STUDIES IN SOCIAL COGNITION: FROM PRIMATES TO PIGS

S Held[1†], M Mendl[1], C Devereux[1] and R W Byrne[2]

[1] Division of Animal Health and Husbandry, Department for Clinical Veterinary Science, University of Bristol, Langford, Bristol BS40 5DU, UK

[2] Scottish Primate Research Group, School of Psychology, University of St. Andrews, UK

[†] Contact for correspondence and requests for reprints

The stressful effects that environments have on farm and laboratory animal welfare are likely to depend on how much animals understand of the behaviour and intentions of their conspecifics as well as on their understanding of their physical environment. However, studies on animal social cognition have primarily focused on primates. Here, we report on our work on social cognition in domestic pigs. It focuses on the ability of domestic pigs to assess and use to their advantage the behaviour of conspecifics, and uses approaches pioneered in studies on primates. Our work has shown that dominant pigs use the privileged knowledge of a subordinate to their own advantage in a competitive foraging situation. While such exploitative behaviour is likely to be based on rapid learning about the subordinate's behaviour, it is also possible that 'higher' cognitive abilities such as visual perspective taking could be involved. Ongoing work uses an adaptation of the Guesser-Knower paradigm to test whether pigs are indeed capable of visual perspective taking.

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Social cognition and welfare

The extent to which domestic animals are positively or negatively affected by the environments we provide for them is likely to depend (amongst other things) on their cognitive abilities. It has long been known that predictability of and control over the variable aspects of the physical environment reduce the physiological symptoms of stress in captive animals (Weiss 1971). For the environment to be predictable to an animal, not only must it 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. To this end, the animal must be able to perceive, store and use appropriately the pertinent environmental information. This applies as much to the social as to the physical aspects of an animal's environment.

However, this does not mean that an ability to predict what will happen and to understand what is happening would automatically reduce potential stress and resultant suffering in any situation. It is feasible that, in some situations, animals which are unable to form expectations or anticipation are less likely to be negatively affected than animals which do expect

something to happen. Nor does it imply that animals with better-developed cognitive abilities are more or less likely to be capable of suffering per se than others. For example, the ability to form expectations is unlikely to be related to the ability to experience pain. But it does mean that the cognitive abilities of animals can inform us about the sorts of environments, or aspects of them, in which they might suffer if they are capable of it (Nicol 1996). For example, animals which are only capable of forming short-term memories are unlikely to suffer from memories of negative experiences in the more distant past (Nicol 1996). Similarly, if animals were unable to form expectations based on events in the past in the absence of present external and internal (eg physiological) stimuli, it would be unlikely that they suffered because their expectations are not met.

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 (see Zayan & Dantzer [1990]). The extent to which animals suffer in social environments is likely to be affected by their 'social cognitive' abilities, ie their ability to assess, monitor and predict the behaviour and intentions of their group mates (Wiepkema & Schouten 1990). However, studies of the social-cognitive abilities of animals have so far focused largely on primates (reviews in Heyes [1994]; Byrne [1995]), laboratory rodents (eg Galef [1990]) and birds (eg Nicol & Pope [1999]). They include studies on social learning about food or novel foraging behaviours (recent reviews in Coussi-Korbel & Fragaszy [1995]; Nicol [1995]; Laland *et al* [1996]; Giraldeau [1997]); on the cognitive abilities such as knowledge exploitation and functional deception which underlie the social tactics of individuals in competitive foraging situations (eg Menzel [1974]; Coussi-Korbel [1994]); on the ability to recognize individuals (eg rodents: review in Gheusi *et al* [1994]) and on 'higher' cognitive abilities such as mental state attribution (recent review in Heyes [1998]). Our work aims to extend the study of social cognition to domestic pigs, *Sus scrofa*.

An improved understanding of how much pigs understand about the behaviour, intentions and knowledge of others is likely to facilitate our attempts to improve their housing conditions. For example, being grouped and re-grouped with unfamiliar individuals is a common experience for domestic pigs at various stages in their lives. This husbandry practice often leads to high aggression levels in the newly formed groups (eg Giersing & Andersson [1998]), and increased stress levels in some individuals (eg Mendl *et al* [1992]). A recent study showed that aggression levels were higher when pigs of the same aggressiveness (high or low; as assessed in standardized tests) were mixed than when pigs of different aggressiveness (high and low) were mixed (Erhard *et al* 1997). This implies that some form of social assessment might have taken place between individuals that allowed them to judge each other's aggressiveness, and that the pigs had the cognitive abilities required for such social assessments (Mendl & Erhard 1997). In related work, Rushen (1988) tested younger pigs (5–6 weeks old as opposed to 11 weeks in Erhard *et al* [1997]) in pairwise encounters. He predicted that if pigs could assess their relative body weights, pairs in which weight differences were small would readily fight while, in pairs where weight differences were large, the smaller pigs would not choose to fight. In fact, fights were equally likely in both pair types, suggesting a lack of ability to assess relative body weight. There are several possible reasons for the differences between the results of Rushen (1988) and Erhard *et al* (1997). These include the possibility that pigs can in some way assess propensity to attack, or its correlates, better than they can assess body weight, and that the context of the studies (pairs in Rushen [1988]; groups containing two sets of four littermates in Erhard *et al* [1997]) somehow affected assessment ability. Another possible reason is that the ability to assess relative competitive ability on the basis of any cue develops only at a certain age (eg

between 6 and 11 weeks). If this were found to be the case, then grouping of unfamiliar pigs of demonstrated, different aggressiveness could be recommended to reduce fighting at mixing from a certain age onwards. We could thus use fundamental knowledge of the ability of pigs to assess the aggressive intention of others to help reduce aggression resulting from mixing of unfamiliar individuals. Other examples of social cognitive abilities in captive animals that are likely to have immediate welfare implications, such as social recognition and memory, are discussed by Mendl et al (2001).

Based on the evidence from behavioural studies of wild pigs, feral pigs and domestic pigs kept in semi-natural environments, we would expect domestic pigs to have well developed social cognitive abilities (eg Petersen et al [1989]; Stolba & Wood-Gush [1989]; Mendl [1995]). These studies have shown that domestic pigs retain the foraging behaviour and social organization of their wild ancestors. If given the opportunity, they form social groups consisting of one or more sows and their offspring with differentiated social relationships between group members. Pigs forage in their groups for patchily distributed food in large home ranges. Group cohesion and organization are maintained by frequent social interactions ranging from rare overt aggression to subtle non-agonistic interactions such as exchanges of glances or leader-follower interactions. Most activities performed by one group-member are perceived by others and affect their behaviour. Under such circumstances, an ability to remember information about the location of profitable food patches (spatial memory), an ability to use to their own advantage the relevant information held by others (knowledge exploitation) and an ability to avoid such exploitation by misleading others about the food location (deceptive tactics) would increase the foraging success of individual group members. We use the terms 'knowledge exploitation' and 'deceptive tactics' in a purely functional sense here to describe behaviours whose consequence it is to exploit or deceive, implying nothing about intentions or other underlying psychological mechanisms such as mental state attribution. However, 'higher' social cognitive abilities such as mental state attribution (including knowledge attribution) would allow pigs to adjust their own behaviour not only to the actions of others, but also to their knowledge, beliefs and intentions.

Pigs do have well-developed spatial memory abilities, as has been demonstrated in various food relocation tasks (Mendl et al 1997; Laughlin et al 1999; Held et al 2000). In addition, field observations indicate that feral domestic pigs may adopt specialized rank-dependent foraging tactics, and also that they may be able to change tactics flexibly in response depending on the distribution of the food source and on the presence, social status and behaviour of individual group mates (Krosniunas 1979). Our work on social cognition in pigs uses an experimental approach. It builds on 'classic' primate studies to investigate whether and how pigs use each other's behaviour and visual perspective to their advantage. Both of these abilities – adjusting one's own behaviour to that of another and taking another's visual perspective – are likely to involve social cognitive processes.

Studies on social cognition in pigs

In one study, we investigated whether pigs would learn to use to their advantage the knowledge of another about the location of a monopolizable food source (Held et al 2000). We used as our experimental paradigm a modification of Menzel's (1974) experimental analogue of natural foraging skills in which one group member, the 'informed' animal, is given privileged information about the location of a monopolizable food source in a foraging arena. The whole group is then allowed to forage together. The actions and interactions of the informed animal and its non-informed co-foragers are recorded to reveal social tactics

used by individual group-members. The chimpanzees, *Pan troglodytes*, observed in Menzel's (1974) study and, in a more recent study, mangabey monkeys, *Cercocebus torquatus torquatus*, (Coussi-Korbel 1994) showed the development of exploitative, deceptive and counter-deceptive tactics.

In our study, pigs foraged in pairs rather than in a larger group. In the chimpanzee study (Menzel 1974), it was specifically in circumstances when the informed individual was of considerably lower social rank than one of its group-members that the most revealing results on social cognition emerged. Coussi-Korbel (1994) deliberately informed only a low-ranking mangabey in the social group. To ensure that the co-foragers in our study would differ in competitive ability, we paired a light pig with a heavy one which was able to exclude the lighter one from access to the food source. Both pigs in each foraging pair were trained to expect food in one of several possible locations in an open arena. In training trials, they searched the arena individually. Locations were baited with food at each trial in random order. The subordinate pig of each pair visited the arena twice per session. In its second visit, the same location was baited as in its first. Appropriate measures and controls were carried out to make sure pigs did not relocate the baited location using odour cues. The purpose of our training phase was to accustom the subordinate member of each pair to search for the food in its first visit to the arena and to relocate the food location in its second visit. The dominant pig visited the arena only once and learnt to search at random for the one location that was baited. This schedule turned the subordinate pigs into informed foragers or 'I-pigs' at the end of the training phase, but kept the dominants naïve or 'non-informed'. In the test phase, we tested the two pigs of each pair together. The I-pig still got its solitary search trial first, but for the relocation it was now paired with its non-informed, but heavier partner, the 'NI-pig'. In pair trials, the subordinate, therefore, knew where the food was hidden, the dominant did not. Figure 1 summarizes our procedure.
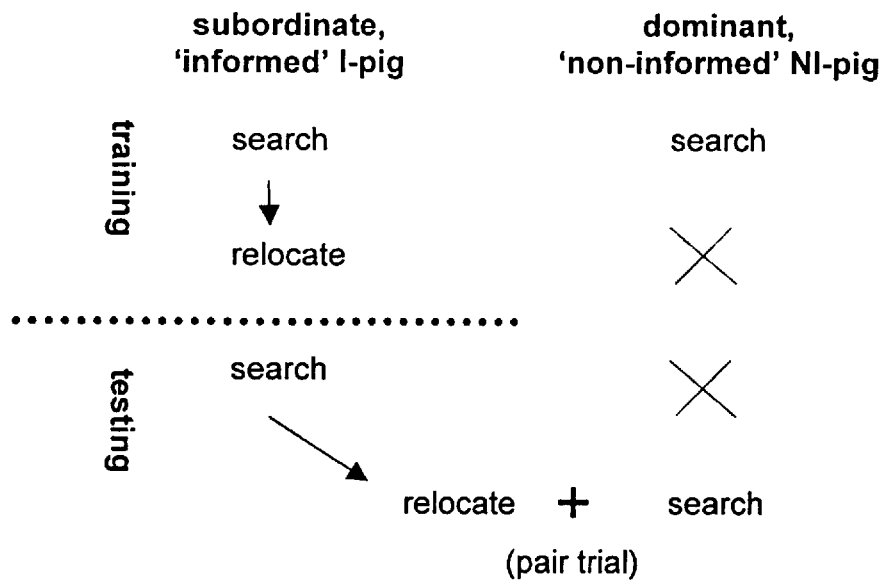
Figure 1   Summary of experimental procedure. Stippled line indicates criterion level of performance in training task for I-pigs.

The crucial question was what the non-informed dominants would 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? The dominant individual in Menzel's group of chimpanzees soon learned to follow the subordinate group member that knew where the food was and monopolized the food reward (Menzel 1974). In a similar study, Coussi-Korbel (1994) found that the same was true for mangabey monkeys. She allowed one subordinate group member to watch when one of several hiding places in an outdoor enclosure was baited with peanuts. The informed subordinate was then returned to its group, and the whole group of seven monkeys was released to search the arena for the hidden food reward. The top-ranking male soon started to follow the informed subordinate and relieve it of the food.

We found that in our pairs of pigs, the non-informed individuals abandoned searching for food for themselves and also learnt to follow their informed partners to the baited location. Once at the baited location, they displaced the subordinates and monopolized the food bait. We used as a measure of following how often an NI-pig investigated a location just after an informed one had been there and compared the proportion of these investigations with the random expectation. There were some differences between individuals, which reflected how soon after the start of the testing period NI-pigs had learnt to follow their informed partners to food locations and how persistently they followed once they had learnt to. Nonetheless, all eight NI-pigs followed more often on average than expected by chance (Figure 2).
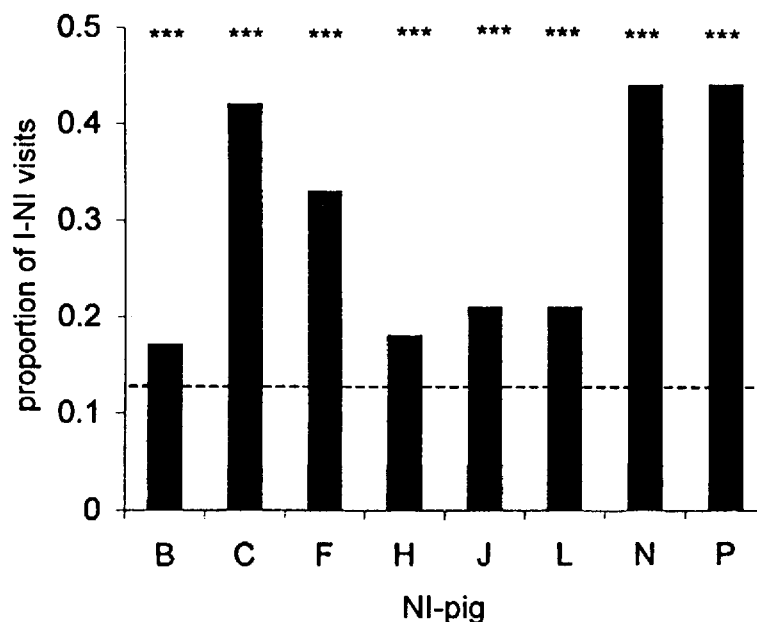
Figure 2   **Proportion of I-NI visits by NI-pigs in pair trials as a measure of the extent of following the I-pigs. An I-NI visit occurred when the next location to be investigated was the one that had just been investigated by the subordinate I-pig. The stippled line indicates proportion of I-NI visits occurring by chance; *** indicates significantly higher ($P <$ 0.0001) proportion of I-NI visits than chance level.**

We also found that following the informed subordinates dramatically increased the foraging efficiency of the dominants (Held *et al* 2000). In solitary training trials, NI-pigs had investigated as many locations as expected of a randomly searching animal before they found the baited one. But in pair trials, when they followed their informed co-foragers, the number of locations visited before they reached the baited location dropped dramatically (Figure 3). All eight NI-pigs investigated fewer buckets in pair trials than expected from a random searcher.
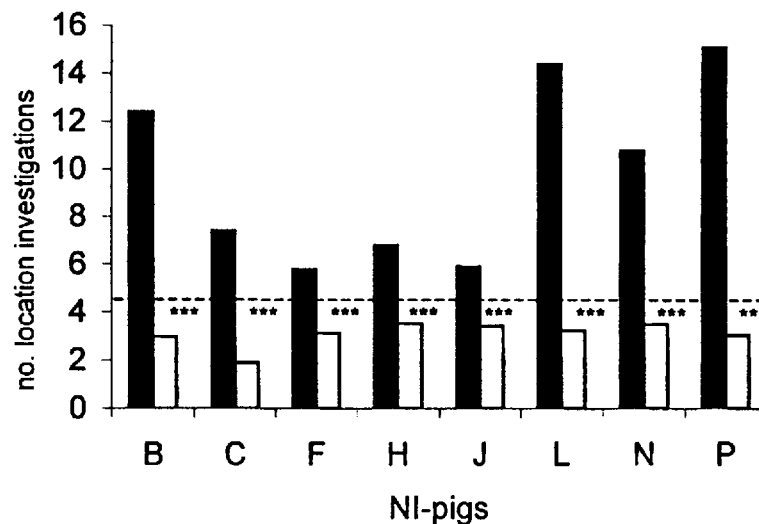
Figure 3   **Average number of location investigations made by NI-pigs before baited location was found. Black bars give solitary training trials, white bars give pair trials. The stippled line indicates the number of location investigations expected of a randomly searching animal; *** indicates significantly fewer ($P < 0.0001$) location investigations in pair trials than expected from random searchers.**

This demonstrates that pigs, like chimpanzees and mangabey monkeys, can use flexible foraging tactics dependent on the presence of an exploitable and knowledgeable co-forager, and will use the knowledge of another to their own advantage. There was also some indication that individual pigs differed in the speed with which they acquired the new 'social' foraging tactic. The question remains how subordinates might overcome continued exploitation of their privileged knowledge by dominant group members when emigration from the group is not a viable tactic. In animals living in complex social groups, natural selection may favour the development of advanced social tactics, such as deception, which could be used by subordinates to counter exploitation (Humphrey 1976; Byrne & Whiten 1988). In Menzel's group of co-foraging chimpanzees, for example, the informed subordinate had learned to use functional (rather than intentional) deceptive tactics (*sensu* Byrne & Whiten [1985, 1992]) to shake off the exploiting dominant (Menzel 1974). The exploited subordinate monkey in Coussi-Korbel's study (1994) acquired different behavioural tactics which all resulted in functional deception of the dominant and guaranteed its own foraging success. Given the evidence provided by our work on knowledge

exploitation in pigs and given their complex social ecology, we suggest that further study of pig social cognition might also focus on potential functionally deceptive behaviour in exploited subordinates, using an extension of our previous experimental paradigm (Held *et al* 2000).

Whilst it is likely that the change in behaviour of the dominant foragers in the presence of exploitable subordinate co-foragers is based on a rapid learning about the outcome of the subordinates' behaviour, it is also possible that the dominants actually understand what the subordinates know. Our work to date does not allow a distinction between these two cognitive processes in pigs.

Ongoing research is investigating explicitly the ability of pigs to take the visual perspective of others. Several experimental paradigms have been devised to test whether primates are capable of attributing knowledge, or ignorance, or other mental states such as false beliefs or intentions, to others (review in Heyes [1998]). Some of these studies on 'higher' cognitive abilities have focused on visual perspective taking, which we are testing in pigs. Our experimental approach is based on a classic study by Povinelli *et al* (1990). In it, a chimpanzee had to pick one of four containers, two of which were pointed at by human trainers. One trainer, the 'Knower', had been in a position to see which of the containers had been baited with food, but the other trainer, the 'Guesser', had not seen the baiting taking place. The chimpanzee could see that baiting was happening, but not which container was baited. Chimpanzees quickly learned to pick the container pointed at by the 'Knower'. In the transfer phase, when experimenters changed the ways in which the knowing trainer could see the baited container, and the way in which the 'Guesser' could not, chimpanzees again appeared to prefer the containers pointed at by the 'Knower'. Initially, this was interpreted as indicating that chimpanzees can attribute knowledge and ignorance using visual perspective taking (Povinelli *et al* 1990). However, rapid discrimination learning during the first few trials of the transfer phase could have caused this result (Heyes 1993). In fact, the chimpanzees' performance was at chance level in the very first transfer trials (Povinelli 1994), and a series of subsequent experiments in this paradigm failed to find clear evidence of visual perspective taking in young chimpanzees (Povinelli & Eddy 1996). Our current adaptation of the original Guesser-Knower experiment aims to address some of the problems of the original design. It differs from Povinelli *et al*'s (1990) design in three main aspects. Firstly, transfer tests are unrewarded probe trials to rule out learning of a correct response. Secondly, we use conspecific companions in the 'Guesser' and 'Knower' roles such that subjects do not have to interpret the behaviour of another species. And, finally, we aim to use companions in the two roles that are equally trained and unaware which response was the correct one for the subject. Test animals would thus be unable to learn to use cues from either companion indicating the 'correct' response.

Animal welfare implications

We discussed earlier in the paper how the cognitive abilities of animals might affect their welfare. Our studies address specifically the social cognitive abilities of pigs. We have shown that pigs adjust their behaviour in the presence of an exploitable co-forager (Held *et al* 2000), probably by learning about the co-forager's more efficient foraging behaviour. If pigs were also shown to have the cognitive abilities that allow them to take the visual perspective of others, this would have far-reaching consequences for understanding circumstances that affect their welfare.

Acknowledgements

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