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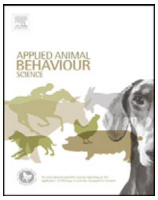

The effect of domestication and ontogeny in swine cognition (*Sus scrofa scrofa* and *S. s. domestica*)

Anna Albiach-Serrano[a], Juliane Bräuer[a], Trix Cacchione[b], Nele Zickert[a], Federica Amici[a,*]

[a] *Department of Comparative and Developmental Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*
[b] *Department of Psychology, Cognitive and Developmental Psychology, University of Zürich, Binzmühlestrasse 14/21, CH-8050 Zürich, Switzerland*

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ABSTRACT

Domesticated animals show physical, behavioural and cognitive differences from their closest wild relatives. This may have resulted from the former's long and continued selection by humans throughout history, but in some cases it could just reflect developmental differences between wild and domestic animals, given that their environments usually differ significantly. In order to investigate possible effects of domestication and ontogeny on swine cognition, we tested wild boars and two groups of domestic pigs living in more and less enriched conditions. In an object choice paradigm subjects had to find food hidden in one of two containers. They received either a physical cue (i.e., the slope of the board hiding the food, the presence or absence of noise from a shaken container, the sight of a baited container changing position) or a human social cue (i.e., touching, pointing, gazing). According to the domestication hypothesis, given similar rearing conditions domestic pigs should perform better than wild boars when receiving social cues but worse when receiving physical cues. According to the developmental hypothesis, more experienced swine should perform better than less experienced swine both in the physical and in the social domain. Subjects performed better when provided with cues on which they had received adequate experience from their environment, thus providing support to the developmental hypothesis. We conclude by suggesting that specific experience on particular stimuli rather than general experience on a wider range of stimuli may explain swine ability to solve both social and physical tasks.

1. Introduction

Domestication has been defined as a process of natural and artificial selection, with adaptation to an often captive environment achieved through genetic changes occurred over generations and environmentally induced developmental changes recurring during each generation (Price, 1984). In comparison to their closest wild relatives, domestic animals show greater gregariousness, less wariness, more playfulness, earlier sexual maturity and more frequent receptivity (Zeder, 2006). Some of these behavioural traits may have been actively (although not necessarily intentionally) selected by humans to increase benefits or to facilitate management, whereas others may be by-products of this selection or mere consequences of life in captivity.

Compared to natural environments, captive environments are usually more stable and predictable. The space available and the number of conspecifics are limited, the likelihood of being attacked by a (non-human) predator is low, resources usually appear recurrently at the same time and location and they are easily accessible. Moreover, domestic animals live close to and depend on humans for obtaining food. It is possible that their long history of

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* Corresponding author. Tel.: +49 341 3550 455.
E-mail address: abbepu@yahoo.it (F. Amici).

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domestication has impoverished their ability to cope with the physical environment, with human intervention relaxing selective pressures on species' specific behavioural patterns (Frank, 1982). On the other hand, this background may have equipped them with the ability to use human cues for their own benefit (Hare et al., 2002; Hare and Tomasello, 2005; Miklosi et al., 2003; Virányi et al., 2008).

The main aim of the current study was to compare the cognitive skills of domestic and wild animals, both in the physical and in the human social domains, using swine as a model. Indeed, wild boars (*Sus scrofa scrofa*) and domestic pigs (*Sus scrofa domestica*) are reported to share common wild ancestors (Larson et al., 2005, 2007). Swine are especially interesting because, unlike the other main domesticates (i.e., goat, sheep, cattle and dog), they are omnivorous. For that reason, wild boars require good general skills to exploit their complex natural physical environment, whereas domestic pigs might have lost some of these skills in their captive environment, as they are potentially redundant (but see Held et al., 2002b). On the other hand, being omnivorous has determined a particular domestication history for pigs, characterized by a close contact with humans, that partially resembles that of dogs. In an initial phase, wild boars (especially the ones that were less scared of humans) might have been attracted to leftover food and cultivated plants in human settlements. Deemed useful as meat stock and in order to recycle waste, some of them (especially the tamer ones) were probably tolerated in the camps or, alternatively, caught and kept in captivity (Hongo and Meadow, 1998). Such close contact with humans might have enhanced those abilities related to the use of human cues by domestic pigs, although probably to a lesser extent than dogs which, in addition to being camp scavengers and potential meat stock, served as hunting companions and house pets (Clutton-Brock, 1995; Hongo and Meadow, 1998).

However, when comparing domestic animals and their wild relatives one needs to consider that they usually experience different environments throughout their ontogeny and cognitive differences could therefore be explained by developmental factors rather than evolutionary ones. A second aim of the present study was consequently to assess the extent to which possible cognitive differences between wild boars and domestic pigs reflect genetic variation or simply porcine behavioural flexibility during ontogeny.

To investigate the potential effects of domestication and ontogeny on swine cognition we used an object choice paradigm in which subjects have to choose between two opaque containers, only one of which has been baited with a food reward. The experimenter provides a physical or a social cue as to where the food has been hidden. Physical cues are given when the subject is provided with physical information about food location, for example the inclination of a board that has food below it, the noise coming from a shaken container that has food inside it or the visible displacement of a baited container from one location to another. The choice of the correct container implies that the subject understands something about basic principles of the physical world, such as the causal connection between objects, how objects affect the orientation of other objects and produce noises under different circumstances or the way objects move (Bräuer et al., 2006; Call, 2004, 2006, 2007). Social cues, on the other hand, are given when the behaviour of the experimenter provides information about where the food reward is hidden. This information can be either behavioural (i.e., reaching towards the correct container) or communicative (i.e., if the experimenter is looking at the subject while indicating the food location using gestures such as pointing, gazing or touching the correct container). To what extent animals use these gestures and understand their communicative intent or whether simpler mechanisms like local enhancement are at play is still a matter of lively debate (Miklosi and Soproni, 2006; Povinelli et al., 1997).

Previous studies have investigated domesticated species' abilities to use social cues in order to locate hidden food. For example, domesticated species reliably use touching (horses: McKinley and Sambrook, 2000; goats: Kaminski et al., 2005) or pointing as a cue (cats: Miklosi et al., 2005; horses: Maros et al., 2008; Proops et al., 2010; goats: Kaminski et al., 2005). Moreover, domestic dogs show a flexible use of a variety of social cues from the first trial onwards and even at the age of 6 weeks, they appear to perceive the situation as being communicative and they are more adept at using human cues than their wild relatives, the wolves (e.g., Bräuer et al., 2006; Hare et al., 1998, 2002, 2010; Miklosi and Soproni, 2006; Riedel et al., 2008). Some authors have therefore argued that, at least in dogs, the ability to read human cues has been mainly developed during domestication, with ontogeny playing a less important role. However, other studies suggest that ontogenetic experience is important to understand human social cues, with dogs' ability to use human cues improving with age, and wolves raised with intensive social contact to humans also being able to read complex human social cues (e.g., Barrera et al., 2011; Dorey et al., 2010; Elgier et al., 2009; Udell et al., 2008, 2010a,b).

On the other hand, very few studies have investigated domesticated species' abilities to use physical cues to locate hidden food. These studies have shown that, in contrast to their good performance in social tasks, both cats and dogs can only master the easiest conditions of transposition tasks (i.e., object permanence tasks; cats: Doré et al., 1996; dogs: Collier-Baker et al., 2004; Rooijakkers et al., 2009). When Bräuer et al. (2006) compared the performance of chimpanzees and domestic dogs on a series of object choice tasks, dogs were especially skillful when being provided with a social cue and chimpanzees performed better when provided with physical cues. The authors argued that domestic dogs might have evolved human cue reading skills during the domestication process, but might have lost some of their skills for understanding physical cues, since humans solve many causal problems for them (Bräuer et al., 2006; Frank, 1980).

Previous studies on domestic pigs have shown that they have good spatial memory (Laughlin et al., 1999; Mendl et al., 1997) and can discriminate food sites on the basis of quantity (Held et al., 2005). Pigs are also able to use cues provided by conspecifics to find food, following informed partners to a food location, and they adjust their foraging behaviour to maximize food intake when they are victims of exploitation (Held et al., 2000, 2002a). However, to our knowledge swine have not been tested in object choice tasks before, and no direct experimental comparison between wild boars and domestic pigs has so far been conducted.

In the present study we aimed at doing a first exploration of the roles that domestication and ontogeny might play on swine cognition. With this purpose, we systematically compared wild boars and domestic pigs using a series of object choice tasks which have already been successfully used with several other species to measure their ability to use social and physical cues to infer the location of hidden food (see Bräuer et al., 2006). We compared (i) the performance of wild boars and domestic pigs living in similar environments (WB+ and DP+, respectively) and (ii) the performance of domestic pigs living in environments that allowed them more versus less physical and social experience (DP+ and DP−). We wanted to contrast two different hypotheses, (i) whether domestic pigs are more capable than wild boars at using human social cues to locate hidden food, but less adept at using physical cues (domestication hypothesis, or DOM), and (ii) whether swine whose rearing conditions have allowed more physical and social experience during ontogeny perform better than swine who have been raised in “poorer” rearing conditions (developmental hypothesis, or DEV_GENERAL). An alternative version of the DEV hypothesis would be that (iii) rather than generally richer conditions (i.e., exposure to a greater variety of stimuli) leading to a generally better performance, it is specific experience (with specific stimuli) which allows the mastery of related specific problems, regardless of them belonging to the physical or the social domain (DEV_SPECIFIC).

2. Methods

2.1. Subjects

Between July 2008 and July 2009, we tested 7 wild boars (*S. s. scrofa*) from the Wildpark in Leipzig, Germany (WB+), 12 domestic pigs (*S. s. domestica*) from a farm in Colfiorito, PG, Italy (DP−; breed: large white), and 15 domestic pigs from a farm in Leipzig, Germany (DP+; breed: Edelschwein, Deutsches Sattelschwein, Angeln Saddleback, Bentheim, Duroc). Since we were interested in comparing swine at the subspecies level, we did not consider breed in our analyses. All three groups had members of both sexes (WB+: 3/7 males, DP+: 3/9 males, DP−: 8/12 males) and contained both adults and subadults (WB+ and DP+: 03–72 months, DP−: 03–24 months; because exact ages could not be ensured for some subjects, we decided to use a broader classification; see Table 1 for details). Unfortunately, we do not have information about kin relationships within groups. None of our subjects had participated in any study before. The reduced number of WB+ as compared to the other subspecies was due to the difficulty of habituating them to the set-up and separating subjects from the group to perform testing (see below).

2.2. Area descriptions

WB+ lived together with 15 other wild boars in a large outdoor enclosure (2.6 ha) situated within a forested area and thus containing natural vegetation, water sources, mud ponds, rocks and other natural features. They were usually fed only in winter, once daily, with a variety of fruit, bread and fodder that was poured in a specific area of their enclosure. Although we tested the wild boars in summer–autumn, we provided them with some food that helped us directing them to the area of their enclosure where we carried out the tests. In addition, WB+ were usually exposed to the public, who could throw food over the fence from any point in the perimeter of their enclosure (although people did not have direct contact with the boars, thanks to a second fence situated about 1.5 m from the main one). When performing experiments, signs around the testing area successfully prevented the public from interfering with the experiment by, for example, attracting subjects with food towards another part of the enclosure.

DP+ had diverse living arrangements: (i) single- or pair-housed in indoor stalls (approximately 2 m × 4 m), (ii) pair or group-housed in indoor stalls with access to an outdoor enclosure (approximately $40\,\mathrm{m}^2$), and (iii) pair- or group-housed in outdoor stalls (approximately $100\,\mathrm{m}^2$). Individuals had access to the outdoor areas in a rotating system according to the needs of the farm. Male breeding pigs lived outside all year round, accompanied by one or two females whenever they came into heat. Females and juveniles were rotated every two months so that all pigs had similar outdoor-access. The ground was covered with bark mulch and muddy puddles in the outdoor enclosures, and with straw bedding in the indoor ones. All pigs had daily hands-on contact with various keepers and visitors both in- and outdoors. Pigs were fed twice a day with bruised grain, soilage and swill. Additionally, they were fed irregularly by visitors with fruit and vegetables under the supervision of the farm keepers.

Finally, DP− lived in groups of 12–15 individuals. Each group shared an indoor area made of concrete (4 m × 3 m) and had brief weekly access to an outdoor area (12 m × 8 m) with earth ground and other basic natural features. Pigs were fed four times a day with liquid pig food and only had brief daily contact with familiar farmers during cleaning procedures or when being moved to the outdoor area, which did not include petting or feeding by hand.

Although ideally WB+ and DP+ would live in similar, rich environments whereas DP− would live in different, poorer conditions, the samples available were limited and only partially we fulfilled this requirement. For example, WB+'s enclosure was larger than DP+'s and their group size was also bigger. Also, DP+'s living conditions differed from DP−'s not only in the physical and human social input but also in group size and in that both groups were managed differently and fed different food. Nevertheless, note that these variables do not seem especially relevant for the problems presented here, whereas groups differed in the aspects critical for our tests, in the required way: on the one hand, both WB+ and DP+ had experience with solid food, different types of substrate (that could sometimes work as a visual barrier for the food) and humans moving the food, often by throwing it towards the vicinity of the subject. On the other hand, DP− fed from automatic dispensers of liquid food, which reduced their opportunities of interaction with humans, and spent most of their time on a hard

Table 1
Subjects participating in the study.

Group	Subject	Name	Breed	Sex	Age (months)	Age (group)
WB+	01	Rudi	–	M	72	Adult
	02	Blackie	–	F	13–36	Adult
	03	Brush	–	F	13–36	Adult
	04	Spot	–	M	13–36	Adult
	05	Zorro	–	M	13–36	Adult
	06	Moon	–	F	03	Subadult
	07	Cut	–	F	03	Subadult
DP+	08	Wolfgang	Deutsches Sattelschwein	M	36	Adult
	09	Balduin	Bentheim	M	12	Adult
	10	Eik	Duroc	M	36	Adult
	11	Schecki	Angeln Saddleback/Bentheim	F	24	Adult
	12	Orthrun	Edelschwein	F	36	Adult
	13	Seelchen	Deutsches Sattelschwein	F	72	Adult
	14	Perle	Bentheim	F	10	Subadult
	15	Merle	Angeln Saddleback	F	10	Subadult
	16	Wanja	Duroc	F	72	Adult
	17	Nemo	Bentheim/Duroc		03	Subadult
	18	Arrow	Bentheim/Duroc		03	Subadult
	19	Pinpoint	Bentheim/Duroc		03	Subadult
	20	Argus	Bentheim/Duroc		03	Subadult
	21	Edward	Bentheim/Duroc		03	Subadult
	22	Blacktop	Bentheim/Duroc		03	Subadult
DP−	23	01	Large white	M	13–24	Adult
	24	02	Large white	M	13–24	Adult
	25	03	Large white	F	13–24	Adult
	26	04	Large white	M	13–24	Adult
	27	05	Large white	M	13–24	Adult
	28	06	Large white	M	13–24	Adult
	29	07	Large white	F	13–24	Adult
	30	08	Large white	F	13–24	Adult
	31	09	Large white	F	13–24	Adult
	32	10	Large white	M	03–12	Subadult
	33	11	Large white	M	03–12	Subadult
	34	12	Large white	M	03–12	Subadult

Name, breed, sex and age of the subjects included in the study. WB+: wild boars; DP+: domestic pigs from an enriched, similar environment to that of WB+; DP−: domestic pigs from a less enriched environment; M: male; F: female; adult: older than 12 months, subadult: younger than 12 months; blank space: information is unknown because the keepers in the farm were not able to determine the sex of young piglets.

ground with no objects to explore apart from their conspecifics. Most of our subjects were born in the same place where we tested them, being together with their mother and siblings at least until weaning. DP− were moved to the farm in which testing took place before 3 months of age, from a close-by farm in which reproduction took place and subjects were housed in comparable conditions. Therefore, in principle, the descriptions above account for all the experience they had with space, materials, types of food, conspecifics and contact with humans. As we already noted above, none of the subjects had participated in any cognitive study before.

In all three groups subjects were tested individually. In the case of swine living indoors, they were isolated in a partition within their enclosure (DP+: 2 m × 1 m, DP−: 4 m × 3 m). In the case of swine living outdoors (DP+, WB+), the experimenter attracted the subject to the testing area while keeping the others away by using food. Because wild boars lived in a large group, a helper (NZ) was needed. She provided food to the boars from a point in the fence 8 m from the testing area, which permitted the experimenter to test subjects without too much disturbance from other boars. Importantly, although this meant testing different groups under different conditions (i.e., outside or inside), it allowed us to test all subjects in areas that were equally familiar to them (Hare et al., 2002; Udell et al., 2008; Virányi et al., 2008). In all cases, subjects kept visual, auditory and potentially tactile contact with the rest of the group. To allow a better comparability of data, subjects of all species were only tested after having been habituated to the experimenter and the apparatus (i.e., when they were not afraid of the experimenter or to retrieve food from the apparatus through the bars of the fence). Importantly, the habituation phase never consisted in subjects retrieving food from baited cups or boards but only from the table that would later be used to support the testing materials (see below). During the test, subjects were never food deprived and water was always available. None of the subjects had participated in any kind of study before.

2.3. Materials

A low table placed against the fence outside the subjects' enclosure provided a flat support for a plastic platform (180 cm × 50 cm; Fig. 1). All subjects of all groups were tested in this way, with the fence between the subject and

Fig. 1. Experimental set-up.

the experimental set-up. Subjects could retrieve food from one of two potential positions on the platform, about 50 cm apart from each other, by inserting their snout through the fence. Food was always shown to the subject before being placed in one of the two positions. In some conditions (see Section 2.4), the baiting process was hidden from the subject by interposing a plastic barrier (170 cm × 60 cm) between the subject and the table. Food was either hidden beneath one of two identical opaque plastic cups (Ø 11 cm × 10 cm), in some cases covered with lids (15 cm Ø), or below one of two opaque plastic boards (30 cm × 20 cm) which could be positioned in different ways (i.e., flat versus inclined 45° with the help of a concealed wooden leg). Dog food (Frolic) was used as a reward for WB+ and DP+, and little vanilla biscuits were used for DP−, following the advice of the keepers of each group. Both of these were highly preferred foods for the animals and were not included in their usual diets.

2.4. Procedure

In case of necessity, before starting a trial the experimenter (E) used low-value food (e.g., bread) to position the subject (S) centred with respect to the platform. Then, E showed the food to S and, as soon as S paid attention, she baited the cups or boards. Baiting was performed either behind a visual barrier or in full view of the subject, according to the condition (see below). The barrier was removed after the baiting procedure was over. For the social tasks E gave a cue (lasting approximately 3 s) to indicate the location of the food. E then pushed the platform towards S while looking directly ahead. If no choice was made within 1 min, E stopped the session and continued it later on the same or another day, to avoid that motivational issues might affect individuals' performance. In this case, subjects were not shown where food had been placed by uncovering it, to avoid that subjects interrupting more sessions gained more experience than the other ones. However, the necessity to interrupt a session was rare for the domestic pigs (less than 5 times across all trials for each group) and wild boars (10 times across all subjects, mostly because other boars sometimes displaced the subjects, eventually distracting them). When S made a choice, by touching a container or by putting its snout within less than 10 cm of it through the fence, E lifted the chosen container. In the event of a correct choice, S could access and eat the food, if necessary with the help of E. In the event of an incorrect choice, E showed S the empty container, pulled the platform back and then showed S the content of the non-chosen, baited container. Subsequently, a new trial started. Subjects received a pre-test phase, 2 control conditions and 7 different experimental conditions, with either social or physical cues being given (see Fig. 2). Videos of each condition are available in supplemental online material.

2.4.1. Pre-test phase

E showed S two empty cups and then, in full view of S, baited one of the cups and pushed the tray forwards. The pre-test phase ended when S had chosen the correct cup in 4 consecutive trials (see Bräuer et al., 2006). This phase aimed to ensure that motivation and the appropriateness of both the set-up and the general procedure were comparable across subspecies. However, food in this phase was never manipulated like in the experimental conditions, to avoid that subjects receiving more pre-test trials could benefit from a more extensive experience in the experimental conditions. Success in this phase was reached in 4–30 trials for all subspecies (mean number of trials (WB+): 12.57; (DP+): 4.66; (DP−): mean not available). Note that none of these subjects had ever been tested before on a cognitive task and the set-up and the procedure were thus completely novel to them. In addition, WB+ were not used to the close presence of humans, which might explain why some subjects needed many trials before succeeding in the pre-test.

2.4.2. Social cues

1. *Gazing*. While occluded by the barrier, E hid the food below one of two cups. After releasing the barrier, she alternated her gaze twice (with head movement) from S's eyes to the correct cup, before looking straight ahead and pushing the platform forwards.
2. *Pointing*. The procedure was identical to that of the previous condition but, in addition and coordinated with the gazes, E stretched out her arm twice to point at the correct cup with the index finger of her ipsilateral hand (see Bräuer et al., 2006). The index finger only extended once the arm had reached its final position and the fingertip was approximately 10 cm from the cup upon completion of the gesture.
3. *Touching*. The procedure was identical to that of the previous condition with the following exception. E stretched out her arm twice to touch the upper part of the baited cup with the palm of her hand while maintaining her gaze on the cup. Note that both in the pointing and in the touching conditions the trajectory of the hand was directed from the body to the final extension rather than in an arc motion from above.

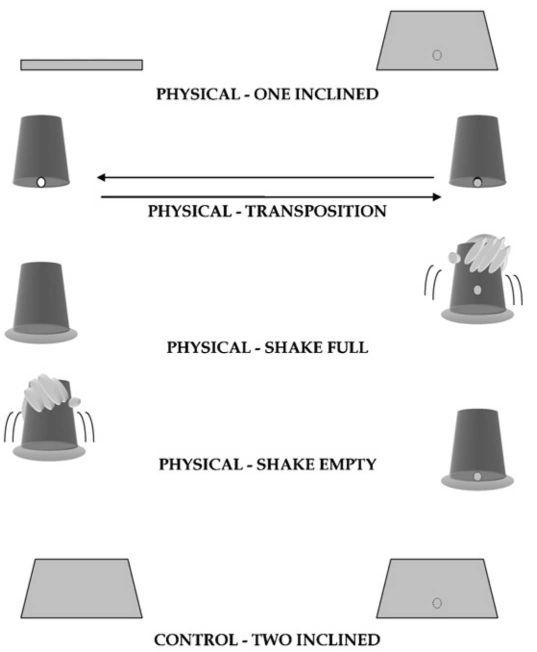

Fig. 2. Schematic representation of the social, physical and control conditions in the experiment. Food rewards were not visible to the subject and are represented here with grey little dots. White dots represent the original position of the food reward, before transposition took place (as indicated by the arrows).

2.4.3. *Physical cues*

4. *One inclined*. While occluded by the barrier, E hid the food below one of two boards. One board had an inclination of approximately 45° and allowed the food to be hidden beneath; the other remained flat on the platform and did not permit this. S could therefore infer the location of the food reward by the fact that the board was inclined (see Call, 2007).
5. *Transposition*. In full view of S, E baited one cup and then performed a transposition, so that the baited cup and the un-baited cup switched their locations. Each cup was moved with E's ipsilateral hand and upon reaching the middle of the platform E switched her hands in order to complete the transposition.
6. *Shake full*. While occluded by the barrier, E hid the food below one cup. After removing the barrier, E raised the baited cup with her ipsilateral hand and shook it twice to make a clear noise while looking at it. S could infer the position of the food because noise should be caused by the presence of food (see Bräuer et al., 2006; Call, 2004).
7. *Shake empty*. The procedure was similar to that of the previous condition, but this time E shook the un-baited cup. S could infer the position of the food by exclusion (i.e., food should cause a noise in the shaken container, thus the reward has to be in the other cup). This condition also controlled for the possibility that subjects used the cup shaking as a social cue rather than as a physical cue, since the cup touched by E was the empty one.

2.4.4. *Controls*

8. *Two cups*. While occluded by the barrier, E hid the food below one of two identical cups and subsequently did not provide a cue. This condition controlled for the possibility that S could smell or see the food or used cues given inadvertently by E in order to find it.
9. *Two inclined*. While occluded by the barrier, E hid the food below one of two identical boards both of which were inclined 45° from the platform. Thus, food could potentially be under both boards. This condition controlled for the possibility that S could smell or see the food or used cues given inadvertently by E in order to find it.

2.5. *Design*

After passing the pre-test phase, each subject completed 2 sessions of 18 trials each (2 trials for each of the 9 conditions described above, alternating the side of the baited cup within conditions). Within each session, subjects were first presented with conditions 1, 2, 3 and 8 ("social block") and then with conditions 4, 5, 6, 7 and 9 ("physical block"), or vice versa. This order was counterbalanced between subjects and also for each subject, between the two sessions. The order of the trials within a block was random, with the only constraint being that the food could not appear on the same side more than twice in a row. Consequently, every subject underwent a total of 36 trials, 4 for each of the 9 conditions. None of the subjects received more than one session per day.

2.6. *Ethical approval*

All our experiments complied with the International Guiding Principles for Biomedical Research Involving

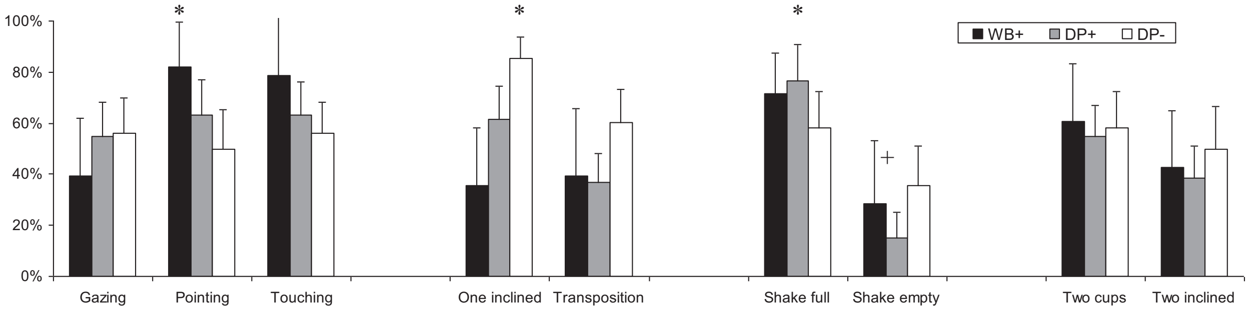

Fig. 3. For the wild boars (WB+) and the two groups of domestic pigs (DP+ and DP−), mean percentage of correct choices and confidence intervals at 95% in each of the nine administered conditions. '*' denotes a performance significantly above chance level; '+', a performance significantly below chance level ($p < 0.05$).

Animals as issued by the Council for the International Organizations of Medical Sciences.

2.7. Data analysis

All trials from WB+ and DP+ and DP− were coded live and recorded by AAS, NZ and FA, respectively. A second observer coded 25% of all the trials from the video-recordings. The second observer was naïve to the hypotheses and blind: as soon as the subject made a choice, she stopped the tape and coded before seeing the experimenter's reaction to the subject's choice. In both cases, inter-observer reliability was excellent (Cohen's *kappa* (WB+) = 1.00, $n = 61$; Cohen's *kappa* (DP+) = 0.97, $n = 132$; Cohen's *kappa* (DP−) = 0.98, $n = 105$). Tapes from DP− were not kept after having been coded for inter-observer reliability.

We minimized the negative consequences of using different experimenters (AAS, NZ and FA) by using very basic experimental procedures. Moreover, NZ tested DP+ only after having assisted AAS testing WB+ (see Section 2.1) and FA tested DP− only after having observed videos of AAS testing WB+. We minimized the influence of learning by administering a reduced number of trials per task.

Our dependent variable was the percentage of correct trials. Because the homogeneity of variance assumption was violated, we used nonparametric statistics. For each of the three groups, we analysed deviation from chance across conditions and in the general task categories (social, physical and control; Wilcoxon test). Also, we analysed the effect of group on the percentage of correct trials in each condition and in each of the general task categories (Mann–Whitney test). All tests used exact and two-tailed probability, with the α level set at 0.05. We decided not to use any correction for multiple testing, to avoid being overly conservative and promoting type II errors (e.g., Perneger, 1998; Nagakawa, 2004). When small sample sizes ($n < 6$) occurred due to tied observations, we did not conduct within-subject tests of significance, since the impossibility to reject the null hypothesis would render the tests uninformative (Siegel and Castellan, 1988). In those cases, we simply indicated this in Section 3. Only significant results are reported.

3. Results

3.1. Performance in the different conditions

Fig. 3 shows the overall performance in each condition (percentage of correct choices in all trials) for all three groups of subjects. WB+ were significantly above chance in the "pointing" ($n = 6$, $T = 21$, $p = 0.031$) condition, and at chance level in the "shake empty" condition. In the other conditions, we conducted no statistics for the WB+ due to the reduced sample size. DP+ were above chance in the "shake full" condition ($n = 13$, $T = 93.5$, $p = 0.005$) and significantly below chance level in the "shake empty" condition ($n = 13$, $T = 91$, $p < 0.001$). Finally, DP− were above chance in the "one inclined" condition ($n = 12$, $T = 78$, $p < 0.001$). None of the groups was above chance in either of the control conditions (although, due to tied observations, no analyses were run for the WB+ in the "two inclined" control condition).

3.2. Performance in the general task categories: social, physical and control

For a more general analysis we grouped the various conditions into three categories: social ("gazing", "pointing" and "touching"), physical ("one inclined" and "transposition") and control ("two cups" and "two inclined"). The fact that DP+ were above chance in the "shake full" condition but below chance level in the "shake empty" condition suggests that the "shake" conditions could have been interpreted by some subjects as social conditions (i.e., S provides social information to S by shaking a cup) rather than physical conditions (i.e., if the shaken cup produces noise, then it must be baited; if it does not, then food must be in the other cup). Therefore, we excluded both the "shake full" and the "shake empty" conditions from all the following analyses. Fig. 4 presents the mean percentage of correct choices for the two groups of domestic pigs and the wild boars in all three task categories. DP+ were significantly above chance in the social tasks ($n = 8$, $T = 51$, $p = 0.014$), and DP− were above chance in the physical tasks ($n = 11$, $T = 66$, $p = 0.001$). Importantly, all groups performed at chance level in the tasks controlling for olfactory cues ("two cups" and "two inclined").

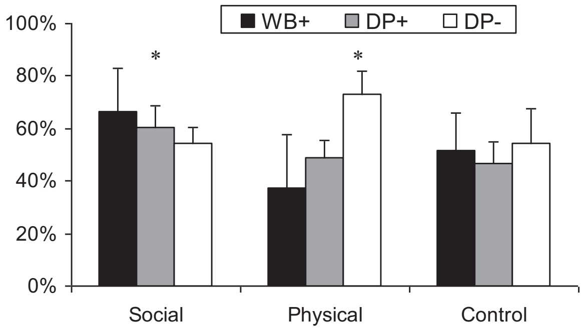

Fig. 4. For the wild boars (WB+) and the two groups of domestic pigs (DP+ and DP−), mean percentage of correct choices and confidence intervals at 95% in each of the three general task categories (social, physical and control), without "shaking" conditions. '*' denotes a performance significantly above chance level ($p < 0.05$).

3.3. *Comparison between subspecies living under similar conditions (WB+ versus DP+)*

DP+ outperformed WB+ in the "one inclined" condition ($n_1 = 7$, $n_2 = 15$, $U = 23.5$, $p = 0.039$; Fig. 3). They did not differ in any other condition. Also, they did not differ in either of the general task categories (Fig. 4).

3.4. *Comparison between groups of the same subspecies living under different conditions (DP+ versus DP−)*

DP− were significantly better than DP+ in the "one inclined" condition ($n_1 = 12$, $n_2 = 15$, $U = 36.5$, $p = 0.007$), in the "transposition" condition ($n_1 = 12$, $n_2 = 15$, $U = 39.5$, $p = 0.012$), and in the "shake empty" condition ($n_1 = 12$, $n_2 = 15$, $U = 45.5$, $p = 0.028$), but they performed significantly worse than DP+ in the "shake full" condition ($n_1 = 12$, $n_2 = 15$, $U = 46$, $p = 0.032$; Fig. 3). With regard to the general task categories, DP− outperformed DP+ in the physical tasks ($n_1 = 12$, $n_2 = 15$, $U = 16.5$, $p < 0.001$), but not in the social tasks (Fig. 4).

4. Discussion

In contrast to DOM, wild boars did not outperform domestic pigs in the physical tasks and domestic pigs did not outperform wild boars in the social tasks. Instead, both groups performed similarly in both task categories. Also, in contrast to DEV_GENERAL, domestic pigs raised in more enriched conditions did not outperform domestic pigs raised in less enriched conditions, neither in the physical nor in the social domain. On the contrary, the latter outperformed the former in the physical tasks. However, more detailed analyses suggest that success in particular tasks might depend on subjects having acquired specific experience with particular stimuli in their environment, rather than on their general experience in a given domain, as predicted by DEV_SPECIFIC.

Importantly, none of the groups was above chance level in any of the control conditions, showing that subjects could not rely on olfactory, visual or inadvertent cues given by the experimenter to solve the task.

In the experimental conditions, only WB+ solved the social task "pointing". Note that the fact that wild boars use the human pointing gesture is remarkable as to date this has only been shown in either domesticated animals or in individuals that grew up with close human contact, which was not the case for these boars. Our results could be explained by the fact that WB+ often receive solid food from humans. People throw the food into their enclosure performing a gesture that potentially resembles pointing, and they occasionally even point to the food if an individual has not found it, for pointing is a very natural gesture for humans (Tomasello, 2008). In contrast, DP− obtain their liquid food from dispensers, and therefore the availability of food for them does not strictly depend on any obvious action from humans or even on their presence. Also DP+ could not solve the social task "pointing": although they live in closer contact to humans, however, food is not thrown in their enclosures and pointed to with the same frequency as in the case of WB+. Thus, it is possible that the ability to use pointing cues in swine is not innate but is rather developed during ontogeny. The question remains whether WB+ really learnt something about the communicative nature of these cues or if they just learnt the connection between a human hand and food (Giret et al., 2009; Proops et al., 2010). A similar question stands for the fact that swine also use conspecifics' cues to find food (Held et al., 2000).

The "touching" condition was not solved by any group. This is surprising, as this condition should be easier to master than any of the other administered social conditions, given that the touching cue is quite obvious. Also "gazing" was not solved by any group. In domestic pigs, exchanges of glances are used as non-agonistic interactions in order to maintain group cohesion and organization (Stolba and Wood-Gush, 1989). Moreover, it is conceivable that gaze following plays a role in predator avoidance in swine as it happens in other species (Jaime et al., 2009). However, gaze is a subtle cue and using another species' gaze to find food does not seem very relevant for swine, either in the wild or in captivity. Many species other than swine do not follow human gaze to locate hidden food (Call et al., 1998; Kaminski et al., 2005; Neiworth et al., 2002; Peignot and Anderson, 1999; Proops et al., 2010) and evidence suggests that even dogs, which are well known for using human communicative cues, may not be able to do this (Bräuer et al., 2006; Hare et al., 2002).

With regard to the physical tasks, the "one inclined" condition was only solved by DP−, who outperformed DP+ who in turn outperformed WB+. Interestingly, this correlates positively with each group's level of exposure to hard ground. Whereas the floor in DP−'s main enclosure is made of concrete and therefore any solid object occupies a volume above the ground level (and any cover resting on top of this object will necessarily be inclined), most of the area of DP+'s enclosure has earth as a substrate, so that small objects are not so salient. Finally, WB+'s enclosure is a parcel of humid forest including a stream, where mud is the main substrate. As a consequence, solid objects sink into the mud and any cover resting on top of these objects will not necessarily show an incline from ground level. Indeed, WB+ spend most of their foraging time searching for food in the mud.

None of the swine solved the “transposition” condition, since the three groups of subjects were at chance level. However, according to the literature only primates (e.g., Amici et al., 2010; Beran et al., 2005; Rooijakkers et al., 2009) and two bird species (Pepperberg et al., 1997; Zucca et al., 2007) have solved this problem so far. It is interesting that the domestic pigs that had closer contact with humans (DP+) performed worse than DP− and seemed to rely on the strategy of choosing the location where the food had last been seen, similarly to domestic dogs (Rooijakkers et al., 2009). This could be due either to worse physical cognitive skills with regard to tracking invisible displacements or to enhanced attention to the baited location as a social cue from the experimenter.

Only DP+ solved the “shake full” condition. This condition is unique in that it can be solved by either attending to the significance of the presence of sound during shaking or through stimulus enhancement. The “shake empty” condition controls for the second possibility: In order to solve it the subject cannot simply choose the cup that has been shaken, but should instead infer that if the shaking cup does not produce noise the food reward cannot be in there and has to be in the other cup (Call, 2004; but see Penn and Povinelli, 2007). Interestingly, DP+ performed significantly above chance in the shake full condition and below chance in the “shake empty” condition, choosing the cup shaken by E even if it made no noise. These results support the idea that in the conditions involving shaking cups subjects made their choices according to stimulus enhancement, or considering shaking as a social cue, without a deep causal understanding of the physical properties of the containers and similarly to what has been already evidenced for dogs (Bräuer et al., 2006; Hare et al., 2010).

In conclusion, neither an analysis by categories (i.e., physical versus social tasks) nor an analysis of individual tasks gives any support to the DOM hypothesis, which predicted that DP+ would outperform WB+ in the social tasks and the contrary would occur in the physical tasks. In addition, the fact that DP+ did not outperform DP− in neither of the tasks or categories does not support the DEV_GENERAL hypothesis, which predicted more enriched pigs outperforming pigs living in less enriched conditions. Moreover, our results actually contradicted the DEV_GENERAL hypothesis, since DP− outperformed DP+ in the physical domain, both in the one inclined and the transposition tasks, and DP+ outperformed WB+ in the one inclined task. Indeed, both in the physical and in the social tasks most of the results can be potentially explained by specific features in the subjects' environment, as the type of ground (hard versus soft), the type of food (solid versus liquid) and the degree and type of human contact experienced by subjects during ontogeny, as predicted by the DEV_SPECIFIC hypothesis. The skills subjects showed in this study, therefore, rather than reflecting some general cognitive capacity acquired in more or less complex environments, seem to reflect their experience with specific stimuli. In other words, rather than having an overall richer environment, what apparently helped subjects solving particular tasks was having a particular environment that provided the adequate experience for that.

Although one should consider our data as preliminary, they suggest that the cognitive complexity of domestic pigs, both in the physical and in the human social domain, has not gone through special changes linked to domestication and might thus be similar to that of their closest wild relatives. Some observational studies on free-ranging swine also point in this direction (e.g., Graves, 1984; Gustafsson et al., 1999). This could be partially explained by the fact that pig domestication has occurred several times throughout history in different areas of the northern hemisphere (e.g., Giuffra et al., 2000; Larson et al., 2007). Pigs have often escaped from human control, becoming feral and mixing with local populations of wild boars, only to be caught again for domestication (Vilá et al., 2005). This lack of complete genetic isolation may therefore have maintained cognitive homogeneity in both subspecies. In contrast, dogs were domesticated only once or twice (Savolainen et al., 2002), much earlier than pigs – 15,000 years ago (Vilá et al., 1997) –, and they show more overt behavioural and cognitive differences from their wild relatives (Frank, 1982; Gacsi et al., 2005; Virányi et al., 2008).

Another possible explanation for these results might be linked to the reasons of the enormous evolutionary success of the *Sus* genus. In the physical domain, behavioural flexibility, good learning skills, good sense of smell, perfectly equipped snouts and powerful teeth to crack open any encapsulated food would make any complex cognition to exploit the environment unnecessary. In the social domain, given that domestic pigs were not selected to accompany humans but commonly as meat stock, their human social environment would be less demanding than that of dogs, for example, and they might not need special cognitive adaptations to deal with it. If this was true, domestication would not have entailed drastic cognitive changes in pigs. Instead, they would only need to apply their already extant learning abilities to a new environment.

Ideally, in order to investigate the potential effects of domestication and ontogeny on swine cognition: (a) all groups would have the same size and age and sex composition, and all subjects would be tested under identical circumstances and with similar motivation levels; (b) WB+ and DP+ would live in identical conditions, with their physical and social experience controlled from birth; and (c) DP+ and DP− would be of the same domestic breed, preferably siblings separated just after weaning and kept under controlled conditions differing only in the intended ways. As we already commented in Section 2, unfortunately the study presented here is not a balanced and strictly controlled study with respect to a number of these points. However, we believe it is a first approach to the question of the influence of domestication on cognition that can provide some hints for future studies on this topic.

5. Conclusion

In conclusion, we regard this study as a first approach to the problem of the roles played by life history and evolutionary history in swine cognition. Although one should consider our data as preliminary, our results suggest that specific experience on particular stimuli during ontogeny best explains swine ability to solve both social and physical tasks. For further clarification of this topic studies will need to be conducted where variables such as the age and sex of the subjects are counterbalanced and genetics and experience strictly controlled (e.g., Hare et al., 2005; Plyusnina et al., 1991). Also, future studies would benefit from larger sample sizes, more trials and more tasks, which should cover all of the cognitive domains that may differ between swine subspecies. Moreover, according to our results the predictions for these tasks should consider subjects' specific experience relevant to each problem, rather than their general experience in the physical or the social domain.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.applanim.2012.07.005.

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