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Original study

A note on pigs' knowledge of hidden objects

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Abstract

Object permanence is the notion that objects continue to exist even when they are out of observer's sight. This ability is adaptive for free ranging animals who have to cope with a dangerous and highly changeable environment and allows them to be aware of predators sneaking in their proximity or to keep track of conspecifics or food sources, even when out of sight. Farm animals might also benefit from object permanence because the ability to follow the trajectory of hidden food or objects may lead to a higher predictability of subjects' environment, which in turn might affect the level of stress under husbandry conditions. We conducted two experiments to examine the ability of object permanence in young domestic pigs (Sus scrofa domestica). For this purpose, we used a test setup that was formerly developed for primates and adopted it to the behavioural constraints of pigs. A rewarded object was hidden in one of three hiding locations with an increasing complexity of the object's movement through successive test sessions. Subjects were confronted with visible and invisible displacement tasks as well as with transpositions of hidden objects in different contextual settings. Pigs solved visible, but not invisible displacements or transpositions, indicating that they have difficulties to keep track of once hidden and then moved objects. This should be taken into account when designing husbandry environments or studying designs.

Keywords: physical cognition, object permanence, transpositions; domestic pig

Abbreviations: E: experimenter; DVD: double visible displacement; fSVD: fixed single visible displacement; SID: single invisible displacement; SVD: single visible displacement

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Introduction

Free ranging animals have to cope with a dangerous and highly changeable environment. They have to be aware of predators sneaking in their proximity or keep track of conspecifics or food sources, even when out of sight. Therefore, following the trajectory of a previously seen but now hidden subject or object is highly adaptive - an ability called object permanence. In short definition, object permanence refers to the notion that objects are perceived by subjects as separate entities that continue to exist even when they are out of the observer's sight (Piaget 1954). In the Piagetian classification, there are six stages within the sensorimotor period during which sensorimotor intelligence in infants develops (Piaget 1954; for a summary see Table 1). Success in the recognition of single visible displacements (i.e., an object transferred in full view to a single hiding place) indicates Stage 4b of object permanence. However, subjects at this stage still commit the A-not-B or perseveration error, that means, they continue to search an object that was repeatedly hidden and successfully found at location A in previous trials, even if it afterwards has been hidden fully visible at location B. Only at Stage 5a, they overcome this kind of error and are able to solve such sequential visible displacements. At Stage 5b, subjects can solve double visible (i.e., sequential visits of more than one location before final hiding in one trial) and single invisible displacement (i.e., an object is first hidden in a particular box which is then transferred to a second fixed hiding location while the box was removed), but they fail to solve sequential invisible displacements (i.e., an object is first hidden in a particular box which is then transferred to a second randomly chosen hiding location). Solving sequential invisible displacements marks the beginning of Stage 6a. Subjects at Stage 6b can solve double invisible displacement, meaning that they can mentally reconstruct the movements of an unperceived object (Doré & Dumas 1987).

Animal studies on object permanence have been conducted so far with primates and several other mammals as well as with different species of birds. Whereas several monkeys (Japanese macaque: Natale *et al.* 1986; rhesus monkeys: de Bois & Novak 1994; squirrel monkeys: de Blois *et al.* 1998), dogs (Collier-Baker *et al.* 2004) and cats (Doré 1990) failed in a single or double invisible displacement task, for example apes (Call 2001, de Bois & Novak 1994, Natale *et al.* 1986), cotton top tamarins (Neiworth *et al.* 2003), psittacine birds (Pepperberg & Funk 1990) and the Eurasian jay (Zucca *et al.* 2007) succeeded in following the trajectory of a hidden object in a double invisible displacement task and therefore show evidence of real object permanence.

Research on object permanence in mammalian farm animals is of two-way interest. First, it is a general concern whether object permanence exists not only in non-human primates and humans but also in mammals in general. If this is true, it may point to the ecological conditions that have led to the development of this mental ability as well as its phylogenetic origin in evolution. Second, it is important to recognize that when designing housing and husbandry systems as well as methods of enriching the environment for farm animals, their cognitive capabilities should be taken into account (Held *et al.* 2002a, Broom 2010, Kornum & Knudsen 2011). Studies with domestic pigs have previously shown some sophisticated cognitive abilities of these animals, including the use of a mirror to obtain information (Broom *et al.* 2009), the discrimination between attentive and inattentive humans (Nawroth *et al.* 2013), potential perspective taking of conspecifics (Held *et al.* 2001) and social exploitation behaviour in a spatial foraging task (Held *et al.* 2000, Held *et al.* 2002b).

From an applied perspective, not only social but also physical cognitive abilities and constraints of domestic animals have to be considered for animal welfare in modern husbandry systems. In a natural environment, object permanence has obvious advantages in various respects for the non-domesticated counterparts of husbandry animals (see above). That is why this capacity could affect today's animals under husbandry conditions as well. For example, the ability to follow the trajectory of hidden food or objects may increase the environmental predictability for the subject, which might either lead to a decrease of stress in husbandry management or to an increase in boredom (thus negatively affecting animal well-being) in enrichment items and food supply (van Rooijen 1991).

Two experiments were conducted to examine object permanence in domestic pigs (Sus scrofa domestica). To our knowledge, there are no systematic studies which examined mammalian farm animals tested for object permanence (but see for domestic chicken: Etienne 1973, Regolin et al. 1995). Although pigs heavily rely on olfactory and spatial cues and despite their poor visual acuity (Zonderland et al. 2008), they are able to visually discriminate large stimuli like humans (Tanida & Nagano 1998), conspecifics (McLeman et al. 2008) or arbitrary symbols (Gieling et al. 2012). Taking this into account, an experimental setting similar to that of de Blois et al. (1998) and Call (2001) was adapted to the behavioural abilities and constraints of domestic pigs. Subjects were presented with visible and invisible displacements in Experiment 1 (corresponding to Stage 4b to 6a) as well as transpositions of hidden objects in different contextual settings in Experiment 2. The results of both experiments are presented together. Our aim was to investigate to what extent domestic pigs are able to mentally represent an object that is no longer visible.

Table 1 Summary of the stages of object permanence (after de Blois *et al.* 1998)

| Stage | Description |
|---------|--|
| 1 and 2 | No search for hidden objects. |
| 3 | Subjects can retrieve a partly hidden object. |
| 4a | Subjects can retrieve a totally hidden object if they initiated search before the object was completely hidden. |
| 4b | Subjects can retrieve a totally hidden object, but they persist searching a previously rewarded screen even if they saw the object disappear behind a new screen (perseveration of »A not B« error). |
| 5a | Subjects overcome the perseveration error, and they can find an object that was hidden behind a different screen on every trial. |
| 5b | Subjects can find an object that was hidden behind various screens within the same trial. |
| 6a | Subjects can find an object that was invisibly hidden behind a different screen on every trial. |
| 6b | Subjects can find an object that was invisibly hidden behind various screens within the same trial. |

Material and methods

Subjects & Housing

Subjects in Experiment 1 and 2 were four pigs at the age of seven weeks at the beginning of the study and at the age of ten weeks when tests were completed. They were housed in an indoor pen $(2.5 \, \text{m} \times 1.7 \, \text{m})$, each with a companion pig, at the department facilities. All testing trials took place at the home pens of the animals. Subjects were tested individually and the

experimental apparatus was cleaned after each test. The room temperature was maintained between 22 and 25 °C. Pigs had water and food access ad libitum all the time. Before the experiments began, the animals had been subjected to behavioural observations but no other choice tasks were administered. Subjects received one training or test session per day at the time between 10:00-14:00.

Apparatus

For every training and test session, a mesh with three holes (diameter: 11 cm, distance from each other 11 cm) in a horizontal line was inserted into the pen entrance while the door was open (see Figure 1). The mesh was fixed vertically and horizontally at the pig pen, covered the whole entrance area and should prevent subjects from directly interfering with the test procedure. In front of the mesh, a grey sliding table (60 cm×25 cm) was placed. Depending on the test, two or three pots (dark brown cloured; diameter: 11 cm; height: 10 cm) were placed upon the table, each corresponding to one hole of the mesh. A blue plastic egg (length 7 cm) was used as rewarded object. As pigs are able to discriminate blue from other colours (Tanida et al. 1991), this was expected to facilitate training and help them to keep track of the moving object. An empty white cup was used as displacement device for invisible displacements. The bottom of the cup was cut out and by squeezing the displacement device the object could not pass through the cup unless the experimenter (»E«) released the pressure. To prevent acoustic cues, the bottom of all pots was filled with cotton.

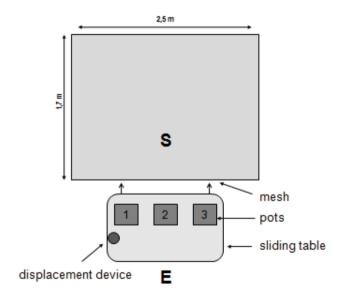


Figure 1
Experimental setup. Pots at location 1-3 were used in Experiments 1a and 1b, only two pots were used in Experiment 2, depending on condition. E: place of experimenter during sessions; S: subject

Clicker Training

Pigs heavily rely on spatial, olfactory and haptic cues while foraging. Due to their poor visual acuity (Zonderland *et al.* 2008), it seems hard for them to follow small food rewards (Nawroth, unpublished data). However, pigs seem to be able to use visual information to locate food if

a secondary reinforcement is used (Croney et al. 2003). Therefore, a secondary reinforcement method (»Clicker training«) was used in this study, too. Because only one pig of each pen was trained and rewarded, the animals did not have to be separated and were therefore not exposed to a novel environment, which might have probably induced stress or distraction and thus could have led to an impaired performance in the tests.

During the clicker training, subjects completed three classical conditioning training sessions consisting of ten trials on consecutive days with the clicker sound and a following reward (a slice of apple). One trial consisted of E producing a clicker sound and subsequently rewarding the subject. Afterwards subjects proceeded to the operant conditioning. The plastic egg was held in E's hand, slightly higher than the pig's head. The pig was rewarded every time by a clicker sound and a slice of apple when it touched the plastic egg with its snout. Again, three sessions of ten trials were conducted on three consecutive days. Previous pilot tests indicate that 30 trails are sufficient for the subjects to reliably snout the reinforced object.

Choice Training

In order to teach the subjects how to make a choice, additional training sessions were administered. Here, the object (i.e., the plastic egg) was placed on the sliding table (either at location 1, 2 or 3) in front of the pots which were set with their opening towards the subject. This configuration allowed the subject to get familiar with the hiding places and to visually explore that these pots have a bottom and are empty. Each subject was presented with training sessions of twelve trials. First, it experienced four forced choice sessions each consisting of twelve trials where the object was placed behind the mesh until the subject snouted it and therefore got rewarded. After those sessions, free training began. The subject passed a trial when it touched the object with its snout immediately (e.g. within a delay of 2 s) after the object was presented at the sliding table. The order of the rewarded location in training trials was chosen pseudorandomly, with every location (1, 2 or 3) being rewarded four times per session. Training criterion was set at ten correct choices out of twelve trials on two consecutive sessions. Three subjects needed two training sessions and one subject needed three sessions to reach the criterion.

Experiment 1a: Visible and invisible displacements

Pre-Test

A pre-test was conducted before each test session to raise motivation and to re-establish the learned response. The procedure was the same as in the choice training sessions except for the fact that subjects passed the pre-test after three consecutive correct trials. The order of the rewarded location in the pre-test was chosen randomly, with the restriction that a specific location was not baited two times in a row. If this criterion was not reached after ten trials, the session was terminated and started again the next testing day. All subjects passed the pre-test in each test session.

Test

Before a test session started, subjects got 5 min to re-habituate to the apparatus, but without food rewards. Each test trial started when E was lifting the rewarded object in the middle

position at an approximately height of 30 cm and, if necessary, called the subject to approach. Before baiting, E made sure that the subject was visually tracing the object by moving it a few centimetres in a horizontal line. Subsequently, E put the object into one of the available pots. Care was taken that no noise was produced during the procedure. After baiting one pot, E moved the sliding table towards the subject where it was able to indicate a choice by snouting one of the pots. If the subject chose the correct pot it was rewarded with a clicker sound and a slice of apple, whereas an incorrect choice led to no reward and the beginning of a new trial. Test sessions were conducted consecutively in the following order: fixed single visible displacement, A-not-B-error trials, random single visible displacement and double visible displacement. In the fixed single visible displacement task (fSVD), the same out of three pots (either Position 1 or 3, Position 2 was never baited in fSVD trials though the pot in this location was still present) was used as hiding place in three subsequent trials. After the three fSVD trials, three A-not-B-error trials followed in the same session, using the opposite hiding location as in the previous trials $(1,1,1\rightarrow 3,3,3 \text{ or } 3,3,3\rightarrow 1,1,1)$. Each of the following test conditions contained twelve trials, presented in one session. In the random single visible displacement task (SVD) the baited pot was chosen pseudorandomly out of the three pots. Each pot was baited four times per session, but not more than three trials in a row. In the double visible displacement task (DVD), two of the three pots were visited with E's hand (i.e. E briefly touched the pot) and either the pot visited first or the pot visited second was baited with the reinforced object. The baiting started either from the left or the right side to avoid a potential side bias caused by E's hand. In the DVDs, the direction of baiting (from left to right and vice versa) and the baited pot (first or second visited) were pseudorandomly distributed and counterbalanced across trials. At the end of a single or double baiting trial, the hand was fully opened and shown to the subject to signal that the reward was not in the hand anymore. In single invisible displacement (SID) tasks, the procedure was almost the same as in SVD trials except that the baiting procedure took place while the reward was first put into a separate opaque displacement device held by E and was thus not visible to the subject anymore. The displacement device was then moved to one of the three baiting locations and, while stopping to squeeze the displacement device, the object passed through the cup into one of the designated pots. At the end of a baiting trial in the SID task, the displacement device was rotated to show the subject that the reward was not in the device anymore and was then put at the extreme left or right side of the sliding table, in a pseudorandom order. To check if subjects were only following the displacement device, we further conducted another SID session where the displacement device was removed from the table after baiting (SID_noDD). After baiting one of the cups, E looked straight ahead to prevent inadvertent cueing. A trial was either finished when the subject chose a pot or after 30 s (failed trial). Failed trials were repeated at the end of a session and after three consecutive failed trails a session was terminated and repeated the next day. When a subject made a correct choice, E took the object from inside the pot and simultaneously made a clicker sound, followed by a slice of apple as a reward. When the subject chose incorrectly, E lifted the object from the correct pot and the next trial began. If the companion pig interfered with the testing procedure, trials were repeated or paused. Though companion pigs never received a reward, interference only happened in some trials. After testing a subject, the testing apparatus was cleaned before the next session started.

Data scoring and analysis

For individual data we conducted binomial tests. When pigs chose the correct pot eight times or more out of twelve trials on an individual level this was counted as significant (P=0.036) above chance level (33 %).

Experiment 1b: Controlling for experimenter cues

Test

To check if subjects really followed the rewarded object and were not distracted by E's hand, we conducted two additional control sessions, each containing twelve trials, with single and double visible displacement tasks (SVD_free and DVD_free, in this order) where the object was attached to a 30 cm long fishing line. Subjects could hereby still see the hand and the object, but both had no direct contact. While baiting, E released the fishing line and the object slowly into the designated pot. In DVD_free trials where the first pot was baited, E moved his hand to the second pot and executed the same hand movement as if he was baiting it as well. Pre-tests were conducted as in Experiment 1a before each session. All other procedures were the same as in Experiment 1a.

Data scoring and analysis

Data scoring and analysis were the same as in Experiment 1a.

Experiment 2: Transpositions

Although solving classic transposition tasks requires Piagetian level 6 of object permanence, little is known of how contextual modifications of the setup may influence performance. For example, Rooijakkers *et al.* (2009) found that for dogs it was easier to follow a non-crossed compared to a crossed transposition. For this reason, we conducted a classic transposition task as well as transposition tasks with changes in the size, colour or movement of the pots to investigate whether any of these changes will affect the performance of the subjects.

Pre-test

Before each test session, a pre-test was conducted. Only the left (location 1) and the right pot (location 3) were used. The rewarded object was randomly put into one of the pots. After five out of six correct choices, the subject proceeded to the test session.

Test

We administered four different context specific conditions to the subjects, using (1) a crossed movement of two identical pots (same context: both dark brown coloured; diameter: 11 cm; height: 10 cm), (2) of two pots differing in colour (dark brown and light brown coloured, diameter: 11 cm; height: 10 cm), (3) of two pots differing in size (both dark brown coloured; diameter: 11 cm; height: 10 cm and diameter: 13 cm; height: 12 cm) and (4) a non-crossed movement with two identical pots (dark brown coloured, diameter: 11 cm; height: 10 cm). Each condition included twelve trials where conditions 1-3 were mixed within three sessions of twelve trials and condition 4 was presented in a separate session of twelve trials after the mixed conditions. In the crossed conditions, both pots changed their place after baiting from location

1 to location 3 and vice versa. In the non-crossed condition, pots were placed at location 1 and 2 or at location 2 and 3. After baiting in the non-crossed condition, both pots were moved one location to the right or to the left, respectively. In the crossed condition, the pot at location 1 was moved slightly earlier than the pot at location 3 to make it easier for the subject to follow the movements. Baiting location and different sized or coloured pots were randomized throughout the trials. One subject was excluded from the tests in Experiment 2 because it lacked motivation to participate at the end of Experiment 1. All three remaining subjects received the crossed sessions first. All other procedures were the same as in Experiment 1a.

Data scoring and analysis

For individual data, we conducted binomial tests. When a pig chose the correct pot ten times or more out of twelve trials this was counted as significant (P=.039) above chance level (50%).

Results

One subject refused to participate after the DVD trials and was therefore excluded from further testing. In Experiment 1a, only one subject (»2«) reliably chose the baited pot in all three fSVD trials but failed to choose the baited pot in the first A-not-B-error trial. Because all other subjects did not choose the baited pot reliably in all three fSVD trials, we did not analyse their choice behaviour in A-not-B-error trials in more detail. Three of four subjects performed above chance in the SVD trials, but none of them exceeded chance level in the DVD trials or in the two invisible displacement conditions (see Table 2). All three remaining subjects performed above chance in the SVD_free trials and one subject (»1«) did so in the DVD_free trials (see Table 1). In Experiment 2, none of the three subjects performed significantly above chance in any condition (see Table 3), but one subject was below chance in the non-crossed condition (two out of twelve correct choices).

Table 2 Individual performance of subjects (# of correct trials) in the eight conditions of Experiment 1a and 1b

| | Experiment 1a | | | | | | Experiment 1b | |
|---------|---------------|----------|-----------|-----------|-----------|-----------|---------------|-----------|
| Subject | fSVD | A-not-B | SVD | DVD | SID | SID_noDD | SVD_free | DVD_free |
| | 3 trials | 3 trials | 12 trials | 12 trials |
| 1 | 1 | 3 | 9 | 6 | 6 | 4 | 8 | 8 |
| 2 | 3 | 1 | 6 | 6 | 6 | 5 | 9 | 6 |
| 3 | 1 | 2 | 10 | 3 | - | - | - | - |
| 4 | 0 | 2 | 9 | 6 | 5 | 4 | 9 | 6 |

Performance was significantly above chance (33 %) when eight of twelve trials were correct (binomial test; *P*=0.036; excluding fSVD and A-not-B trials).

Table 3 Individual performance of subjects (# of correct trials) in the four conditions of Experiment 2

| Subject | Crossed – same features 12 trials | Crossed – different colour 12 trials | Crossed – different size 12 trials | Non-crossed – same features 12 trials |
|---------|---|--|--|---|
| 1 | 4 | 4 | 6 | 4 |
| 2 | 5 | 5 | 6 | 2 |
| 4 | 7 | 3 | 4 | 4 |

Performance was significantly above chance (50%) when ten of twelve trials were correct (binomial test; P=0.039).

Discussion

The results of Experiment 1 and 2 indicate a limited ability of young pigs to mentally represent hidden objects and especially movements of hidden objects seem to be difficult to track. At the beginning of testing, only one out of four subjects reliably chose the baited pot in all three fixed single visible displacement trials, but subsequently failed to choose the baited pot in the first A-not-B-error trial. Although being the performance of a single subject, one can speculate whether this error indicated a real perseveration error as found by non-human primates and human children - but unlike cats and dogs which skip the phase of committing A-not-B errors (Gómez 2004). For example, the subject could have relied on local enhancement or associative learning processes due to the sequential presentation of the reward on the opposite side in the fixed single visible displacement trials. Another explanation would refer to pigs' foraging behaviour, where they, contrary to most other species, exhibit a win-stay strategy in spatial foraging tasks (Mendl *et al.* 1997).

Three of four subjects solved the random visible displacement task and three out of three subjects solved the task when it was controlled for local enhancement. Surprisingly, only one subject solved the double visible displacement task when it was controlled for local enhancement whereas all subjects failed in the standard double visible displacement task, indicating individual difficulties to track a more complex movement of a particular object.

Individual performance in tasks involving invisible movements (single invisible displacements and all transpositions) did never exceed chance level nor did contextual modifications affect performance in transposition tasks.

Especially in the non-crossed transposition pigs preferred to choose the location where they have last seen the object disappearing, even when there was no pot present anymore. This pattern was also observed in dogs (Rooijakkers *et al.* 2009, Fiset & Plourde 2012). Interestingly, dogs were able to solve transpositions when the task was modified and the baited locations were only rotated for 90° instead of 180° (Miller *et al.* 2009). Nonetheless, by solving single and, under certain circumstances, double visible displacement tasks, subjects, even at this young age, may reach Stage 5b of object permanence (Piaget 1954). At this point, one might argue that pigs solved visible displacements relying on other cues (e.g. odour of the plastic or »Clever Hans« effects) or learned specific contingencies (e.g. choose the pot last touched by E's hand), but negative results in the invisible displacement and transposition tasks indicate that this was not the case.

From an applied perspective, future studies might address the question of how a basic grasp of object permanence affects animals' well-being. An increasing stage of object permanence may lead to (or cause) a higher environmental predictability, especially for re-appearing objects that first went out of sight. It remains to be clarified in particular whether this elicits boredom or whether it reduces stress by reducing surprising events in the environment. Physiological measures might contribute to answer this question (von Borell et al. 2007). On the other hand, the present study showed that an advanced object permanence in terms of tracking the movement of hidden objects is not existent at least in young pigs. The resulting novelty and/or suddenness of the (re-)appearance of particular objects and individuals can be a potential stressful event, eliciting physiological responses of different degree (Désiré et al. 2002), such as fear (Forkman et al. 2007). For example, a

study by Désiré *et al.* (2004) showed that lambs responded to suddenness of an appearing object with a startle response coupled with an increase in heart rate. Until now, there are no studies available investigating the physiological effects of (re-)appearing objects in pigs. It thus remains an open question, which housing and husbandry conditions might lead to such negative reactions in the animals due to their potential lack of full object permanence. The study presented here has also some limitations. First, the tested subjects were quite young and adult pigs, which remain to be tested, may have less problems in dealing with more complex movements of hidden objects. Second, the setup involved arbitrary stimuli, not present in the subjects' everyday experiences. Though speculative, setups that include highly familiar objects or conspecifics may reveal different results.

Nevertheless, examining the physical-cognitive capabilities of domestic pigs and farm animals in general can be integrated into new approaches to improve husbandry conditions and therefore animal well-being. Additionally, it might provide new insights into the phylogenetic origins of that trait and the ecological conditions causing its development. In summary, the results suggest that even a species that heavily relies on other, non-visual perceptual inputs like spatial or olfactory information, develops a basic understanding of object permanence. This should be taken into account when designing husbandry environments or future study designs.

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References

- Broom DM, Sena H, Moynihan KL (2009) Pigs learn what a mirror image represents and use it to obtain information. Anim Behav 78, 1037-1041
- Broom DM (2010) Cognitive ability and awareness in domestic animals and decisions about obligations to animals. Appl Anim Behav Sci 126, 1-11
- Call J (2001) Object permanence in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and children (*Homo sapiens*). J Comp Psychol 115, 159-171
- Collier-Baker E, Davis JM, Suddendorf T (2004) Do Dogs (*Canis familiaris*) Understand Invisible Displacement? J Comp Psychol 118, 421-433
- Croney CC, Adams KM, Washington CG, Stricklin WR (2003) A note on visual, olfactory and spatial cue use in foraging behavior of pigs: indirectly assessing cognitive abilities. Appl Anim Behav Sci 83, 303-308
- De Bois ST, Novak MA (1994) Object permanence in rhesus monkeys (*Macaca mulatta*). J Comp Psychol 108, 318-327
- De Blois ST, Novak MA, Bond M (1998) Object permanence in orangutans (*Pongo pygmaeus*) and squirrel monkeys (*Saimiri sciureus*). J Comp Psychol 112, 137-152
- Désiré L, Boissy A, Veissier I (2002) Emotions in farm animals: a new approach to animal welfare in applied ethology. Behav Processes 60, 165-180
- Désiré L, Veissier I, Després G, Boissy A (2004) On the Way to Assess Emotions in Animals: Do Lambs (*Ovis aries*) Evaluate an Event Through Its Suddenness, Novelty, or Unpredictability? J Comp Psychol 118, 363-374
- Doré FY, Dumas C (1987) Psychology of animal cognition: Piagetian studies. Psychol Bull 102, 219-233

- Doré FY (1990) Search behaviour of cats (*Felis catus*) in an invisible displacement test: Cognition and experience. Can J Psychol 44, 359-370
- Etienne AS (1973) Searching behaviour towards a disappearing prey in the domestic chick as affected by preliminary experience. Anim Behav 21, 749-761
- Fiset S, Plourde V (2012) Object permanence in domestic dogs (*Canis lupus familiaris*) and gray wolves (*Canis lupus*). J Comp PsychoL 127, 115-127
- Forkman B, Boissy A, Meunier-Salaün MC, Canali E, Jones RB (2007) A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. Physiol Behav 92, 340-374
- Gómez JC (2004) Apes, monkeys, children and the growth of mind.
- Harvard University Press, Cambridge, Mass., USA
- Gieling ET, Musschenga MA, Nordquist RE, van der Staay FJ (2012) Juvenile pigs use simple geometric 2D shapes but not portrait photographs of conspecifics as visual discriminative stimuli. Appl Anim Behav Sci 142, 142-153
- Held S, Mendl M, Devereux C, Byrne RW (2000) Social tactics of pigs in a competitive foraging task: the 'informed forager' paradigm. Anim Behav 59, 569-576
- Held S, Mendl M, Devereux C, Byrne RW (2001) Behaviour of domestic pigs in a visual perspective taking task. Behaviour 138, 1337-1354
- Held S, Mendl M, Laughlin K, Byrne RW (2002a) Cognition studies with pigs: Livestock cognition and its implication for production. J Anim Sci 80 (E-Suppl.), E10-E17
- Held S, Mendl M, Devereux C, Byrne RW (2002b) Foraging pigs alter their behaviour in response to exploitation. Anim Behav 64,157-165
- Kornum BR, Knudsen GM (2011) Cognitive testing of pigs (Sus scrofa) in translational biobehavioral research. Neurosci Biobehav Rev 35, 437-451
- McLeman MA, Mendl MT, Jones RB, Wathes CM (2008) Social discrimination of familiar conspecifics by juvenile pigs, *Sus scrofa*: Development of a non-invasive method to study the transmission of unimodal and bimodal cues between live stimuli. Appl Anim Behav Sci 115, 123-137
- Mendl M, Laughlin K, Hitchcock D (1997) Pigs in space: spatial memory and its susceptibility to interference. Anim Behav 54, 1491-1508
- Miller HC, Gipson CD, Vaughan A, Rayburn-Reeves R, Zentall TR (2009) Object permanence in dogs: Invisible displacement in a rotation task. Psychon Bull Rev 16, 150-155
- Natale F, Antinucci F, Spinozzi G, Potí P (1986) Stage 6 object concept in nonhuman primate cognition: A comparison between gorilla (*Gorilla gorilla gorilla*) and Japanese macaque (*Macaca fuscata*). J Comp Psychol 100, 335-339
- Nawroth C, Ebersbach M, von Borell E (2013) Are juvenile domestic pigs (*Sus scrofa domestica*) sensitive to the attentive states of humans? The impact of impulsivity on choice behaviour. Behav Processes 96, 53-58
- Neiworth JJ, Steinmark E, Basile BM, Wonders R, Steely F, DeHart C (2003) A test of object permanence in a new-world monkey species, cotton top tamarins (*Saguinus oedipus*). Anim Cogn 6, 27-37
- Pepperberg IM, Funk MS (1990) Object permanence in four species of psittacine birds: An African Grey parrot (*Psittacus erithacus*), an Illiger mini macaw (*Ara maracana*), a parakeet (*Melopsittacus undulatus*), and a cockatiel (*Nymphicus hollandicus*). Anim Learn Behav 18, 97-108
- Piaget J (1954) The construction of reality in the child. International Universities Press, New York, USA
- Regolin L, Vallortigara G, Zanforlin M (1995) Object and spatial representations in detour problems by chicks. Anim Behav 49, 195-199
- Rooijakkers EF, Kaminski J, Call J (2009) Comparing dogs and great apes in their ability to visually track object transpositions. Anim Cogn 12, 789-796
- Tanida H, Senda K, Suzuki S, Tanaka T, Yoshimoto T (1991) Colour discrimination in weanling pigs. Anim Sci Technol 62, 1029-1034

- Tanida H, Nagano Y (1998) The ability of miniature pigs to discriminate between a stranger and their familiar handler. Appl Anim Behav Sci 56, 149-159
- Van Rooijen J (1991) Predictability and boredom. Appl Anim Behav Sci 31, 283-287
- Von Borell E, Langbein J, Després G, Hansen S, Leterrier C, Marchant-Forde J, Marchant-Forde R, Minero M, Mohr E, Prunier A, Valance D, Veissier I (2007) Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals A review. Physiol Behav 92, 293-316
- Zonderland JJ, Cornelissen L, Wolthuis-Fillerup M, Spoolder HAM (2008) Visual acuity of pigs at different light intensities. Appl Anim Behav Sci 111, 28-37
- Zucca P, Milos N, Vallortigara G (2007) Piagetian object permanence and its development in Eurasian jays (*Garrulus qlandarius*). Anim Cogn 10, 243-258