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

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Abstract

A non-invasive method was developed to study the transmission of cues that are used in social discrimination by pigs, *Sus scrofa*. We investigated the ability of juvenile pigs to discriminate between pairs of familiar, similar-aged conspecifics in a Y-maze learning task, using either single or paired visual, olfactory and auditory cues. The stimulus pigs (\(n = 12\)) were littermates that were familiar but unrelated to the test pigs (\(n = 12\)). For the bimodal task, test pigs (four per treatment) were presented with cues of two modalities: olfaction and vision (OV), vision and audition (AV), or audition and olfaction (AO). Approaches to a pre-determined correct stimulus were rewarded with food in daily sessions, each of 10 consecutive trials. Three consecutive successful sessions of \(\geq 8/10\) correct choices (\(P = 0.00016\)) fulfilled the criterion for starting the unimodal task, during which test pigs were given either olfactory, visual or auditory cues only using the same success criterion. Eight pigs learnt the bimodal task (OV: 4, AV: 2, AO: 2) of which six pigs subsequently completed the unimodal task successfully (O: 3, V: 2, A: 1). These findings indicate that juvenile pigs have the cognitive capacity to discriminate between same-sex littermates that are also familiar group-members in the absence of either visual, olfactory or auditory cues.
cues, and that some can use just one of these modalities. A larger-scale study is needed to determine the sensory hierarchy of social discrimination in pigs.

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1. Introduction

Social stability in small (<30) groups of juvenile pigs relies upon the swift and decisive determination of dyadic relationships following mixing, as well as the ability to continue to discriminate different group members. The ability to discriminate between individuals begins shortly after birth with the piglet able to distinguish its dam from other sows using initially olfactory, and then auditory, cues (Horrell and Hodgson, 1992b; Walser, 1986). As pigs mature, cues used in social discrimination become increasingly multimodal with groups apparently able to function socially, albeit in a modified fashion, when one or more modalities are disrupted. Meese and Baldwin (1975) and Ewbank and Meese (1974) used contact lenses, hoods or surgical ablation of the olfactory bulbs to demonstrate this, although such invasive procedures may have affected the pigs’ social behaviour in a number of ways, e.g. by impeding navigation, increasing fearfulness, or interfering with social discrimination.

Several studies have shown that pigs are able to discriminate between familiar and unfamiliar conspecifics using various cues, e.g., urine, faeces, bedding material (Horrell and Hodgson, 1992b), recorded vocalisations (Illmann et al., 2002), whole body odours and live conspecifics (Kristensen et al., 2001). These and similar studies rely on subjects responding more vigorously to one stimulus than the other, spending longer investigating one stimulus over another, or showing a functional response such as aggression towards the unfamiliar animal. Such differential responses might be expected given that one of the stimuli may be novel; however, this approach can also give ambiguous results or poor repeatability due to conflicting motivational priorities, differing preferences according to context, neophobia, the emotional state of the subject during the test, or individual differences in propensity to show aggressive behaviour. Also, the approach lends itself less readily to studies of group-member discrimination where both stimuli are equally familiar.

Given the limited availability of cues (excepting large weight advantages) that predict success in agonistic encounters (Andersen et al., 2000), it is often assumed (e.g. Jensen, 2002), and seems highly likely, that pigs discriminate between group-members by recognising individuals according to their individually unique characteristics (see Zayan, 1994), although this has never been demonstrated explicitly. Furthermore, the cues that pigs use and need for group-member discrimination are unknown, hence the focus of this paper on cue use by pigs in a social discrimination task.

Although olfaction is thought to be the dominant sense used in pig social communication (Jensen, 2002), pigs use visual cues when signalling aggression and submission (Jensen, 1982; Jensen and Woodgush, 1984) and produce many vocalisations, of which at least one appears to have individually unique characteristics (Blackshaw et al., 1996) and could therefore be used in individual recognition. Encounters between two unfamiliar pigs often end in overt aggression. They are characterised by a nosing phase, in which individuals repeatedly touch and sniff one another, especially on the facial and anal-genital regions; and a biting phase (Jensen and Yngvesson, 1998), in which they butt the head and body, bite (especially the head and ears), press and lever, until one pig signals submission and retreats (Rushen and Pajor, 1987). Nosing is
thought to be used for information gathering (Jensen and Yngvesson, 1998) during which cues that are unique to individuals may be committed to social memory. As neither the nosing phase itself, prior exposure to individuals in neighbouring pens (Fraser, 1974), nor exposure to olfactory cues from individuals (Kennedy and Broom, 1996) seem to prevent the biting phase (even when large weight asymmetries exist), it seems that information about relative fighting ability is not gathered until the fighting phase (Rushen et al., 1988). This is consistent with the idea that pigs may be becoming familiar with the unique array of cues from individual opponents, rather than assessing specific status-related cues prior to the onset of aggression; otherwise easily outmatched pigs would more commonly submit without a contest. Although a proportion of all unfamiliar dyads in a newly mixed group of pigs are not observed to fight after mixing (see discussion in Arey and Edwards, 1998; Arey and Franklin, 1995), this does not necessarily mean that dominance relationships between them are settled. It could be that less successful pigs lower their assessment of relative fighting ability following social defeat, becoming less likely to engage in fights, or even that they are able to avoid fighting all potential opponents by observing the outcomes of encounters between other dyads and inferring their own relative status (e.g. Hogue et al., 1996). An opponent’s unique sensory cues, linked to the memory of success or defeat against them during the fighting phase, may be the mechanism for hierarchy maintenance in the established group. Therefore, the cues and sensory modalities that may be used by pigs during nosing and during subsequent benign social interactions are of interest, as these moderate and help to avoid further overt aggression.

We have shown previously, using an operant Y-maze method, that juvenile pigs can discriminate between unrelated same-sex group-members, between group-members that are also same-sex littermates, and between two unfamiliar pigs that are same-sex littermates when the full range of visual, olfactory and auditory cues is available (McLeman et al., 2005). In the current study, we aimed to assess bimodal and unimodal discriminatory abilities. Although some previous studies have removed sensory cues, the methods used were either invasive (surgical/chemical anosmia: Baldwin and Shillito, 1974; Meese et al., 1975; Ferreira et al., 2000), potentially ineffective (deodorants/perfumes to mask odours: Horrell and Hodgson, 1992a; Koba and Tanida, 2001), or potentially lacking in fidelity (photographs, recorded vocalisations to represent live conspecifics: see D’Eath and Dawkins, 1996). To overcome these problems, we developed engineering solutions to manipulate the transmission of olfactory and auditory cues, whilst a simple opaque barrier eliminated visual cues when required. This approach allowed the use of live stimuli, but removed the need to impair perception physically as transient sensory manipulation occurred only in the test apparatus.

This paper discusses the development of this non-invasive method and its initial use for training pigs in a social discrimination task using either bimodal or unimodal cues. Success in a bimodal task would suggest that the lack of at least one important sensory modality was not essential for social discrimination while success under unimodal conditions would identify those modalities that could be used alone. The results can thereby improve our understanding of the effectiveness of each of three sensory modalities in social discrimination in pigs.

2. Materials and methods

2.1. Subjects, housing and husbandry

Two batches of 12 Landrace × Large White × Duroc female pigs were obtained at weaning (ca. 4 weeks old) from a commercial outdoor pig unit. Each batch comprised six unrelated pigs to be used as test subjects,
and a further six (two littermates from each of three litters) to serve as stimulus pigs. Batch 2 was obtained 12 weeks after batch 1; each batch was housed together as one social group for at least 2 weeks before testing began to ensure that all pigs were familiar with one another. The 12 test subjects were divided into two batches in order to maximise the number of training sessions per pig before the weight limit for the apparatus was reached, as only six pigs could be tested each day.

Each batch was housed indoors as a single group in a 16 m² pen, and bedded on wood-shavings and straw. Fluorescent light was supplied on a 12:12 h cycle of light:dark with lights switched on at 07:00 h at an illuminance of approximately 70 lx (measured at 0.5 m above the floor). Overhead heaters provided a minimum temperature of 26 °C at weaning, reducing to not less than 9 °C when the pigs weighed 60 kg. Soiled bedding was replaced daily with fresh shavings and straw, and enrichment devices were provided, e.g. robust toys and destructible materials. Water was available ad libitum; food was available ad libitum except on test days, when it was removed (08:00–12:00; 13:00–17:00) to enhance motivation for rewards.

2.2. Apparatus

A Y-maze (Fig. 1; Plate 1; McLeman et al., 2005) was located in the same room as the animal accommodation. The apparatus consisted of an octagonal central arena (Ø 2 m) and five rectangular chambers (1 m × 0.8 m), each resting 0.15 m off the floor on castors. Light intensities in the arms of the

![Fig. 1. Plan view of the apparatus. Chambers are drawn to scale.](image-url)
The configuration of the apparatus was modified as necessary to exclude or transmit olfactory, visual and auditory cues by changing the airflow direction and pressure, using opaque or transparent drop-doors and/or using a sound system. There were six permutations of the apparatus; unimodal conditions were met by combining two of the three methods described below.

To prevent transmission of olfactory cues, the central arena and stimulus boxes were placed under positive pressure with respect to the atmosphere using a fan (Ø 315 mm), with air drawn from another (animal-free) room within the building, rather than from outdoors, to ensure a stable air temperature. The combined volumes of the central arena and the reward chambers, and each stimulus chamber, were ventilated separately at about 53 air changes per hour using secondary ducting to supply fresh air to each stimulus chamber. The direction of the airflows and the pressure differential ensured that there was minimal air exchange between the stimulus and reward chambers. The effectiveness of this technique was verified using a tracer gas (pure SF$_6$; McLeman, 2005 after Demmers, 1997) released at a constant rate (0.3 ml min$^{-1}$) into the secondary ducting supplying fresh air to one stimulus chamber. The concentration of the tracer gas in air was then measured in the stimulus chamber, and in the central arena at the entrance to one arm of the Y-maze (where a test pig would be standing whilst investigating a stimulus pig). Over a sampling period of 102 min, that was much longer than the duration of a test session, the mean ± S.E. concentration of SF$_6$ in the stimulus chamber was 470 ± 0.3 ppb compared with 3 ± 0.1 ppb in the central arena, demonstrating minimal cross-contamination. In tests that allowed olfactory communication between the stimulus and test pigs, the airflow was circulated between the stimulus boxes and the central arena at over 100 air changes per hour, as measured using the tracer gas method described above.

To prevent transmission of visual cues, opaque PVC doors were placed in front of the stimulus chambers; each contained an ‘audio window’ (an airtight, circular opening, Ø 200 mm, covered with black
polythene film) to allow transmission of auditory cues. Secondary, steel mesh doors (50 mm mesh) were placed inside these doors to protect the audio windows from damage by the stimulus pigs. In tests that allowed visual communication, the opaque doors were replaced with transparent PVC doors, with transparent audio windows.

It was not feasible to prevent the transmission of auditory cues because the secondary ducting used for exchange of olfactory cues inevitably also transmitted auditory cues. We were reluctant to mask the pigs’ sounds because of the high sound volume that would be needed to obscure the loud, high-pitched vocalisations typically produced by young pigs when isolated in a confined space (see Hutson et al., 1993). Instead, test subjects were prevented from using sound to locate each stimulus pig by a ‘surround’ sound system that replayed each vocalisation at four other locations around the apparatus (see Kristensen et al., 2001; Fig. 1). Tie-clip voice microphones (Labtec Verse-313) were placed in both stimulus chambers to detect sound signals that were then mixed (Eurotrack MX602A), amplified (Marantz PM40 SE; Rotel stereo power amplifier RB-960BX; Rotel control amplifier RC-980BX), and then replayed via four loudspeakers (Goodmans 12\" professional loudspeakers Audiom-12P-D, 50 W, 8 Ω). Three additional measures were put in place to reduce the likelihood of the test subject identifying the source of vocalisations. The sound volume at the loudspeakers nearest the start box was set to be slightly louder than that nearest the reward chambers to offset any perceived differences in amplitude between the stimulus chambers. Solid PVC doors without audio windows were also used to minimise direct sound transfer through the door; as direct sound would reach the pig’s ears marginally sooner than sound coming from the speakers. Finally, an echo box (AXL EAD2), connected to the mixing deck, provided further confusion about the location of the sound source by generating an acoustic overlap between near synchronous vocalisations. In all tests allowing auditory communication, microphones were removed and the sound system was switched off.

2.3. Procedures

In the bimodal task, the test pig (n = 12) had to learn to discriminate between a pair of littermates that were familiar but unrelated to it using two of three principal modalities (AO = audition + olfaction but no vision; VO = vision + olfaction but no audition; AV = audition + vision but no olfaction; n = 4 animals per bimodal type). Each test pig was assigned to one of the three types of bimodal test and one of the six pairs of stimulus pigs throughout the experiment. Each stimulus pair served two different test pigs and each stimulus pig acted as a positive stimulus for just one test subject; this reduced the likelihood of the stimulus animals learning to behave in a particular way contingent on the behaviour of the test pig. If a test pig reached the criterion for learning this task, she was then tested on a unimodal task with the same stimulus pair and positive stimulus as used previously. The unimodal task required discrimination between the same pair of littermates using only a single modality (A = audition; V = vision; O = olfaction) and testing continued until the subject met the criterion for learning or had been tested in a maximum number of sessions (24 and 30 in batches 1 and 2, respectively, see below), whichever came first. For unimodal tasks subjects were pre-allocated to one of the two modalities available during their bimodal task, this was done before the bimodal task and was balanced in each batch.

Test and stimulus pigs were acclimatised to the Y-maze apparatus for 1 week prior to testing. Stimulus pigs were acclimatised to the stimulus boxes in all configurations, e.g. with opaque as well as transparent doors, in order to minimise distress caused by novelty, temporary confinement, or separation from groupmates. Test pigs were acclimatised to moving through the Y-maze from the start box to the reward chamber, especially to the opening and shutting of drop-doors, ensuring that they visited each side of the maze an equal number of times during an acclimatisation session.

Subjects were tested in daily sessions, each of 10 consecutive trials, in which an approach to the positive stimulus of a pair of familiar littermates was rewarded with a preferred food (4–5 raisins). The location of the positive stimulus was randomised but balanced so that it was presented on each side of the apparatus an equal number of times in each session, but never on the same side for more than two consecutive trials. The criterion for learning was three consecutive sessions with ≥8/10 correct choices (P = 0.00016) for both the bimodal and unimodal tasks. The order of sessions within a day was arranged so that each subject was tested
every weekday, and each type of test (bimodal, \( n = 3 \); unimodal, \( n = 3 \)) occurred a maximum of once per half-day. Each stimulus pig was used as a positive stimulus for one test pig and a negative stimulus for another, once per day in sessions separated by at least 1 h. This ensured that stimulus pigs were not confined for long periods and that they had time to rest, drink, and exercise between periods in the apparatus.

During a trial, stimulus pigs were placed in the stimulus chambers at the end of each arm of the Y-maze and the test pig was placed in the start box. The test pig was released from a start box into the central arena in which bimodal or unimodal cues from both stimulus pigs were available. It was held here for 15 s to encourage it to attend to cues from the stimuli before making a choice. The steel mesh drop-doors to the reward chambers were then opened and the test pig could choose to approach either stimulus pig. If it approached the positive stimulus and placed all four trotters in the reward chamber the mesh drop-door was immediately closed behind it; a dog clicker was used as a reinforcer to bridge the delay (1–2 s) between the subject’s correct response and the arrival of the food reward, which was delivered via the air inlet as soon as the drop-door was lowered. The stimulus pigs were also given a food reward of 4–5 raisins during each inter-trial interval regardless of the trial’s outcome to ensure that they also experienced frequent and predictable positive events whilst serving as a stimulus in the relative confinement of the chambers. If the test pig approached the negative stimulus, the mesh drop-door was closed behind her, but neither a reinforcing click nor a food reward was given. Following either a correct or incorrect choice, the start box was then wheeled to the back of the reward chamber that the pig had entered, and the test pig gently encouraged in to the start box. The start box was then returned to the start position for the next trial.

Upon reaching criterion in the bimodal task the pig was tested in the unimodal task in its next session. Subjects continued with the unimodal task until they had either achieved the learning criterion or been tested in the maximum number of sessions, which was 24 and 30 sessions in total (including both bimodal and unimodal tests) in batches 1 and 2, respectively. Fewer sessions were conducted in batch 1 because replacement of a sick animal and the subsequent social disturbance delayed the start of the experiment.

2.4. Analysis

Each animal’s performance in each session was measured by its overall score, i.e. the proportion \( p \) of correct choices per session. The probability, \( P \), of \( p \geq 0.8 \) occurring by chance in a single session is 0.0547 from the Binomial law. It is most improbable that similar choices would occur randomly in three consecutive sessions (\( P^3 = 0.00016 \) by the Multiplication rule) and this level of performance was used as the learning criterion to ensure that a performance plateau had been reached in the bimodal and unimodal tests. A generalised linear regression of score \( p \) on session number was used to estimate the rate of learning for each modal test type; the data were transformed with a Logit (\( \log_e(p/(1-p)) \)) to stabilise the variance. The data for the bimodal and unimodal tests were analysed separately using Genstat$^\text{TM}$ (5th Edition). The treatment structure, or fixed model, in Genstat notation was test$^*session$ for both analyses, where session describes the daily session number (1–30), and test (1–3) is the type of bimodal or unimodal test. Differences between test types were determined from the analysis of deviance; the deviance ratio is approximately distributed as \( F \). The sample sizes were small; therefore, test grouped the subjects by modality treatment rather than by each subject pig individually. However, some pigs did not complete the bimodal test and their results were later analysed individually to determine the rate of learning.

3. Results

3.1. Bimodal discrimination task

Eight pigs (\( n; AO-2; VO-4; AV-2 \)) learned the bimodal discrimination task (Table 1); the number of sessions needed to reach a third consecutive session with \( p \geq 0.8 \) ranged from 13 to 22. There was no significant difference in the rate of learning between these pigs (accumulated analysis of deviance: \( D_{2,138} = 1.18, P = 0.311 \)), i.e. there was no interaction between session and
test for the estimates of the regression’s gradient. There was also no main effect of test (accumulated analysis of deviance: $D_{2,138} = 1.40, P = 0.250$), i.e. there were no significant differences in the regression intercepts, or initial scores, between pigs on the different bimodal treatments. The regression model was therefore simplified to exclude test with a new fixed model of just session. The rate of learning for those eight pigs that reached criterion could then be described by a single regression of score on session (Generalised linear model: gradient ($\pm$S.E.) = 0.0803 ($\pm$0.0150), $P < 0.001$).

### Table 1
Session scores for individual pigs in the bimodal discrimination task

<table>
<thead>
<tr>
<th>Subject #</th>
<th>Test type</th>
<th>Batch 1</th>
<th>Batch 2</th>
</tr>
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<tbody>
<tr>
<td>Stimuli</td>
<td></td>
<td></td>
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<tr>
<td>B:A</td>
<td>Auditory and olfactory cues (AO)</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>E:F</td>
<td>Auditory and olfactory cues (VO)</td>
<td>4</td>
<td>11</td>
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<tr>
<td>C:D</td>
<td>Auditory and visual cues (AV)</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>F:E</td>
<td>Auditory and olfactory cues (AO)</td>
<td>2</td>
<td>10</td>
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<tr>
<td>D:C</td>
<td>Auditory and olfactory cues (VO)</td>
<td>3</td>
<td>10</td>
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<tr>
<td>A:B</td>
<td>Auditory and visual cues (AV)</td>
<td>5</td>
<td>12</td>
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</table>

Scores are out of 10 trials except where indicated. Pigs completing three consecutive sessions with $p \geq 0.8$ correct trials (indicated by shading) were promoted to the unimodal test in their next session. Pigs in batches 1 and 2 were given a maximum of 24 and 30 sessions, respectively. Stimulus pigs used for each test subject are identified by letters A–L with the positive stimulus in bold. AO: auditory and olfactory bimodal task; AV: auditory and visual bimodal task; VO: visual and olfactory bimodal task.
Four test pigs (AO, \(n = 2\); AV, \(n = 2\); 1 and 3 pigs in batches 1 and 2, respectively) failed to reach the bimodal task criterion within the experiment’s time limits (ca. 5 weeks). Problems with training included a tendency to lie down in the apparatus and lack of food motivation (pigs 8 and 12), despite the provision of a preferred food as a reward. In batch 2, this was probably due to the high ambient temperatures that occurred during training over the summer and caused lethargy and inappetence, thereby affecting the pigs’ motivation to work.

The regression gradients for three of these test pigs were not significantly different from zero, indicating that they did not learn the task; only pig 11 improved her score over time at approximately half the rate of those pigs that learnt the task (Table 1; accumulated analysis of deviance: \(D_{1,28} = 14.54, P < 0.001\); gradient (±S.E.) = 0.0464 (±0.0124)). Furthermore, three subjects achieved at least five non-consecutive scores of \(p \geq 0.8\), except for pig 8, which did not achieve any significant scores and failed to complete all 10 trials in 11 of her 30 sessions. There were no obvious problems with motivation of pig 5; all trials were completed and all rewards were consumed. As all stimulus pairs were used for two test subjects, and despite four pigs not meeting criterion, all six pairs of stimuli used in the experiment were discriminated successfully by at least one test subject in the bimodal task (Table 1).

Table 2
Session scores for individual pigs in the unimodal discrimination task

<table>
<thead>
<tr>
<th>Previous bimodal test</th>
<th>AV</th>
<th>AO</th>
<th>AO</th>
<th>VO</th>
<th>VO</th>
<th>AV</th>
<th>VO</th>
<th>VO</th>
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<tbody>
<tr>
<td>Sessions to reach bimodal criterion</td>
<td>21</td>
<td>14</td>
<td>13</td>
<td>13</td>
<td>20</td>
<td>21</td>
<td>20</td>
<td>22</td>
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<tr>
<td>Unimodal test</td>
<td>A</td>
<td>A</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>V</td>
<td>V</td>
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<tr>
<td>Subject #</td>
<td>3</td>
<td>4</td>
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<td>6</td>
<td>9</td>
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<td>Session</td>
<td>1</td>
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Session scores are number of trials correct out of 10; shaded scores are \(p \geq 0.8\) correct trials. Criterion for the unimodal test was three consecutive sessions at \(p \geq 0.8\) correct trials (\(P \leq 0.00016\)). The bimodal test given and number of sessions to meet bimodal criterion are shown for each pig above the unimodal test results. Pigs in batches 1 and 2 were limited to a maximum of 24 and 30 sessions, respectively to complete both bimodal and unimodal tests; unimodal sessions were therefore stopped after 3 sessions for subject #3, and 4 sessions for subject #2, without pigs having met the unimodal criterion. Stimulus pigs used for each test subject are identified by letters A–L with the positive stimulus in bold. AO: auditory and olfactory bimodal task; AV: auditory and visual bimodal task; VO: visual and olfactory bimodal task; A: auditory unimodal task; V: unimodal visual task; O: unimodal olfactory task.
3.2. Unimodal discrimination task

Six of the eight pigs that progressed to the unimodal task successfully reached criterion by discriminating consistently in three consecutive sessions when given unimodal cues (Table 2; O, \( n = 3 \); V, \( n = 2 \); A, \( n = 1 \)). All of the eight pigs scored \( p \geq 0.8 \) in at least one session but two pigs failed to do so in three consecutive sessions. There was no effect of session on score (gradient (±S.E.) = −0.0481 (±0.091), \( P = 0.601 \)) suggesting that these pigs were no longer learning during the unimodal test. All stimulus pairs were discriminated successfully by at least one test subject. Although there were significant differences in the mean accuracy of pigs using different modalities averaged over all unimodal sessions, i.e. a main effect of test (accumulated analysis of deviance: \( D_{2,32} = 5.50, P = 0.009 \)), this result must be treated with caution due to the small sample size for each test type and the possibility that individual differences were, at least in part, responsible for the observed difference. Olfactory discriminations (back-transformed mean proportion correct = 0.90; Table 3) were significantly more accurate than the two other test types whilst auditory and visual discriminations did not differ significantly from one another (back-transformed means = 0.61 and 0.68, respectively; Table 3). Our informal observations suggest that stimulus pigs screamed and squealed a lot in early sessions but gradually vocalised less frequently across successive sessions and trials within a session, producing fewer high-pitched vocalisations whilst continuing to grunt. Some loud sounds, such as screams, produced by one stimulus could have masked quieter vocalisations produced by the other stimulus. During some trials, stimulus animals sometimes failed to answer grunts produced by the test subject or their fellow stimulus pig, and often only produced a single grunt before test subjects made a choice.

4. Discussion

To the best of the authors’ knowledge, this study is the first explicit demonstration that pigs are capable of discriminating between closely related group-members when cues from only one or two of the three principal sensory modalities are available. The Y-maze method was successful in testing each modality separately; it provides opportunities for further work on social discrimination, such as the importance of relative dominance or degree of familiarity. Given the study’s small scale and the sixfold combination of bimodal and unimodal cues that the pigs could have experienced, individual differences in rate of learning could have been attributed to either order effects or individual differences in cognitive capacity, rather than to differences in the effectiveness of each sensory modality for individual discrimination. It was therefore not possible at this stage to determine a hierarchy of sensory cues that are used in social discrimination of group members.

The use of a learning paradigm to test group-member discrimination circumvents the potential problem of transitory preferential relationships or avoidance of particular individuals that can arise in a preference test. It can also demonstrate discrimination even where there is a lack of
preference, and this might be of particular relevance to group-member discrimination, when both familiar stimuli are equally attractive in a novel environment, for example. The use of engineering methods that allowed cue transmission to be manipulated effectively had several advantages: (i) there was no need to impair – by surgical or other means – the sensory abilities of test subjects, either temporarily or permanently; (ii) artificial representations of conspecifics, such as photographs (Ryan and Lea, 1994) or recorded vocalisations (Illmann et al., 2002) which can lack fidelity were avoided; and (iii) live stimuli allowed the dynamic interactions that occur between animals in dyadic encounters.

However, the main experimental difficulty with a method that uses live stimuli is the lack of control of cues between trials. While the exchange of air within the apparatus ensured that odours were transmitted, we have no knowledge of the concentration or composition of the odourants that were released. Visual cues were provided at a distance of 1 m (via mesh and Perspex panels) by stimulus animals that were free to turn around, stand up, lie down or otherwise alter their appearance. Auditory cues were available only if the stimuli vocalised. Our overall impression was that pigs tended to vocalise less frequently and produce fewer high-pitched vocalisations with successive sessions, and trials within a session and sometimes only produced a single grunt before test subjects made a choice. Similar differences in stimulus activity and vocal behaviour were also found by Hagen and Broom (2003) and Horrell and Hodgson (1992a).

Another potential limitation of the method is that the stimulus pigs could have influenced the choices made by the test subject through their behaviour. Each pig was used as both a positive and negative stimulus to limit the emergence of differential patterns of behaviour that might aid discrimination. Furthermore, the stimulus animals had no incentive to attract or repel the test subjects, other than their own motivation to interact with, or avoid, the test subject. Our previous work demonstrated that providing stimulus animals with incentives to attract or repel the test subject, contingent on their own rewards, can alter the rate of learning of test pigs (McLeman et al., 2005). If this potential difference in behaviour, outwith behavioural idiosyncrasies, was a major concern, then a more complex learning paradigm that utilises symmetrical reinforcement would be required (e.g. Gheusi et al., 1994).

Four out of twelve subjects failed to learn the bimodal discrimination task within the experiment’s time limits. This failure rate was lower than in our previous study with a similar method in which all social cues were available (McLeman et al., 2005), perhaps because the number of training sessions given this time was more than twice as high. Differences in learning ability, arousal, attention to stimuli, food motivation, a preferential relationship with the negative stimulus, an aversion to the positive stimulus, or potential differences in discriminability of the stimulus pairs, are plausible explanations for individual differences in task performance. However, we believe that the most likely explanations for three of the failing subjects in the second batch are lethargy and inappetence associated with the high ambient temperature during the experiment. Given the time invested in training subjects, it might also be advisable in future to keep subjects on a restricted diet to improve motivation (e.g. Laughlin and Mendl, 2004 after Kyriazakis et al., 1993), though this might require authorisation by a regulatory body, and to provide air conditioning if possible or alternatively avoid training during the warmest periods of the year.

The results of the bimodal discrimination task indicated that juvenile pigs can learn to discriminate between individual conspecifics in a Y-maze task using just two modalities. This is in agreement with previous work involving sensory disruption, which suggested that established social relationships could be maintained in the absence of visual (Ewbank and Meese, 1974) or olfactory cues (Meese and Baldwin, 1975): these experiments involved either the insertion of
opaque contact lenses or surgical removal of the olfactory bulb, respectively. We have shown that our improved stringency of control over olfactory and auditory cues enabled the role of modality in social discrimination of live conspecifics to be studied without the need to impose physical impairment.

There was no significant difference in the rate of learning under the different bimodal conditions, implying that pigs are quite versatile in the cues needed for social discrimination. However, the sample size was small due to the heavy demands of the experimental schedule and the rapid growth of the animals that made them too large to handle safely. Only approximately six pigs could be trained daily with this method. Similar studies in other domestic species using a series of successive discrimination tasks, and following the failure of some subjects to learn a task, have also yielded only a small number of subjects meeting criterion (1 hen: Bradshaw, 1991, experiment 1; 3 pigs: Tanida and Nagano, 1998, experiment 2; 5 cows: Rybarczyk et al., 2001, experiments 3 and 4).

Given the suggested primacy of olfaction for communication in pigs (Jensen, 2002), it could be hypothesized that subjects in the AV treatment would have been the slowest to learn the task. However, little is known about the mechanisms of social discrimination within groups of pigs; the behavioural ecology of wild and feral pigs suggests that the cues utilised will depend upon distance as well as context. Attempts to compare directly the efficiency of modalities may be futile, as we cannot be sure that the essential cues are provided under optimal conditions for transmission. With regards to visual cues, Koba and Tanida found that visual discrimination in pigs deteriorated both with increased distance, and decreasing illuminance (Koba and Tanida, 2001). Groups of commercial pigs are often homogeneous in terms of size and sex, and therefore perception of small differences in appearance could be impaired under dim light. In addition, disruption of auditory cues in this study, by disguising the source, differed fundamentally from the removal of visual and olfactory cues. Sound attenuation to background noise levels (≥50 dB reduction) would require very heavy chambers that would be cumbersome to move manually. However, this technique might be feasible with smaller animals.

The rate of task acquisition is particularly important when complex questions are to be answered about perception and cognition based on learning paradigms but the rapid growth rate of our pigs constrained the duration of the experiment. Test pigs reached criterion between 13 and 22 sessions. Although this is considerably longer than in our previous experiment in which all social cues were available (between 4 and 11 sessions, McLeman et al., 2005), it does not necessarily follow that pigs were hampered in their rate of learning because they normally use all three modalities for social discrimination. The slower rate of learning may also have reflected general disturbance following the disruption of a modality that affected attention or memory formation, or changes in the reward procedure; stimuli in this study were fed a reward after each trial regardless of the performance of the test subject, whilst in our previous work stimuli were rewarded contingent on the test subject’s success. This procedural change may have reduced activity, vocal rate and other high-arousal behaviours and hence affected discrimination (McLeman, 2005).

Six of the eight pigs that learned the bimodal task were subsequently able to discriminate familiar, closely related conspecifics using only one sensory modality. Pigs can use unimodal sensory information to discriminate between stimuli; for example, sows discriminated recorded vocalisations of their offspring from unrelated piglets of the same age (Illmann et al., 2002), while juveniles discriminated between whole body odours from familiar vs. unfamiliar pigs (Kristensen et al., 2001). Yet, these discriminatory cues differ in their familiarity to the test subject, and not necessarily in their unique characteristics. Our results are the first to show that individual discrimination is possible with all three primary modalities using live, familiar conspecifics. The
ability to discriminate between individuals using idiosyncratic cues, rather than differences in broader social classes such as age, sex, familiarity, etc., has been suggested as a prerequisite for true individual recognition (Zayan, 1994; Zayan and Vauclair, 1998), whereby a concept or mental representation of an individual is held by the observer. This is because in order to retain a memory of the identity of an individual, one must first possess the ability to tell an individual apart from other conspecifics (see Gheusi et al., 1997). This could be as simple as using one single, reliable cue in one modality, or it could be possible using any of a number of cues. As such, the ability may be used in the maintenance of not only dominance relationships, but also affiliative social bonds (Durrell et al., 2004; Kendrick et al., 1995). The possibility that pigs could possess multimodal mental representations of familiar conspecifics provides an opportunity to investigate further the nature of the mental representations that animals may hold, such as what cues might be included in the concept of an individual. To date, this has only been demonstrated using generalisation between different cues from a single sensory modality (two distinct odours in rodents: Johnston and Jernigan, 1994; two different photographs in primates: Parr et al., 2000). Given their ability to discriminate individuals using three different sensory modalities, pigs may be able to generalise between cues from the same familiar individual from two different modalities.

5. Conclusion

In summary, discrimination of individual group-members by juvenile domestic pigs using either bimodal or unimodal cues was demonstrated in a simple Y-maze test. The method enables further questions to be answered about social discrimination. These include the effects of the physical environment on discrimination, the importance of specific cues within a modality, and the existence of social categories or relationships between stimuli. Such work may also have important implications for the management of aggression in pig production and hence for pig welfare. Unfamiliarity (Stookey and Gonyou, 1998) and uncertainty over fighting ability (Rushen, 1988) are known to be causative factors of aggression, while pre-exposure of unfamiliar pigs can reduce the time needed to settle dominance relationships once the animals are placed together (Jensen and Yngvesson, 1998). However, the cues that pigs need to recognise group-members and hence reduce aggression, especially after periods of separation, are less well understood. Further fundamental study of the mechanisms of social recognition could complement applied studies of social interaction in groups of pigs by providing knowledge of thresholds for perception and discrimination of social cues, or the time-course for formation and decay of social memory, under controlled conditions.

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