an experiment by Pluske and Williams (1996) on the effects of feed and feeder type on postweaning feed intake. Piglets were weaned at about 30 d and put into weaner groups of nine piglets each. Their feed intake and growth rates were measured for 4 wk after weaning. Feed was dispensed either from single-space feeders wet and dry, or only dry or from multispace feeders. To operate single-space feeders, the piglets had to operate a latch mechanism with their snouts to make feed drop into a trough. Piglets in the "wet and dry" treatment group had to coordinate the flow of water from a drinker inside the bowl with the delivery of food into the bowl. Multispace feeders were

conventional troughs with enough feeding spaces for all nine weaners to feed at the same time. The expectation was that voluntary feed intake would be greater in single-space feeders, because fighting at the feeders would be reduced, because potential attackers could not reach the feeding piglet's head or ears (Pluske and Williams, 1996). Pluske and Williams also predicted that adding water to the feed would increase voluntary feed intake even further. However, against expectation, there was no difference in feed intake or weight gain over the 4 wk after weaning. In the 1st wk after weaning, the feed intake was actually 27% higher in the multispace treatment than in the two single-feeder treatments. Weight gain in the 1st wk after weaning was significantly lower in the single-space feeder treatment with wet and dry feed (Pluske and Williams, 1996). As mentioned above, weaners had to learn how to operate the single-space feeders, and with the "wet and dry" feeders they also had to learn how to coordinate water flow and food delivery. Pluske and Williams observed that it took the piglets about a week to learn how to use the single-space feeders. They suggest that this led to the initial postweaning growth-check and concluded that any potential increase in feed intake caused by lower aggression levels at the single-space feeders was overridden by the piglets' problems with learning how to operate these feeders (Pluske and Williams, 1996).

Young commercial weaners often show a characteristic growth-check in the 1st wk after weaning, which is thought to be associated with abrupt weaning at ages when piglets would still be nutritionally dependent on the sow under natural conditions (cf. Pajor et al., 1991). One of the main factors limiting growth immediately after commercial weaning is thought to be voluntary feed intake (Pluske et al., 1995). Voluntary feed intake, in turn, may be determined by cognitive processes such as learning, as suggested by Pluske and Williams' (1996) study. It might also be affected by the disruption of proper cognitive functioning through separation stress or neophobia (cf. Mendl, 1999). Under natural conditions, the number of sucklings begins to fall after the 1st wk after birth and continues to decline gradually (Jensen, 1988; Jensen and Rećen, 1989). The sow begins to terminate more and more sucklings (Newberry and Wood-Gush, 1986; Jensen and Rećen, 1989), and she spends increasing amounts of time away from the nest to forage and feed (Jensen and Redbo, 1987; Stangel and Jensen, 1991). The frequency of sucklings continues to decrease steadily, with the steepest fall during the first 4 wk (Jensen, 1988). Feeding on solids by the piglets is well established when they are 4 wk old and increases considerably between the 6th and 10th wk after birth (Newberry and Wood-Gush, 1985; Jensen, 1995). In the Petersen et al. (1989) study, for example, piglets started to graze when they were between 24 and 36 d old and to feed on pelleted feed between 28 and 39 d of age. For the piglets, the natural weaning process is thus

accompanied by increasing experience of new sources of food and gradual nutritional changes.

One common practice thought to decrease the postweaning growth-check by facilitating a more gradual change in diet and increasing preweaning experience of new food sources is the provision of supplementary creep feed during lactation. Piglets typically start to eat it when they are 2 to 3 wk old (e.g., Pajor et al., 1991). However, there is large within- and between-litter variation in the amount of feed consumed before weaning, and the effect of providing creep feed on postweaning feeding behavior and growth rates is not clear-cut (Pluske et al., 1995; Held and Mendl, 2001). Weaning age also affects voluntary feed intake immediately after weaning. Generally, all weaners tend to spend less time feeding on the day after weaning than on subsequent days regardless of weaning age. However, the younger the piglets are at weaning, the stronger is this effect (Held and Mendl, 2001). Efficient feed intake seems to develop gradually with age and experience, with the younger piglets taking longer to pick up feeding on solids (see also Appleby et al., 1991; Fraser et al., 1995). We suggest that not only age-dependent gut maturity, but also cognitive maturity, may contribute to this age effect.

Both preweaning experiences and weaning age affect the ability of piglets to cope with the weaning challenge. In general, weaning practices that mimic certain aspects of the natural weaning process ameliorate some of the behavioral problems in young commercial weaners such as low feed intake in the first few days after weaning (Fraser et al., 1995; Held and Mendl, 2001). Early indications are that piglets reared outdoors up to weaning, for example, spend more time feeding at weaning (and mixing) into straw yards than indoor-reared piglets (Webster and Dawkins, 2000; Cox and Cooper, 2001). Cox and Cooper (2001) also observed that outdoor-reared piglets fought less at weaning and mixing. The suggestion is that outdoor piglets have better-developed social and general cognitive skills than conventionally reared piglets. Similarly, de Jonge et al. (1996) found that female piglets reared under conventional indoor conditions up to weaning were more aggressive to each other when weaned into littermate pairs than piglets from enriched farrowing pens. These differences carried over into the later postweaning period and puberty, with the subordinates in pairs originating from conventional conditions (only) showing symptoms of chronic social stress (de Jonge et al., 1996). De Jonge et al. (1996) suggest as one possible explanation that rearing piglets in relatively barren conditions negatively affects the development of their social skills, leading to increased aggression levels. More direct indications for a link between rearing environment and cognitive development in pigs come from a study by de Jong et al. (2000). They found that pigs reared in standard farrowing and finishing pens had impaired long-term spatial memory abilities compared to pigs reared in larger pens with straw (de Jong et al., 2000). In rats,

humans, and nonhuman primates, a strong positive relationship has been established between social and physical environmental complexity early in life and cognitive development and level of cognitive abilities eventually attained (Rosenzweig et al., 1996). It has also been possible to link these effects to changes in brain anatomy and neurotransmitter expression (e.g., Ickes et al., 2000). It might, therefore, be fruitful for wider application to pig welfare and production to further examine the developmental cognitive mechanisms underlying the observed effects of preweaning environment on postweaning feeding (and social) behavior in pigs.

#### *Production Losses Caused by Aggression in Groups of Pigs*

A large proportion of production loss in weaners and group-housed, nonlactating sows can be attributed to aggression (e.g., Tan et al., 1991; Stookey and Gonyou, 1994). Some of the aggression observed directly relates to competition over access to resources such as drinkers or feeder spaces (cf. Gonyou, 2001). Another source is the establishment and re-establishment of dominance hierarchies after mixing and remixing (Meese and Ewbank, 1973; Puppe and Tuchscherer, 1994). At weaning, for example, when piglets are mixed into groups of non-littermates, an initial intensive period of aggression lasting approximately 2 h is commonly observed (e.g., Meese and Ewbank, 1973). This is associated with investigation of unfamiliar individuals by nosing the face, ano-genital region, and belly. The animal that eventually becomes top-ranking deals out most of the aggression. Skirmishes and fights can continue for 24 to 48 h. The frequency of aggressive interactions falls at the same time as a stable social hierarchy emerges. The decrease in aggression and continued low levels are likely to be the result of the piglets' recognition and memory of each other's relative social status. During fighting, pigs may be able to assess each other's relative competitive abilities (Rushen, 1988; Mendl and Erhard, 1997), and their efficiency at this social assessing may determine the frequency and duration of fights.

Various factors influence the speed with which a social hierarchy is established and aggression during mixing decreases. Weight asymmetry in weaner groups facilitates social assessment. Rushen (1987), for example, showed that fights during the first 2 h after mixing lasted longer in groups that consisted of evenly-sized piglets than in groups in which weights differed more. Similarly, Mendl and Erhard (1997) showed that it is possible to split weaner pigs into "fast" and "slow" attackers according to their individual aggressive characteristics. When pigs of the same aggressiveness (fast or slow) were mixed, the number of escalated fights was higher than when pigs of different aggressiveness were mixed. Again, this implies that some form of social assessment took place between individuals that allowed them to judge each other's aggressiveness. Disruption

of social assessment, recognition, memory, or other social cognitive functions might help explain why aggression can occur between previously familiar animals (Mendl, 1999).

### **Cognition Studies with Pigs**

#### *Spatial Memory*

Our first experiment on pig cognition has centered on such disruption of cognitive processes and on how sophisticated the social cognitive abilities of pigs really are. Mendl et al. (1997) investigated whether pigs remembered the location of food hidden in one of 10 possible areas. The task required the pigs to search for and locate the food in their first visit to the arena (the search trial), to remember the location when returned to their home pens (retention interval), and to relocate it during a second visit (the relocation trial). As such it tested the pigs' spatial memory abilities. Pigs did well in relocation trials. They found the food, making fewer errors than would be expected if they had been searching randomly. Pigs remembered food locations over retention intervals of 10 min and 2 h. However, how well they remembered depended on what happened to them during the retention interval. It has long been known that stressors can have deleterious effects on memory formation and recall (recent review in Mendl, 1999). Mendl et al. (1997) therefore tested whether this applied to spatial memory in pigs by presenting them with various treatments or "disturbances" in the retention interval. These were chosen to act as mild stressors or at least to lead to changes in arousal, which are also known to affect cognitive function (e.g., Kavaliers and Colwell, 1995; in pigs e.g., van Rooijen and Metz, 1987). "Disturbances" also mimicked common husbandry events: pigs were confined in a holding pen on the way back to their home pen for 3 min at the beginning of the retention interval, or for 3 min at the end when they were on their way back into the arena for the relocation trial; or they were placed into an unfamiliar isolation pen for the whole of the retention interval; or they received food in the isolation pen after the search trial and were then moved on to their home pen for the remainder of the retention interval; or they were allowed to explore an unfamiliar room for the duration of the retention interval. All disturbances negatively affected the performance of the pigs in the relocation trials. Pigs required more area visits, that is, they made more errors, before relocating the food than in control trials in which they had not been disturbed during the retention interval. The treatments, however, did not totally block or destroy memory of the food location. In "disturbance" trials, pigs still did better than they would had they been searching totally randomly (Mendl et al., 1997).

Laughlin et al. (1999) built on this to investigate whether a more complex spatial memory task might be more susceptible to interference from environmental stressors. Rather than requiring the pigs to remember

and relocate 1 out of 10 locations, they were tested in a win-shift task in a radial eight-arm maze. Four arms were baited with food, the pig was introduced into the maze, and it searched at random until it had found all four baited arms. It was then returned to its home pen for a 10-min retention interval before being allowed back into the maze for a relocation trial. Pigs were trained to a win-shift strategy, that is, they were rewarded for visiting the four arms that had not been baited in the search trial. Pigs, thus, had to remember four out of eight rather than 1 out of 10 locations. When the pigs reached criterion level of performance on the relocation task, tests proper started. There were four disturbance treatments, applied during the retention interval. Again, some were chosen to mimic common husbandry events that are thought to be potential stressors. In the “social encounter” treatment, the test pig spent the retention interval in a pen where it had contact with an unfamiliar pig through a barred gate; in the “novel” treatment, the pig was led to an unfamiliar outdoor area where it spent the 10-min retention interval; in the “maze” treatment, the pig was confined in the central part of the radial maze with all arms closed off; and in the “weigh” treatment, the pig was retained in weigh crate for 10 min then released back into the maze for its relocation trial. All except the “weigh” treatments significantly increased the number of arm visits in relocation trials compared to control trials without disturbance (Laughlin et al., 1999). These disruptive effects were stronger than in the study of Mendl et al. (1997), as the performance of pigs in the study by Laughlin et al. dropped to that expected of a randomly searching animal. One possible explanation for this difference is that more complex memory tasks such as remembering multiple sites rather than just one may be more susceptible to interference from environmental stressors (Laughlin et al., 1999).

These two studies suggest that even common husbandry events may act as mild environmental stressors that can have deleterious effects on spatial memory performance in pigs and may affect how efficiently they deal with their environment. If these effects extended to social memory, this would provide some explanation for the observation that even in previously familiar pigs aggression levels sometimes increase after temporary removal of individuals for routine management procedures (Luescher et al., 1990; Mount and Seabrook, 1993). Such procedures may be at least temporarily stressful enough to disrupt aspects of social memory and resultant social recognition necessitating the re-establishment of relative social status when the animal is put back into the group (cf. Mendl, 1999).

### *Social Cognition*

Our work on social cognition has started by looking at how sophisticated the social cognitive abilities of pigs really are. How much do they understand about the behavior and intentions of others? Do they use this to

their advantage, that is, having taken in information about others, do they change their behavior accordingly to their own benefit? Do they, for example, understand what others can and cannot see?

The first experiment addressed the question of whether pigs use the behavior of others in a competitive foraging situation to forage more efficiently (Held et al., 2000). We adapted the Informed Forager paradigm of Menzel (1974) to test the social tactics of two pigs foraging together for a hidden food bait. We formed eight pairs of one light and one heavy juvenile pig. Lighter pigs were subordinate in a food competition test, heavier pigs dominant. Pairs were housed together in their home pens. Every morning they were allowed to forage for food hidden in an arena. Initially, during training, they foraged alone to learn their respective tasks. Then, during testing, they foraged together. Both pigs learned to expect food in one location (bucket) out of eight possible ones in an open arena with wooden screens providing visual barriers between the food locations. In training trials, they searched the arena individually. A different bucket was baited with food at each trial. The subordinate pig in each pair visited the arena twice. The same bucket was baited in its second visit as in its first. In training, the subordinate member of each pair thus learned to search for the food in its first visit to the arena (search trial), then relocate the food location in its second visit (relocation trial). The dominant pig visited the arena only once and searched at random for the one bucket of the eight that was baited. The purpose of training, thus, was to turn the subordinate pigs into informed foragers or “I-pigs,” but keep the dominants naïve, or uninformed. When the I-pigs had reached criterion level in their relocation task we tested the two pigs of each pair together. The I-pig still got its solitary search trial, but for the relocation it was now paired with its uninformed, but heavier, partner. In pair trials, then, the subordinate knew where the food was hidden, the dominant did not.

What would the uninformed partner do in the pair trials: continue searching at random as in solitary trials during training, or use the knowledge of the subordinates to lead them to the food? We found that uninformed pigs abandoned searching for food for themselves and learned to follow their informed partners to the baited bucket (Held et al., 2000). Once at the baited bucket, they displaced the subordinates and monopolized the food bait. Following the informed subordinates dramatically increased the foraging efficiency of the dominants. In solitary trials, the dominants searched the arena randomly, that is, they visited as many unbaited locations before finding the baited one as expected of a randomly searching animal. When they followed the subordinates in pair trials, however, they visited significantly fewer locations before they reached the baited one (Held et al., 2000). This shows that pigs change their behavior in the presence of a companion that is a better forager and exploitable. Dominant pigs must have had some means of assessing relative forag-

ing efficiency, probably using their co-forager's behavior as the source of information.

These skills are useful if one considers the natural behavior of pigs. Studies on feral and domestic pigs kept in seminatural conditions have shown that domestic pigs retain the social and foraging behavior of their wild ancestors (Graves, 1984; Wood-Gush et al., 1990). They forage for patchily distributed food in family groups in large home ranges (Krosniunas, 1979; Janeau and Spitz 1995). These family groups consist of one or several sows and their offspring with differentiated rank relationships between them (Mauget, 1981; Petersen et al., 1989; Mendl, 1995). Optimality models predict that under such conditions individuals would benefit from the ability to adjust their foraging behavior flexibly to the presence and behavior of other members of their group. The optimal tactics in terms of foraging returns for each individual depend on its social rank or relative competitive ability, and the resource distribution (Barta and Giraldeau 1998). Generally, when food is clumped dominant group members should specialize as scroungers by exploiting subordinates as food-finders or producers (Caraco et al., 1989; Vickery et al., 1991). We would, therefore, expect domestic pigs to have evolved flexible social tactics, and the cognitive abilities that facilitate them, so as to maximize their individual foraging success. Good spatial memory abilities allow individuals to store for future use information about the location of profitable food patches. The ability to use to their own advantage the pertinent information held by another group member (knowledge exploitation) allows pigs access not only to food sources they found themselves, but also to those located by subordinate others.

The next experiment again looked at whether and how pigs use social information in a foraging task. Here we investigated whether pigs understand what another can or cannot see. That is, we tested the visual perspective-taking ability of pigs. A detailed analysis of the results is still outstanding, and we can therefore not draw any conclusions as yet. However, we have included the study here to introduce the type of experimental methodology that allows investigation of more complex social cognitive abilities in farm animals. We adapted a classic primate experiment (Povinelli et al., 1990) to test whether pigs base their foraging choice on the visual perspective of a companion. Visual perspective-taking experiments work on the assumption that animals with perspective-taking abilities will discriminate between individuals that can and cannot see some critical object or event (Heyes, 1998). We predicted that when pigs cannot see for themselves where food is being hidden they should follow an individual that had been able to see where the food was rather than follow one that had not.

Subject pigs initially learned that they had to watch and see where a human trainer went to know which of four corridors contained food. Over differing numbers of training trials, the test pigs learned to enter the

corridor that they had seen the trainer enter. During this training phase, the pigs were also given the experience of not being able to see the baiting event when a visual barrier was placed in front of their start box. Once they had reached criterion level on the training task they were tested in an unrewarded probe trial with two companion pigs in the start boxes on either side. Companions were trained to always enter one particular corridor regardless of the movements of the baiting trainer, and also regardless of whether their view of the arena was blocked by a visual barrier or not. In tests, a visual barrier was then placed in front of the test pig in the middle and in front of one companion, the "blind" companion. The other, "seeing," companion had full view of the arena and corridor entrances. The test pig in the middle could not see the arena, but it could see the "blind" and "seeing" companions on either side, and it could see that one had a visual barrier in front, the same as itself, and the other did not. While the visual barriers were in place, the trainer crossed the arena rattling the bucket noisily to indicate that baiting of a corridor was taking place, then exited the arena quietly to the left or right. After the visual barriers were removed the two companions were released and entered the two corridors that they had been trained to enter. Once they had entered, the test pig was released. Where would it go?

The hypothesis under test was that test pigs will discriminate between "seeing" companions that have visual access to the arena and "blind" ones that do not, if they were able to take the companions' visual perspectives. And the resultant prediction was that test pigs would follow "seeing" companions more often because they understood that only these would lead them to the food. A positive result would show the pigs' understanding of the behavior of their conspecifics to be a lot more complex than previously assumed. As such it would drastically broaden the range of social situation pigs might perceive as stressful. In situations in which they cannot see, for example, they might use "seeing" others as their source of information with resultant expectations of their environment, which may subsequently be thwarted.

## Implications

Modern production systems rely on the ability of livestock to learn and remember how to use unfamiliar equipment, where to find important resources, and so on. That is, they rely on the animals' cognitive abilities. Cognition affects production indirectly through its association with subjective awareness, stress, and welfare. Production may also be directly affected when the cognitive faculties of livestock are underdeveloped or disrupted. Our work shows that pigs have good spatial memory abilities that can be disrupted by common management procedures. If this extended to social memory, it could help explain increased aggression levels in previously familiar pigs after routine procedures.

We have also found that pigs adjust their foraging behavior depending on the presence or absence of a subordinate, exploitable co-forager that knows where the food is. This ability has potential implications for the way feed is best dispensed to pigs such that all group members can maximize their intake.

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