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5 **Cattle discriminate between individual familiar herd members in a leaning**
6 **experiment.**
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13 **Abstract**

14 We tested the ability of cattle to discriminate between socially familiar
15 conspecifics in a Y-maze discrimination experiment. The discriminative stimuli
16 were herd members tethered in the Y-maze side arms (stimulus heifers);
17 approach to one of these was rewarded with food and approach to the other
18 was unrewarded, and their positions were randomly swapped. Each of six
19 experimental heifers was subjected to two pairs of stimulus heifers. All
20 subjects reached the learning criterion (19 out of 20 consecutive choices to the
21 rewarded stimulus heifer's position in the Y-maze) with one pair of stimulus
22 heifers. With the other pair, learning was slower and only three of the subjects
23 reached criterion. All heifers that reached criterion chose correctly in at least
24 five additional trials designed to control for cues emanating from the
25 experimenter's behaviour or from the food reward. We conclude that cattle can
26 discriminate between individual familiar conspecifics, that they can learn
27 discrimination tasks quickly, and that speed of learning and level of correct
28 response can be influenced by the identity of the stimulus individuals. We also
29 explored the experimental heifers' behaviour during the learning process.
30 Behaviours indicative of agitation were observed more often in the second task
31 than in the first and also increased with time during learning tasks ($P < 0.05$),
32 but were not related to whether a heifer made a correct choice. Head
33 orientation predicted the correct direction when this was subsequently chosen
34 ($P < 0.05$), whereas body orientation tended to predict the correct direction
35 when the incorrect arm was subsequently chosen ($P = 0.063$).

36 Keywords: cattle; discrimination learning, social recognition, memory, expressive
37 behaviour

1. Introduction

Social discrimination has been demonstrated in a range of taxa (Colgan, 1983; Halpin, 1986) and can be classified firstly with regard to the social categories that are discriminated and secondly according to the degree of mental complexity involved: discrimination of individuals is distinguished from categorisation of individuals into classes on the basis of kinship, degree of familiarity, sex, social status or other kinds of group membership (Barrows et al., 1975; Gheusi et al., 1994). Further, a distinction is made between discrimination and recognition. Recognition is a more complex mental process than discrimination, as it involves the recollection of the learned idiosyncratic identity of an individual previously met (Gheusi et al., 1994) and the formation of a mental representation (Zayan, 1994). Individual discrimination is however a pre-requisite of individual recognition.

The ability of cattle to recognise individuals has commonly been inferred from their relatively stable dominance–avoidance relationships (Bouissou, 1965; Syme and Syme, 1979; Fraser and Broom, 1997) and may play a role in inhibiting aggression among group members (Abright and Arave, 1997). However, the assumption that individual recognition necessarily underlies stable dominance–avoidance relationships has been criticised (Barnard and Burke, 1979; Zayan, 1987a,b). The development and maintenance of social structures may be supported by mechanisms other than individual recognition (Pagel and Dawkins, 1997; Hemelrijk, 2000).

The ability of sheep to tell apart socially familiar conspecifics was demonstrated by Kendrick et al. (1996), but there is a lack of experimental evidence for individual recognition or discrimination in cattle. Indirect evidence was provided when alteration of visual or olfactory characteristics of individuals influenced aggressive interactions (Bouissou, 1971, 1972; Cummins, 1991). Even on the more general level of social discrimination, experimental evidence is scarce. Barfield et al. (1994) showed that calves prefer the vocalisations of their dams to those of another cow. Calves and their dams are likely to identify each other by olfactory and visual as well as auditory cues, but while this ability has been extensively studied in sheep (Bouissou, 1968; Poindron and Carrick, 1976; Poindron and Lévy, 1990), much less is known about it in cattle. Perceptible individual differences are the basis for individual recognition and calves have been shown to be able to discriminate between unfamiliar individual conspecifics' urine odours in an operant experiment (Baldwin, 1977). Individual differences were also demonstrated in the calls of Chillingham bulls (Hall et al., 1988).

The main aim of the present experiment was to contribute to the understanding of individual recognition in cattle by demonstrating their ability to discriminate between socially familiar conspecifics. We used a Y-maze discrimination paradigm, which has previously been used successfully with cattle (Gramling et al., 1970; Schaeffer and Sikes, 1971; Phillips and Weiguo, 1991; Entsu et al., 1992; Hosoi et al., 1995), and live animals were chosen as stimuli.

We also explored the heifers' behaviour during learning. We wanted to establish whether directional behaviours (orientation of head and body) predicted subsequent choices, and whether they were related to the learning process. In addition, we aimed to detect possible changes with time (experimental experience) or performance in behaviours expressive of agitation.

2. Methods

2.1. Animals and management

Fourteen heifers were kept in a 2.5 ha field in Cambridgeshire, UK, and 10 of them (9 pure-bred South Devon and 1 cross-bred South Devon \times Blonde d'Aquitaine; aged 16–22 months at the start of the experiment) were used in the experiment. The experiment was carried out within the animals' home field during July and August 1998. In the field there was a permanent holding pen (4 m \times 12 m) for temporary confinement of the animals. The field had one permanent water supply.

All animals had been reared together in a suckler herd and weaned at about 9 months. They had been housed together in barns and on fields as part of a larger herd all winter. These 14 heifers had been together in this particular field since March, and there was sufficient vegetation in the field to provide adequate food for the herd until late summer. Prior to the commencement of the experiment, the heifers had been accustomed to being fed barley in the holding pen once or twice a week. During training and the experiment they were each fed, on average, 1.5 kg of rolled barley per day as rewards. The taming, halter-training and preparation process began 2 months prior to the experiment, as none of the heifers had prior experience of intensive handling.

2.2. Apparatus and structure of the experiment

A Y-maze was constructed from electric fencing 10 m away from the holding pen (Fig. 1a). When the experimenter was not in the field, the maze was left with the gates open and the current switched on. During experiments, the current was switched off. Four

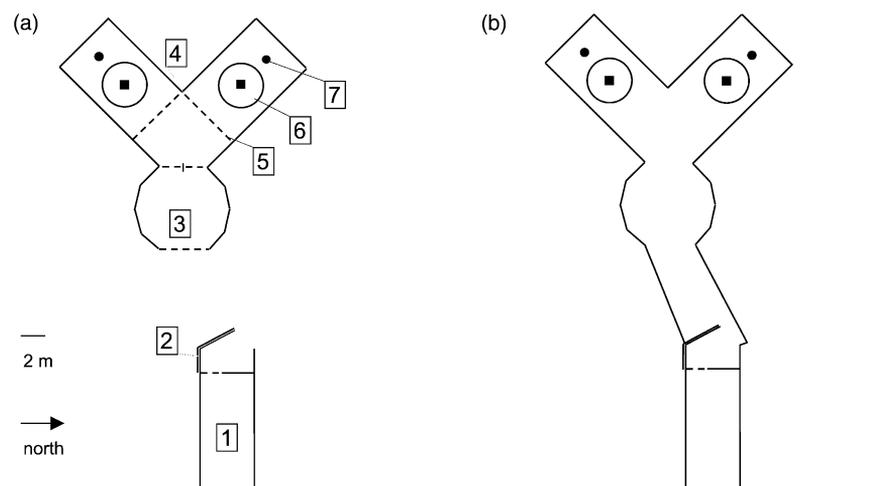


Fig. 1. Map of apparatus for (a) training trials; and (b) test trials: (1), holding pen; (2), visual barrier; (3), start area; (4), corner of maze; (5), gates for confinement after incorrect choices; (6), placement of stimulus heifer in arm (tether at square, radius of movement); (7), food reward bucket.

Table 1
Assignment of stimulus heifers to experimental heifers

E	Round 1			Round 2		
	S pair	S+	S–	S pair	S+	S–
16	A	10	20	B	18	42
39	A	10	20	B	42	18
45	B	42	18	A	10	20
54	A	20	10	B	18	42
72	B	18	42	A	20	10
78	A	20	10	B	42	18

Numbers correspond to original animal eartags and are used for identification of individuals; E, experimental heifer; S pair, stimulus pair; S+, rewarded heifer; S–, non-rewarded heifer.

of the 10 heifers were trained to stand tethered to a ring on to the ground inside the Y-maze arms (point 6 in Fig. 1, stimulus heifers). The other six heifers (experimental heifers) were trained to make a choice between the arms of the Y-maze for a food reward, which was in the bucket behind the correct stimulus heifer. The stimulus heifers were assigned to two pairs (A and B). In pair A, one of the heifers was cross-bred and the other pure-bred; in pair B, both heifers were pure-bred. The experiment consisted of two rounds as each experimental subject was trained and tested for discrimination with each pair as assigned in Table 1.

Training or test sessions were carried out either on consecutive days or with a break of up to 2 days. In the first round, one 12-day break was made for practical reasons after five of the six subjects had learned the task. The subjects had four trials each per training session in a pre-defined, constant order. Each trial consisted of one opportunity to make a choice between the maze arms, as detailed below.

In order to avoid the possibility of position preferences developing, the stimulus heifers' positions in the maze arms were varied randomly except for the following limitations applied to the trial sequences of each experimental subject: (1) within each of the first two sessions, only two consecutive trials with the same position were allowed; (2) in subsequent sessions, no more than three consecutive trials with the same positions were allowed.

2.3. Session and trial procedures

Before each training session, the heifers were gathered in the holding pen (point 1 in Fig. 1) and each fed 150 g barley. The first two stimulus heifers were tethered in the maze arms (point 6) and given a food reward. Whenever the stimulus heifers had to swap places during the session, they were rewarded with 100 g barley each, and sometimes they received randomly dispersed small rewards between swaps. Experimental heifers were tethered behind a barrier (point 2) to prevent them from seeing the maze. The bucket behind the positive stimulus heifer was filled with 300 g barley, the other bucket was left empty.

The experimental heifer was led into the start area (point 3) with the gate between start area and maze arms closed. The rope of the halter was wrapped around her neck, and the entrance gate to the start area was closed behind her. The experimenter walked around her along the north side of the fence and sat down centrally in front of the gate leading to the maze arms. After 50 s, the experimenter turned around via the south, opened the gate from

the middle by throwing the right and left parts of the fencing to the sides simultaneously, and moved straight forward to the corner of the maze (point 4), allowing the heifer to enter the arms. If a heifer's choice was correct, she could eat the food in the bucket behind the positive stimulus heifer (S+). If a heifer's choice was incorrect (S-), she was confined in the wrong arm for about 30 s before she was allowed to go to the other arm where there was food in the bucket. Whether the choice was correct or incorrect, after she had finished eating the heifer was left for another 2 min and then led back to the holding pen.

The learning criterion was set as two possibilities, whichever was reached first: (1) four consecutive sessions (16 trials) without any incorrect choices; or (2) four correct out of five consecutive sessions (only one incorrect choice was allowed in the 20 trials). The probability of either of these criteria occurring by chance is less than 0.001 (binomial test).

After the learning criterion had been reached, test trials were conducted to control for the smell of the food and for possible subtle cues from the experimenter. To make sure that the trained cattle could make choices on the basis of stimulus heifers alone, the maze was altered in that there were no gates and the start area was connected to the holding pen (Fig. 1b). There was no food in either of the buckets and the experimenter was no longer present during trials. The experimental subject was able to walk by herself from behind the visual barrier into the maze. Once a correct choice (to a heifer that had previously been associated with a food reward) had been made, the experimenter gave the heifer the same food reward as during training, but if the choice was wrong, no reward was given. Each experimental heifer had between five and eight such discrimination test trials, however three heifers (16, 54 and 78) did not reach the learning criterion in the second round and because of lack of time discrimination test trials were then not carried out with these heifers.

Between the two rounds, five of the six heifers (all but 45, who had not yet reached the learning criterion) were subjected to one trial each with baited buckets but without stimulus heifers as associative cues. In addition, after the second round, heifers 45 and 72, who had reached the learning criterion quickly, were subjected to a retention test with eight trials each, with the pair of stimulus heifers that they had discriminated in the first round. Heifers 45 and 72 were also given five further trials each with only one stimulus heifer (rewarded stimulus heifer for 45, non-rewarded for 72) in the Y-maze, to find out whether the information provided by only one stimulus heifer was sufficient for them to choose correctly.

2.4. Data collection

For each trial, the outcome could be either success or failure. Learning speed was defined as the number of sessions needed to reach criterion. In addition to the outcome of the trials, in each trial it was noted whether the stimulus heifers were lying while an experimental subject was in the start area.

Pre-choice behaviours of the experimental heifers were recorded from video-recordings made with a stationary camcorder during some of the trials. The orientation of an experimental heifer's body while in the start area was at each second classified as to the left, right or central in relation to a line perpendicular to the gates. The orientation of the head was also recorded each second, as left, right, central or to the experimenter. The number of steps with front feet was counted, from the heifer was taken off the halter until the gate to the maze arms was opened. Further, it was noted whether while the experimenter moved round

the start area, the heifer stayed, moved up to two steps forward, or moved right to the front. Trials were also classified according to whether or not the heifer sniffed/touched the fence while in the start area, whether a heifer moved into a maze arm as soon as the gate opened or waited until after the experimenter had stopped, and whether or not the heifer trotted when she entered a maze arm.

In total, 152 video-recordings were obtained in close-up view of the start area and 187 videos were made with a wide-angle view. All variables could be coded from the 152 close-up videos, and the classifications of time of movement into maze arms and of gait were in addition coded from the 187 wide-angle videos. Before coding, all video clips were edited out of their context and recorded back onto tapes in random order. Videos were coded by the experimenter and in addition by 'blind' observers who did not know the animals or experimental conditions. Inter- and intra-observer agreement was ensured in all cases using Cohen's kappa for classification variables (Bakeman and Gottman, 1997) and Spearman's rank correlations for the number of steps.

For the purpose of statistical comparison, the proportion of time that body/head orientation was to the left or right was calculated for each trial. In order to achieve independence of replicates, the video data were then reduced to subject level in two steps. First, as there were four trials per experimental subject and session, means or proportions of the trial values within each session were calculated. Thereafter, one value per subject and round was calculated by averaging across sessions. This procedure reduced the sample size to the number of subjects and prepared the data for the application of non-parametric matched-pairs and repeated measures tests. All tests are non-parametric and two-tailed and were carried out using the sequential analysis software Gseq (<http://www.gsu.edu/~psyab/sg.htm>) or manually using procedures and tables in Siegel and Castellan (1988). For illustration, graphical presentations in box plots are based on raw data.

3. Results

The stimulus heifers quickly adapted to standing tethered in the maze arms. They would often go to their places in the maze arms by themselves before the start of an experimental session, and they calmly stayed tethered for several hours. They sometimes lay down, in particular heifer no. 10, who suffered from lameness and lay down in 82% of the trials, whereas the others lay down only in 8% (no. 42) and 2% (nos. 18 and 20) of the cases.

All heifers were easy to handle during the experiments, and minor problems with lack of motivation occurred only on a few days, when the weather was very wet and the holding pen that the heifers had to wait in became extremely muddy. The experimental subjects generally accepted the non-activated electric fencing as a boundary, although one of the heifers (no. 45) lost respect for the fence towards the end of the experiment, when she had already reached the learning criterion for the second task, and repeatedly walked right through the gate instead of waiting for it to be opened. Also during the last part of the second round, several of the experimental heifers started to display behaviours directed towards the experimenter that seemed to be aimed at encouraging her to open the gate (pushing, rubbing, staring).

The experimental heifers showed no signs of reluctance to pass any of the stimulus heifers and did not normally interact with them before going to the food bucket. However,

they often interacted with the tethered heifers when confined in the incorrect maze arm, and after they had finished eating. Interactions included licking the udder, mutual licking, play fighting, threats and mounting (when one heifer was in oestrus).

All six heifers learned the discriminations both with pair A and with pair B, but in some cases, they did not reach the pre-set learning criterion (Fig. 2). In the first round, five of the

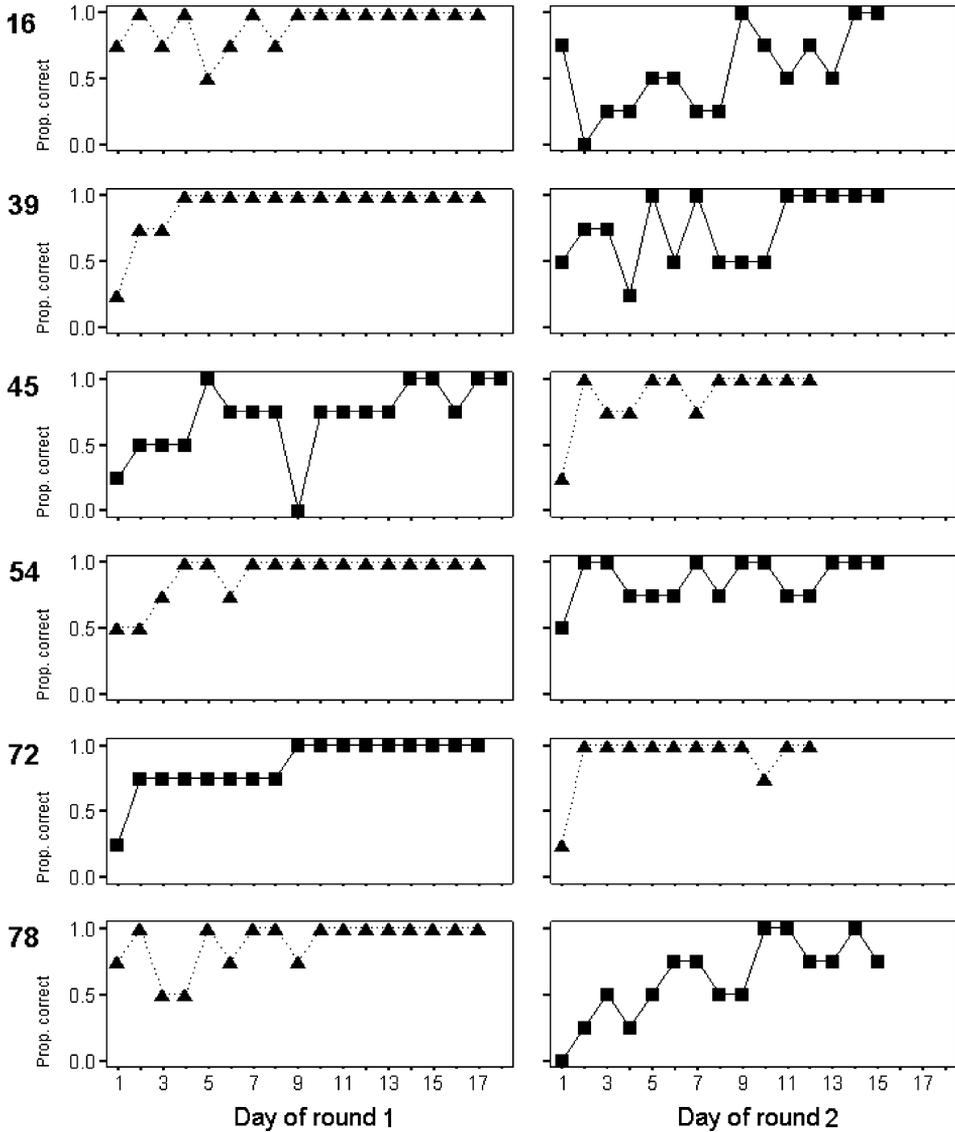


Fig. 2. The proportion of correct outcomes during each session for each experimental heifer (numbers on the left). The point symbols indicate whether the heifer had to learn pair A (▲) or pair B (■). Test trials involving no, or only one, stimulus heifer are not included.

Table 2
Outcome of test trials

Test	E (S)	N	x	P
Round 1 discrimination	16 (pair A)	5	0	0.031
	39 (pair A)	5	0	0.031
	45 (pair B)	8	0	0.004
	54 (pair A)	5	0	0.031
	72 (pair B)	5	0	0.031
	78 (pair A)	5	0	0.031
Without stimulus heifers	All but 45	5 ^a	3	0.81
Round 2 discrimination	39 (pair B)	5	0	0.031
	45 (pair A)	6	0	0.016
	72 (pair A)	8	1	0.035
Retention of round 1	45 (pair B)	8	0	0.004
	72 (pair B)	8	0	0.004
Only one stimulus heifer	45 (S+ from pair B)	5	2	0.50
	72 (S– from pair B)	5	2	0.50

Numbers correspond to original animal eartags and are used for identification; E, experimental heifer; S, stimulus; N, number of test trials; x, number of incorrect choices; P, one-tailed probability of the given values under the binomial distribution.

^a Each of five individuals tested once each.

six heifers (all but no. 45) reached the learning criterion within 14 sessions. They remembered the association over a 12-day break and made the correct choice in the test trials (Table 2), including heifer no. 45, who was tested despite not having reached criterion beforehand. Subsequently, of the five heifers that were tested once each with baited buckets but no stimulus animal present, two made a correct choice and three made a wrong choice. In the second round, three of the heifers (39, 45 and 72) reached criterion within 14 days, and they made the correct choice in all test trials (Table 2). The other three did show a learning effect, but did not reach the criterion within the 14 days (Fig. 2). The two individuals (45 and 72), who were tested as to whether they remembered the first pair after having learned the second, chose correctly on all trials (Table 2). When tested with only one of the stimulus heifers present, the rewarded for heifer 45 or the non-rewarded for heifer 72, each failed in two out of five trials.

Averaging the session outcomes over the six subjects illustrates that learning speed varied with the pair to be learned, pair A being learned more quickly than pair B (Fig. 3; Wilcoxon signed-ranks test: $T = 21$, $N = 6$, $P < 0.05$). There was no effect of which of the two stimulus individuals within pairs was the positive or negative stimulus, nor was there a difference in learning speed between the first and second round ($T = 11.5$, $N = 6$, NS).

On average, an experimental heifer's body orientation was central more than half of the time that she spent in the start area ($\bar{x} \pm \text{S.D.} = 54 \pm 0.4\%$, $N = 152$) and equally likely to be to the left (22%) as to the right (24%). The head orientation was on average 12% to the centre, 25% to the experimenter, 34% to the left and 29% to the right. When categorisations of head or body as central, or to the experimenter, were disregarded, there was 75% agreement between the classification of head and body with regard to left and right.

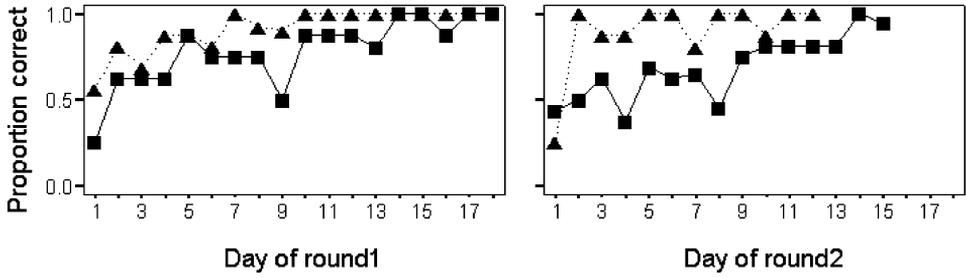


Fig. 3. The proportion of correct choices on each day, mean of the six experimental subjects, depending on whether they were discriminating pair A (▲) or pair B (■).

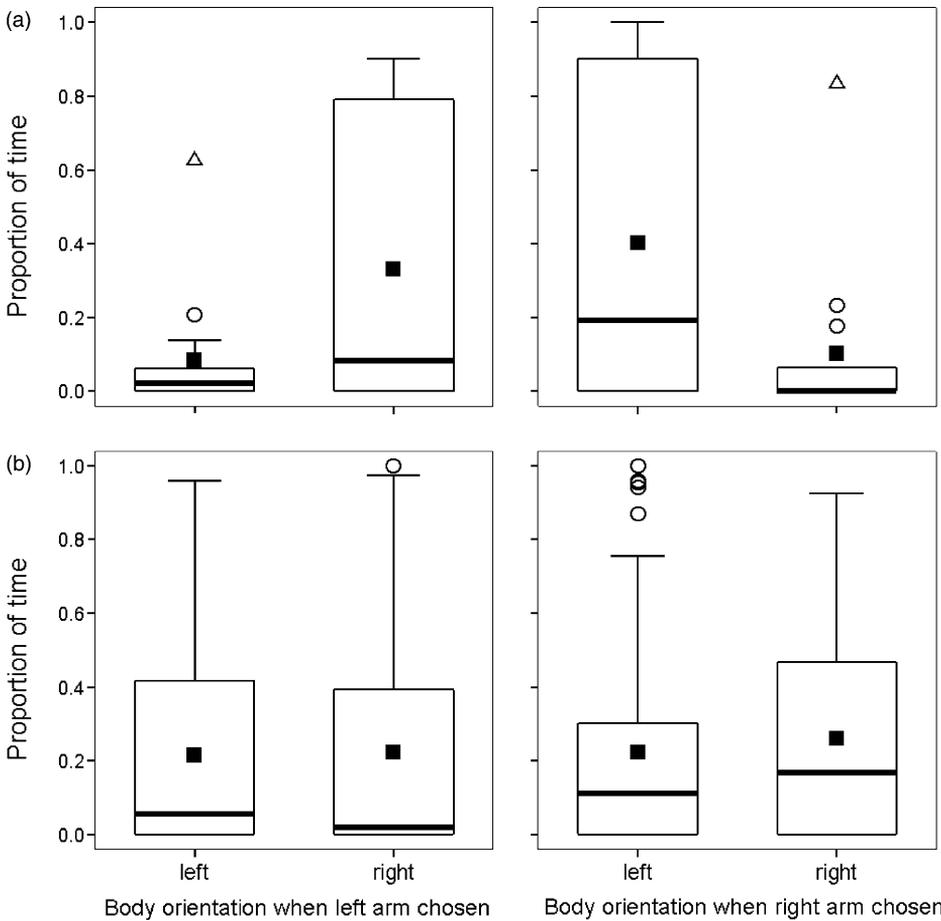


Fig. 4. The proportion of time spent with the body oriented to the left or right (*x*-axis), in relation to whether the left arm (left-hand panels) or right arm (right-hand panels) was chosen, for trials with (a) incorrect choices and (b) correct choices. Box plots based on raw data ($N = 152$) with mean (■), median (—), interquartile range (box), outliers (○); defined as 1.5–3 box lengths from the end of the box), extremes (△); defined as more than three box lengths from the end of the box), range apart from outliers and extremes (whiskers).

Body orientation to the centre decreased from the first to the second round (Wilcoxon signed-ranks test: $T = 21$, $N = 6$, $P < 0.05$). The relationship between body orientation to the left or right, and which arm was chosen, taking into account whether the choice was correct, is shown in Fig. 4. When the choice was wrong, the body orientation appeared to be negatively related to the arm that was chosen. When the right arm was chosen incorrectly, the body tended to be oriented to the left side (Wilcoxon signed-ranks test: $T = 15$, $N = 5$, $P = 0.063$; sample size is five because one of the heifers never chose the right arm incorrectly). When the choice was correct, body orientation was not related to choice.

Head orientation did not change with time. The relationship between head orientation to the left or right, and which arm was chosen, in relation to whether the choice was correct, is illustrated in Fig. 5. When the choice was wrong, there was no clear relationship. When the

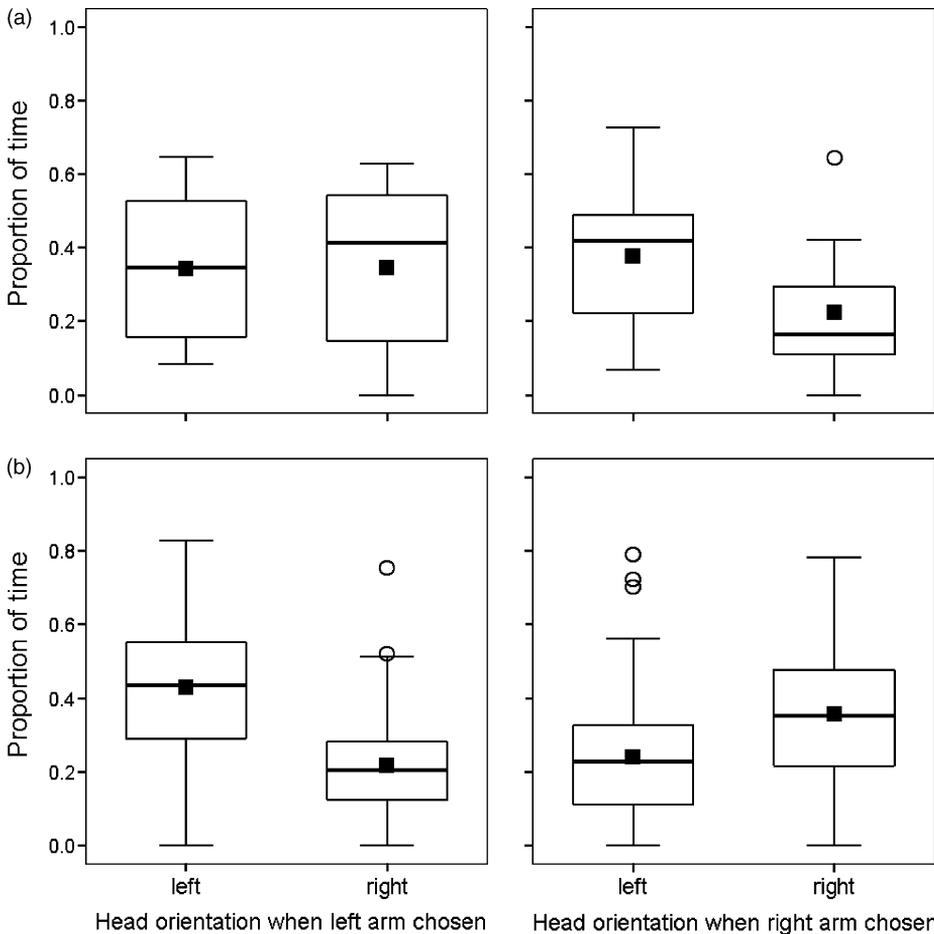


Fig. 5. The proportion of time spent with the head oriented to the left or right (x-axis), in relation to whether the left arm (left-hand panels) or right arm (right-hand panels) was chosen, for trials with (a) incorrect choices and (b) correct choices. Box plots based on raw data ($N = 152$) with symbols as in Fig. 4.

choice was correct, the orientation of the head was positively related to the arm chosen: when the left arm was chosen, the head was orientated to the left more often than to the right; when the right arm was chosen, head orientation to the right occurred more often (Wilcoxon signed-ranks test: $T = 21$, $N = 6$, $P < 0.05$, in both cases).

None of the other behaviours recorded were related to whether the heifers made correct or incorrect choices, but some changed with time. Whereas at the beginning of the tests the heifers frequently stayed near where they had been taken off the halter in the start area while the experimenter moved around to the gate leading to the maze arms, in the second round the heifers mostly moved straight to the gate as soon as they were let off the rope, and they made more steps than in the first round (Wilcoxon signed-ranks test: $T = 21$, $N = 6$, $P < 0.05$, for both variables). All heifers increasingly sniffed or touched the electric fencing gate that led to the maze arms ($T = 21$, $N = 6$, $P < 0.05$). Heifers were observed licking their lips, and in the start area, they sometimes ruminated.

For measures of speed of movement into maze arms and trotting, sufficient video clips were available to investigate not only differences between the two rounds but also changes over time phases (three phases of 5 days each) within rounds. Fig. 6 shows scores for each day on which videos were made. When the gate opened and gave access to the maze arms, in the earlier days heifers tended to wait a little before they moved into one of the arms. However, over the course of the first round the heifers became quicker, and by the end of the first round all of them consistently moved into a maze arm as soon as they could, the three 5-day phases being different (Friedman two-way analysis of variance: $F_r = 11.3$,

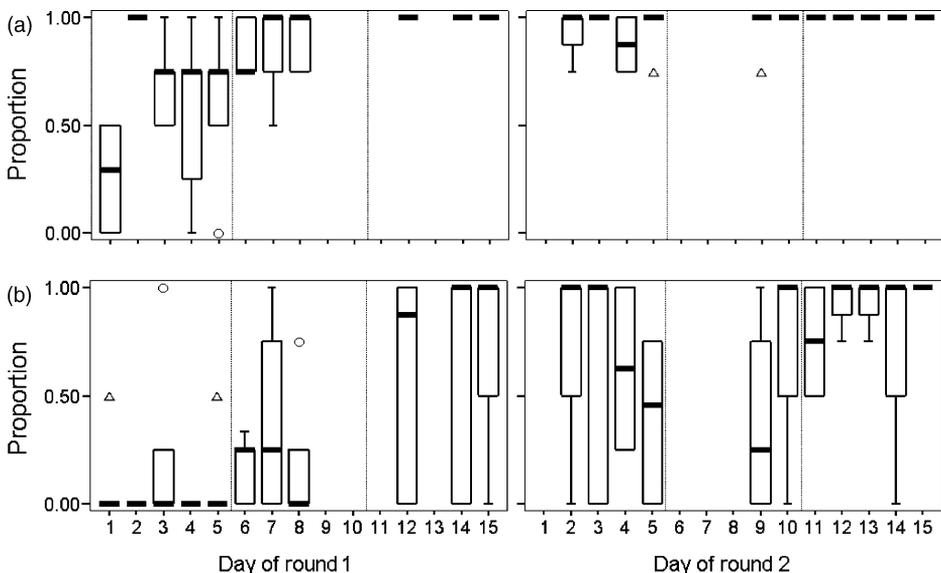


Fig. 6. Scores on each day for (a) proportion moving into the arm as soon as the gate opens and (b) proportion trotting. Vertical reference lines separate phases of 5 days. Box plots with symbols as in Fig. 4. Boxes are based on averages per day for each subject of whom video clips were available: in round 1, $N = 6$ on all days for which boxes are drawn, apart from day 2 when $N = 2$; in round 2, $N = 6$ on days 3, 5 and 9, $N = 4$ on days 2, 10, 12, 13 and 14, and $N = 2$ on days 4, 11 and 15.

$N = 6$, d.f. = 2, $P < 0.001$). Within the second round heifers almost always moved straight into the maze arms. Overall, the heifers went straight into the maze arms more often in round 2 than in round 1 (Wilcoxon signed-ranks test: $T = 21$, $N = 6$, $P < 0.05$). On their way into the maze arms, the heifers usually walked in the first sessions, but increasingly, they trotted (within round 1: $F_r = 7.1$, $N = 6$, d.f. = 2, $P < 0.05$). There was a reduced level of trotting during the middle phase of round 2 (within round 2: $F_r = 8.0$, $N = 4$, d.f. = 2, $P < 0.05$; missing data for two subjects).

4. Discussion

In some of the learning experiments with cattle that have previously been reported, the animals were food-deprived for some time before learning sessions, in order to increase their motivation (Schaeffer and Sikes, 1971; Kilgour, 1981; Entsu et al., 1992). None of the heifers in the experiment reported here were food-deprived. The heifers' completion of the tests in the present study was probably related to their habituation to handling, the high palatability of the food rewards, and their age, as it has previously been shown that yearling cattle are particularly alert and exploratory (Murphey et al., 1981). Cattle are sometimes difficult to use in Y-maze learning because they develop position preferences (Grandin et al., 1994). Position preferences were not a problem here, possibly because the S+ and S- arms were swapped frequently, or/and because the heifers were allowed access to the correct maze arm even when they chose the incorrect maze arm first. Hosoi et al. (1995) found that adult cows changed from win-stay to win-shift foraging strategies in relation to their experience of forage depletion. Wieckert et al. (1966) and Schaeffer and Sikes (1971) also allowed calves access to the correct side and the reward after incorrect choices, so this may be a good technique for the prevention of position preferences.

All six heifers readily learned the discrimination tasks in the Y-maze, although there were individual differences in the number of trials taken to reach criterion. Some of the heifers—with stimulus pair B—did not reach the stringent criterion that had been set in advance, but their learning curves nevertheless clearly demonstrated the acquisition of the discrimination task. In several cases, heifers made no errors at all once they had learned the task. They could retain the learned information for at least 12 days. Furthermore, the two cattle tested both remembered the first discrimination after having learned a second task with different stimulus heifers. The high level of performance in the test trials confirmed that the heifers did not rely on cues emanating from the food alone, or inadvertently given by the experimenter.

It was expected that learning might be quicker in the second round due to practice. However instead, one pair of stimulus heifers was easier to discriminate than the other. There are two possible reasons for this: that social relations made it easier to approach the individuals in pair A, or that additional cues made the formation of an association between stimulus heifer and reward easier in pair A. If the ease of learning pair A rather than B had been caused by some animals being easier to approach than others, subjects with an easily approached individual as the positive stimulus should have learned more quickly. The data do not support this, but on the other hand, the sample size may be too small to detect such an effect. However, this explanation is also rendered unlikely by the fact that none of the

experimental heifers displayed any reluctance to approach any of the stimulus heifers. The fact that heifer no. 10 in pair A tended to lie down could have influenced ease of learning, not because she was easier to approach, but because another obvious cue was added to the distinction between her and heifer no. 20. However, no. 10 did not always lie, and no. 20 did not always stand. In 47 trials when both were standing, a total of eight wrong choices were made (all of these were within the first three training sessions). On three occasions when no. 10 was standing and no. 20 was lying, the experimental heifers chose correctly. However, there was a second distinctive feature about heifer no. 10: she was the only one of the South Devon heifers who was cross-bred with Blonde d'Aquitaine. The differences between heifers 10 and 20 in pair A may therefore have been greater than between the heifers in pair B. The fact that the two heifers who were tested with only one stimulus heifer at a time both made mistakes, also suggests that the experimental heifers might have been using cues about the relation between the two heifers, rather than their idiosyncratic identities, in making the choices.

Live animals were used as discriminative stimuli, so the experimental animals could use a range of different discriminative cues, and several sensory modalities. Further investigation of how cattle experience familiar individuals could involve breaking down the whole-animal stimulus and investigating to what extent discrimination is possible on the basis of particular body parts, perspectives or sensory modalities.

The present experiment only established the occurrence of individual discrimination—it did not address the question of individual recognition as a mental representation of individuals. The topic of mental representation can be addressed by investigating the animals' ability to transfer a discrimination learned using one set of stimuli to tasks with a new, not previously presented, set of stimuli from the same individuals, or with experiments involving cross-habituation. No such experiments are reported for cattle. Sheep have been shown to transfer from slides showing frontal views of herd members to profiles (Kendrick, 1998). Golden hamsters cross-habituate between scents from flank glands and vaginal scents (Johnston and Jernigan, 1994) as well as ear scents (Johnston and Bullock, 2001). Long-tailed macaques matched slides from non-overlapping body parts of familiar conspecifics (Dasser, 1987).

Although individual recognition may not be necessary for the maintenance of social hierarchies, the ability of cattle to discriminate among familiar herd members is appropriate for their stable dominance–subordination relationships and partly non-linear hierarchies. Another important role for individual recognition may be in the development and maintenance of affiliative relationships, which have been repeatedly demonstrated in cattle (Brownlee, 1950, 1954; Broom and Leaver, 1978; Reinhardt and Reinhardt, 1981, 1982; Sato et al., 1993). More research would be needed to determine the relationship between the animals' preferential association with particular herd members in different situations. Also, it would be interesting to investigate the degree to which animals form mental representations of individuals' identities in relation to their social relationships. It is possible that transfer ability across sensory modalities would be greater in tasks that used stimulus animals with which the experimental animals were closely associated socially, than in tasks that used familiar, but less socially bonded, individuals.

Whether body or head orientation predicted a heifer's choice depended on whether that choice turned out to be correct. When the choice was correct, body orientation was not

related to choice, but head orientation was more often towards the arm to be chosen. On the other hand, if the choice was incorrect, head orientation was not related to choice, but body orientation tended to predict where the heifer was not going, that is, the correct maze arm. It may be, that the results reflect a reluctance to go to the incorrect arm when the heifers are close to getting it correct consistently. This interpretation would be consistent with the phenomenon observed in rats (Turner, 1968) that their latencies to choose in discrimination experiments increases for the incorrect, but not for the correct choices, just before they stop making incorrect choices. The effect can be interpreted as showing the gradual strengthening of the association between the positive stimulus and the reward (Pearce, 1997). It is possible that the reason for the directional behaviour observed here could have been a feeling of unease or reluctance caused by the changing associations experienced during choice. However, we are not aware of previous findings of this kind of effect with regard to directional behaviour, and because of the small number of animals and incomplete sample of trials used for the analysis, the results could not be investigated for temporal patterns and should be interpreted with caution. It would be interesting to see whether the tendency for orientation to be towards correct directions during incorrect choices increases with the proportion of correct choices over the course of learning.

The non-directional behaviours did not predict outcomes of trials. Patterns indicative of habituation and increased agitation were observed with regard to moving forward early in the start area, making increased numbers of steps in the start area, sniffing and touching the fence that made up the gate to the maze arms and moving into the maze arms quickly.

In conclusion, cattle can use the identities of individual familiar conspecifics as cues in a discrimination learning task, and they may find this easier when given additional cues such as breed differences. During the process of a learning task they habituate, and get increasingly agitated, and their head and body orientation may indicate subsequent choice in dependence on their stage of learning.

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