

Working and reference memory of pigs (*Sus scrofa domesticus*) in a holeboard spatial discrimination task: the influence of environmental enrichment

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Abstract Interest in cognitive research in pigs is increasing, but little is known about the impact of environmental conditions on pigs' cognitive capabilities. The present study investigated the effect of environmental enrichment on cognitive performance of pigs in a holeboard spatial task, in which they had to discriminate four baited buckets out of 16. Pigs ($n = 32$) were either housed in stimulus-poor, barren pens, or in larger pens enriched with rooting substrates. Pigs were subjected to 30 holeboard trials. Both working memory (WM), that is, the ratio (baited visits/total number of (re)visits to baited buckets), and reference memory (RM), that is, the ratio ((re)visits to baited buckets/total number of visits to all buckets), improved over trials. WM scores were higher in pigs from enriched pens than in pigs from barren pens. Housing did not affect RM scores. Personality type of the pigs, as assessed early in life using a backtest, did not affect WM or RM. In conclusion, housing conditions of pigs did not affect reference memory, but environmental enrichment improved working memory of pigs in a spatial discrimination task. Based on the findings of this study, we suggest that cognitive functioning of pigs may be impaired under commonly used housing conditions.

Keywords Spatial learning · Memory · Chronic stress · Environmental enrichment · Pigs · Personality

Introduction

Interest in cognitive research in pigs has increased during the past decade (Kornum and Knudsen 2011) for different reasons (Gieling et al. 2011). Similarities between the human and porcine brain make the pig a good model for human brain development and disorders (see Kornum and Knudsen 2011; Lind et al. 2007 for review). Furthermore, an enhanced understanding of the cognitive abilities of pigs, and of how these are influenced by environmental conditions, can be used to improve the welfare of both laboratory pigs and intensively kept pigs on farms (Gieling et al. 2011; Kornum and Knudsen 2011). These pigs are frequently housed in stimulus-poor environments that may constrain the development and expression of normal behaviours. Pigs kept in these environments often show behavioural, physiological and pathological signs of poor welfare and chronic stress (e.g. Beattie et al. 2000; Bolhuis et al. 2006; De Jong et al. 2000). Enrichment of the environment of pigs dramatically changes their behaviour. For instance, a threefold increase in play behaviour, which might be relevant for developing cognitive skills and behavioural flexibility (Spinka et al. 2001), was reported when straw bedding was provided to pigs (Bolhuis et al. 2005). Studies in rodents indicate that environmental complexity affects brain development (Rosenzweig and Bennett 1996), which is reflected in improved spatial cognitive abilities (e.g. Leggio et al. 2005; Schrijver et al. 2002). In pigs, studies on effects of environmental enrichment on spatial learning and memory have yielded conflicting results. Beneficial effects of enrichment on

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acquisition of a spatial task have been reported (Sneddon et al. 2000), whereas others found no effects (De Jong et al. 2000; Jansen et al. 2009). It has been suggested that given the good spatial learning and memory skills of pigs (Held et al. 2002), complex tasks are required to reveal a contrast in brain development resulting from environmental conditions (Jansen et al. 2009; Kornum and Knudsen 2011). In addition, emerging studies in rodents have demonstrated that chronically stressed animals perform well or even better than controls when using inflexible, cue-based strategies in spatial tasks (Conrad 2010). Therefore, tasks addressing the spatial learning and memory capacities of animals should rule out the option to use fixed, non-spatial strategies for solving these tasks. Recently, the spatial discrimination ‘holeboard task’ which yields measures of both spatial reference memory and working memory (see Van der Staay et al. 2012 for review) has been adapted for pigs (Arts et al. 2009). Spatial working memory is seen as a form of short-term memory that typically holds information relevant within a spatial test trial, such as a list of locations that have recently been visited, whereas reference memory holds trial-independent information about the rules and solution of a spatial task, such as the baited locations across trials (see Van der Staay et al. 2012). In the current study, we used the spatial holeboard test to assess the impact of housing conditions during rearing on cognitive performance of pigs. Pigs were characterised at a young age by their response in a backtest (see below), which reflects their personality type (Bolhuis et al. 2000, 2004). Pigs diverging in backtest response differ in exploration patterns (Jansen et al. 2009) and respond differently to aversive conditions, including a stimulus-poor environment (Bolhuis et al. 2003, 2004, 2005, 2006) which may potentially affect their performance in spatial tasks. The aim of this study was to investigate the effects of housing conditions during rearing (barren vs. enriched) on cognitive performance of pigs with different personality types in the spatial holeboard task.

Animals

We used 32 pigs (Tempo x Topigs 30), offspring of 16 sows that had been purchased for another study (Oostindjer et al. 2010). Pigs were housed with their mothers until weaning in either 9.2 m² barren farrowing pens or in 18.4 m² farrowing pens enriched with wood shavings (550 L), peat (400 L), straw (1 kg) and branches (3–5). Fresh straw (0.5 kg) and wood shavings (70 L) were added to enriched pens daily, peat (40 L) once a week, and branches were replaced twice per week. At 2 weeks of age, pigs were subjected to a backtest (Bolhuis et al. 2003) in which they were manually restrained in supine

position for 60 s. The number of escape attempts and vocalisations and latency to the first escape attempt were used to classify the pig as high resisting (HR: active response) or low resisting (LR: passive response) as previously described (Melotti et al. 2011). From weaning at 4 weeks of age, pigs were housed in eight groups of four unrelated individuals in a 1:1 sex ratio and 1:1 backtest classification ratio, in 3.2 m² barren (B) or 6.4 m² enriched pens (E) with wood shavings (185 L), peat (135 L), straw (0.5 kg) and 3 branches. At 6 weeks of age, B groups were transferred to barren 7.1 m² pens and E groups to 16.4 m² enriched pens, in a room adjacent to the test arena. All pens contained feeders providing four feeding places, two drinking nipples and an iron chain. A commercial pig diet was available ad libitum until spatial training and habituation started. On test days, pigs were mildly food deprived by removing the feeders from the pen the evening before and placing them back when all pigs in the pen had completed their trials. Growth of the experimental pigs was 91 % of growth in ad libitum-fed, non-trained pigs of the same age and origin. Food-restricted pigs may ingest substantial amounts of straw (Bolhuis et al. 2007; Staals et al. 2007). Therefore, to prevent large differences in feeding motivation between B and E pigs which could affect their performance in the test, from 6 weeks of age, E pens were provided with peat (400 L), wood shavings (550 L) and branches (3) only, but not with straw. Fresh wood shavings (70 L) were added to E pens daily, peat (40 L) once a week and branches were replaced twice per week. Between 8 and 11 weeks of age, pigs were exposed to a simple spatial 2-way choice test (data not reported here). Before this test, pigs were gradually habituated to the experimenters, the test arena, the buckets and the baits used (chocolate raisins) over a 12-day period. Habituation started with exposure to the experimenters, baits and buckets in the pigs’ home pens on two consecutive days. Briefly, an experimenter visited each pen, bringing a bucket and chocolate raisins. She first sat until all pigs within a pen approached her and the bucket, ate a chocolate raisin and allowed her to touch them; after this, she squatted until all pigs approached her, and finally she stood in the pen until all pigs approached her. Thereafter, pigs were exposed to the arena once per day. Pigs left their pens voluntarily, had to enter the corridor, the arena, approach the buckets and were returned to their pens after eating the chocolate raisins. They were first allowed to briefly explore the test arena two times group-wise, subsequently four times in pairs of pen mates and finally four times individually. Before holeboard testing started, pigs were allowed to explore the test arena briefly while eight of the 16 buckets were baited. All habituation steps described took

approximately 10 min per pen per day and, later, per pair or pig per day.

Holeboard task

Starting at 12 weeks of age, all individual pigs were exposed to 30 test trials in total on 15 days (2 massed (for pens) trials/day/pig). The 7 × 7 m arena, confined by wooden walls (height: 1 m), contained four entrances with guillotine doors that could be opened from a central location in the room. As recommended (Arts et al. 2009; Kornum and Knudsen 2011), four entries were used to prevent the pigs from developing a non-spatial, fixed pattern of visits that would reduce their working memory load. The arena was surrounded by corridors serving as waiting areas. The corridors contained three ropes with a tennis ball attached to it (dog toy) for the three waiting pigs while one of their pen mates was tested. Sixteen dark brown, plastic buckets (height 17 cm, radius 17.5 cm), arranged in a 4 × 4 matrix, were screwed on the concrete floor of the arena. Four of the 16 buckets were baited with a chocolate raisin during testing (see Fig. 1). To prevent the use of odour cues to locate the baited buckets, all buckets contained a perforated grid bottom under which fresh chocolate raisins were placed before testing. Individual pigs were trained on a fixed configuration of baited buckets. Four different configurations were used, a configuration baiting buckets 4, 7, 9 and 14, and the 90°, 180° and 270° rotated versions (Fig. 1). Configurations differed between all four pigs within each pen and were balanced for backtest classification and sex. Over four consecutive trials of an individual pig, each entrance was used once, in a random order. Order of testing between and within groups of pen mates was alternated across days. Before the start of a trial, all four pigs of a pen were led into one of the corridors surrounding the testing arena, and the pig to be tested was given access to the appropriate entrance. The trial was terminated when the pig found all four rewards, followed by a clicker sound, or when 180 s had passed, which was signalled by a different sound cue (siren-like sound). After a trial, the pig was led back into the waiting area where its

pen mates were held. Both in the test room and in the room where pigs were housed, a radio played during daytime to minimise the effect of sudden noise. The Animal Care and Use Committee of Wageningen University approved all procedures.

Data recording and analysis

The following variables were scored: latency between entering the arena with the forelegs and visits to the baited buckets; time needed to finish the trial (i.e. either having collected all four rewards or the maximum time of 180 s); number of rewards collected; total number of bucket visits; working memory (WM) errors (i.e. all revisits to baited buckets); and reference memory (RM) errors (i.e. all (re)visits to the unbaited buckets). Afterwards, the WM score was calculated as the ratio between the number of baited visits and all visits to the baited buckets. Also, general working memory (GWM) was calculated, which is the ratio between the number of different buckets visited and the total number of visits (Van der Staay et al. 2012). The RM score was calculated as the ratio between number of visits to the baited buckets and the total number of visits to all buckets (Arts et al. 2009). We also assessed the ratio between the number of baited buckets visited and the total number of different buckets visited as an alternative RM measure (RMalt) which excludes WM performance. Block means of five trials each were calculated for all variables. Skewed distributions of time were logarithmically transformed before analysis. Preliminary analyses showed no effects of sex. A mistake was made in the location of the baits in block 3 for four pigs; for these pigs, data from block 3 and further were omitted from analysis. Effects of housing (E or B), backtest classification (LR or HR), trial-block and their interactions were assessed by analysis of variance using the GLM procedure in SAS 9.1 (SAS Inst. Inc., Cary, NC, USA). Housing effects were tested against the effect of pen within housing (i.e. pen was experimental unit for housing effect); effects of backtest classification and its interaction with housing were tested against the effect of pig within backtest classification, pen and

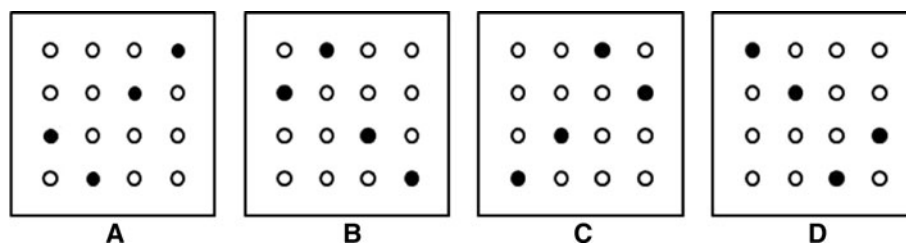


Fig. 1 Configurations of baited buckets (*open circles* non-baited buckets; *closed circles* baited buckets). Configurations **b**, **c** and **d** are the 90°, 180° and 270° rotated pattern of configuration (**a**)

housing. In 96 % of the trials, pigs collected all four baits within 180 s. Effects of housing or backtest classification on successful completion of the task (i.e. collection of all four baits or not) as a binary variable were analysed with a generalised mixed model with logit link function. Incomplete trials (usually with 3 rewards collected) occurred most often in the first 5-trial-block (8.4 %) and thereafter decreased (6.3, 4.5, 3.0, 0.7 and 2.9 % for blocks 2, 3, 4, 5 and 6, respectively). Preliminary analyses showed that omitting the incomplete trials did not change the effects much; therefore, data presented below (mean \pm SEM) include all trials.

Results

No significant interactions between trial-block and housing were found, that is, rate of changes over trial-blocks did not differ between B and E pigs. Trial duration and total number of visits per trial decreased over trial-blocks ($F_{5,129} = 23.8$ and 127.2 , respectively, $P < 0.001$ for both, Fig. 2) and were unaffected by housing. Time to arrive at the first baited bucket and mean interval between visits to baited buckets also decreased over trial-blocks ($F_{5,129} = 8.1$ and 21.1 , respectively, $P < 0.001$ for both). Pigs from

barren housing tended to be faster to visit the first baited bucket than pigs from enriched housing (6.2 ± 0.3 vs. 7.4 ± 0.2 s, $F_{1,6} = 5.7$, $P < 0.06$), but had a longer interval between visiting the baited buckets (18.1 ± 0.4 vs. 17.0 ± 0.4 s, $F_{1,6} = 6.8$, $P < 0.05$).

The number of revisits to baited buckets, that is, working memory (WM) errors, decreased and, correspondingly, WM score increased over trial-blocks ($F_{5,129} = 10.9$ and 12.0 , respectively, $P < 0.001$ for both). Pigs from barren pens had a higher number of WM errors ($F_{1,6} = 9.8$, $P < 0.05$) and a lower WM score than pigs from enriched pens ($F_{1,6} = 10.2$, $P < 0.05$, Fig. 2). GWM was strongly correlated with WM ($r = 0.89$ over all trials; overall means for WM and GWM 0.89 vs. 0.90). Similar to WM, GWM improved over trial-blocks ($F_{5,129} = 22.3$, $P < 0.001$) and was higher for enriched than for barren housed pigs ($F_{1,6} = 7.1$, $P < 0.05$, data not shown).

Reference memory (RM) scores increased with time and number of RM errors decreased ($F_{5,129} = 101.1$ and 150.7 , respectively, $P < 0.001$ for both, Fig. 2). RM scores were not affected by housing. RMalt was strongly correlated with RM ($r = 0.97$ over all trials) and, similarly, affected by trial-block but not by housing (data not shown).

Backtest classification or its interaction with housing and trial-block did not affect any of the variables, except

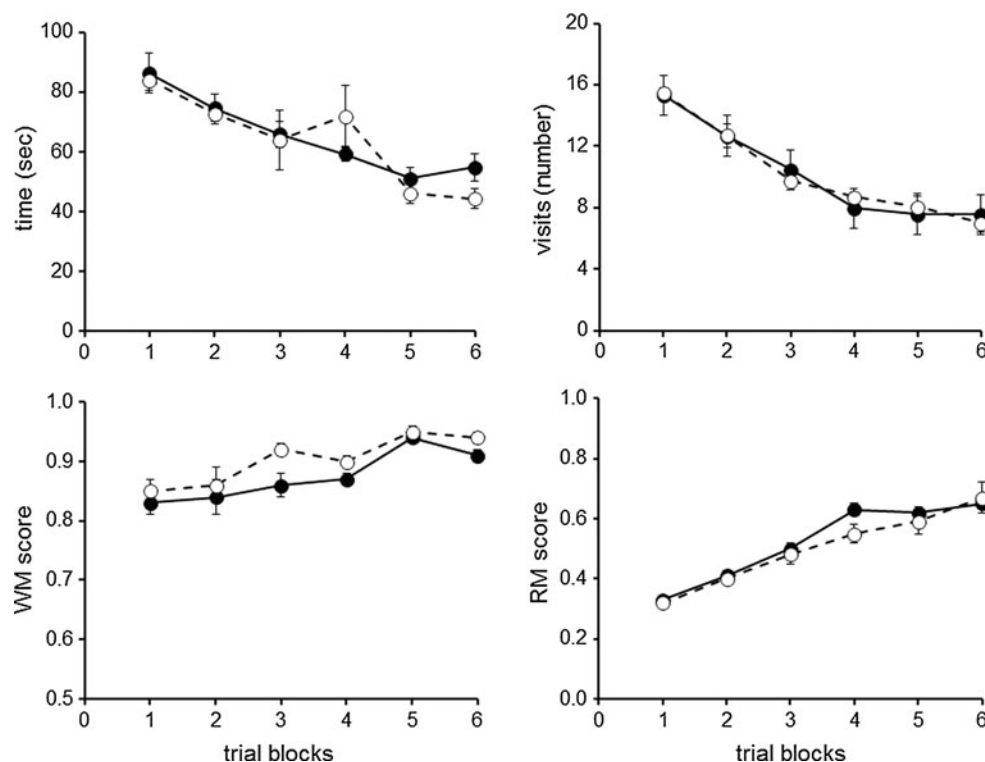


Fig. 2 Time to complete a trial (time), total number of visits (visits), working memory (WM score) and reference memory (RM score) of pigs in barren (closed circles, solid lines) and enriched housing conditions (open circles, dotted lines) for the six trial-blocks

(consisting of five trials each). Different Y-axis scaling for time, visits, WM and RM score. Significance of housing and trial-block effects are given in the text

that LR pigs completed the task more often successfully, that is, collected all 4 rewards within 180 s, than HR pigs (overall: 98.1 vs. 93.0 %, $F_{1,22} = 8.5$, $P < 0.01$), particularly in the first trial-block.

Discussion

Our study confirms previous studies (Arts et al. 2009; Gieling et al. 2011) that pigs are well able to acquire a spatial cognitive holeboard task. RM and WM scores and learning curves were similar to those previously reported in pigs (Arts et al. 2009; Gieling et al. 2012), but individuals in the current study were, from the start, slightly faster to finish a trial which could be due to the mild food deprivation we applied.

This is the first study to show that rearing and housing conditions of pigs affect their cognitive performance in the spatial holeboard task. Pigs from barren pens tended to be faster to reach the first baited bucket, suggesting that they were at least equally, if not more, motivated than enriched pigs to complete the task. It has been suggested that barren housed animals may be more motivated to work for food due to the lack of stimulation in their home pens (Inglis et al. 1997). Enriched pigs, however, had higher WM and GWM scores than pigs from barren pens, indicating that they were better able to memorise which (baited) buckets they had already visited within a trial, and they had shorter inter-visit intervals between baited buckets. The improved cognitive performance of enriched pigs is in accordance with studies in rodents reporting beneficial effects of environmental enrichment on spatial abilities (e.g. Leggio et al. 2005; Schrijver et al. 2002). Conversely, rather than being the result of non-enrichment, the poorer performance of pigs from barren pens can also be seen as a result of stress, as a lack of suitable rooting substrates and a lack of space in their home environment seems to be aversive for pigs (Beattie et al. 2000; Bolhuis et al. 2005, 2006; Pearce and Paterson 1993). Stress may influence cognitive processes in different ways, and sometimes even improves learning and memory (see Mendl 1999 for review). Acute stress induced by mixing pigs with unfamiliar conspecifics, did not affect holeboard performance in pigs of similar age (Arts et al. 2009). Barren, stimulus-poor housing conditions may, however, give rise to more sustained stress in pigs, as indicated by changes in behaviour and HPA-axis functioning. For instance, barren housed pigs, apart from developing maladaptive, damaging behaviours (Beattie et al. 2000; Bolhuis et al. 2005, 2006), were reported to have a blunted circadian rhythm in salivary cortisol (De Jong et al. 2000) and heavier adrenals at slaughter (Beattie et al. 2000) than pigs from enriched pens, and changes in functional activity of the hippocampus have been

suggested (Van der Beek et al. 2000). Studies in rodents indicate indeed that chronic stress impairs cognitive performance in non-aversive, fear-neutral spatial tasks such as the holeboard task (see Conrad 2010 for review).

It should be noted, though, that housing conditions did not affect RM in this study. Apparently, the long-term barren housing conditions in pigs did not affect the acquisition, consolidation or retrieval of spatial reference memory across trials, whereas within-trial memory of already visited locations was impaired compared with enriched housed pigs. The differential effects of housing on RM and WM support the idea that these measurements seem to reflect rather independent memory components related to different neural substrates (see Van der Staay et al. 2012). Indeed, in our study, correlations between RM and WM per trial-block were all non-significant ($r = 0.29$, 0.15 ; 0.34 ; -0.06 ; -0.03 ; 0.11 for trial-blocks 1–6 when considering all trials, and $r = 0.21$; -0.06 ; 0.17 ; -0.18 ; -0.03 ; 0.12 , respectively, when considering completed trials only). Also, in rodent studies, it has been found that stressful conditions may have differential effects on RM and WM (Conrad 2010; Krugers et al. 1997). Chronic stress has been found to impair both spatial RM and WM, or either one of the memory constructs (e.g. Manikandan et al. 2006; Krugers et al. 1997, see also Conrad 2010 for review). It has been suggested that the time course for developing cognitive deficits following sustained stress is different for WM and RM, with RM deficits developing more slowly (Conrad 2010). In addition, the influence of housing conditions on different brain structures may vary, which may have played a role in the differential effects of housing on WM and RM. For instance, both RM and WM in spatial navigation require hippocampal function, while spatial WM also includes the contribution of the medial prefrontal cortex (Yoon et al. 2008).

Personality type did not affect cognitive performance in the holeboard task, except that LR pigs were more likely to collect all four baits within a trial than HR pigs, particularly in the first trial-block. This is in line with other studies reporting that, albeit LR pigs appear to explore their surroundings more thoroughly than HR pigs, the two types of pig do not differ in spatial learning per se (Bolhuis et al. 2004; Jansen et al. 2009). Differences between LR and HR pigs may become more apparent, though, if configurations of baited locations would be changed, because HR pigs are less flexible in changing a learned pattern (Bolhuis et al. 2004).

In conclusion, pigs from barren housing conditions had a poorer WM performance than pigs raised and housed in enriched pens. In many commercial pig housing systems, no adequate enrichment substrates are provided and space requirements for pigs on farms and in laboratories are generally lower than the space allowance of the barren pigs

in the current study. This means that cognitive functioning of pigs may be impaired under commonly used housing conditions.

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