Behavioural Processes 89 (2012) 304–310

Contents lists available at SciVerse ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Investigations on training, recall and reversal learning of a Y-maze by dwarf goats (*Capra hircus*): The impact of lateralisation

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ARTICLE INFO

Article history:
Received 30 March 2011
Received in revised form 2 November 2011
Accepted 19 December 2011

Keywords:
Dwarf goats
Y-maze
Learning
Memory
Reversal-learning
Lateralisation

ABSTRACT

We investigated maze learning in dwarf goats (*Capra hircus*) and the impact of lateralisation on learning. Lateralisation refers to the collection of phenomena in which external stimuli are perceived and processed differentially on the two sides of the brain and/or certain behaviours are preferentially performed by one side of the body. We trained 29 dwarf goats in a Y-maze, directing them to the opposite alley from that chosen in a free pre-run. In total, 13 goats were trained to the left alley (L-goats) and 16 goats to the right alley (R-goats). Recall of the trained alley was tested three months later. We then analysed reversal learning across 10 reversals. During training, the direction of the alley had an impact on learning. The number of runs required to reach the learning criterion was significantly lower in the L- than the R-goats. The goats recalled the trained alley three months later, with no difference between the L- and the R-goats. During the reversal learning, the reversal only tended to impact learning performance, whereas the directions of the new and the initially trained alley did not. Goats did not adopt a general rule with which to master the maze (e.g., win-stay/lose-shift) across the 10 reversals. Our results indicate a right hemisphere bias in the processing of visuospatial cues in the maze during initial training; however, no such impact was detected during reversal learning.

1. Introduction

While former definitions have seen animal welfare chiefly in terms of the body and the physical environment (shelter, feed and health, etc.) (McGlone, 1993; Moberg, 1993), current theories have suggested that welfare is also dependent on the cognitive, mental, and emotional abilities of the animals concerned (Boissy et al., 2007; Duncan, 2006; Manteuffel et al., 2009; Mendl and Paul, 2004). In particular, understanding how animals process visuospatial information about their environment can help to improve the quality of housing for captive animals and to develop management routines to avoid distress and suffering. Differences in learning ability and the impact of external factors on learning have been studied in a wide range of animal species using different types of mazes, including the Morris water maze, the T-maze and the Y-maze (Bolhuis et al., 2004; Lee et al., 2005; Kight et al., 2008; Marinier and Alexander, 1994; Schaeffer and Sikes, 1971; Schwarting and Borta, 2005; Sison and Gerlai, 2010; Wright and Conrad, 2008). However, the learning capacity of different species is difficult to compare. For example, sensory and motor abilities differ between species so that cattle are likely to outperform chickens in an odour discrimination task (Jones and Roper, 1997; Sommerville and Broom, 1998), while sheep and goats have much better visual sense compared to pigs and exhibit advanced visual learning (Tanaka et al., 1995; Zonderland et al., 2008). Attempts to develop relative measures of cognitive skills that can be used with different species were first made by Harlow (Harlow, 1949; Harlow and Warren, 1952; Levine et al., 1959; Macphail, 1996). He proposed practical measures to assess an animal's capacity to develop a learning set. Establishing a learning set refers to an animal's ability to use prior learning experiences to facilitate subsequent learning of new problems of the same kind. An ideally designed learning set task would be able to provide evidence that some species learn a general rule or strategy for solving a particular kind of problem, whereas others do not (Macphail, 1987). One such measure, suggested by Bitterman (1975), is the ability to learn the rule underlying repeated reversals of a discrimination task and to develop a learning strategy (e.g., win-stay, lose-shift). Reversal problems are conducted as follows: the animal is presented with a discrimination problem. Once the learning criterion is met, the positive and negative values of the problem are reversed. In the case of a T- or Y-maze, an animal is initially trained to go to either the left or right alley of the maze. Once a learning criterion is achieved, the trained direction is reversed and the animal's ability to learn this reversal is examined. Each time the

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doi:10.1016/j.beproc.2011.12.013

criterion is met, the values are reversed again. Learning scores can be calculated across a number of successive reversals to determine whether the animal shows progressive improvement in learning.

However, conducting learning studies using T- or Y-mazes can yield misleading results, as recent evidence has revealed a variety of left-right cerebral and behavioural asymmetries among vertebrates (Vallortigara and Rogers, 2005), and lateralised motor behaviour may influence learning performance in maze tasks (Murphy and Arkins, 2007). Lateralisation is a term used to describe the idea that external stimuli are perceived and processed differentially on each side of the brain and/or that some behaviours are preferentially performed by one side of the body. Among the studies on lateralisation that have been conducted using farm animals, this phenomenon has been shown at the individual (Casey and Sleigh, 2001; Forsberg et al., 2008; Hopster et al., 1998; Lane and Phillips, 2004; McGreevy and Rogers, 2005; Morgante et al., 2007; Murphy et al., 2005) and population levels (e.g., Arave and Walters, 1980; Des Roches et al., 2008; Deuel and Lawrence, 1987; Hosoi et al., 1995; McGreevy and Thomson, 2006; Versace et al., 2007). All of these studies investigated primarily motor laterality. The impact of lateralisation bias on maze learning has primarily been investigated in laboratory animals. Mice were found to adapt more easily to situations that favoured their preference bias compared to situations that were contralateral (Collins, 1975). A number of studies have revealed spontaneous asymmetric spatial tendencies in a T-maze in rats, with a preference for the right arm (Lorenzini et al., 1990; Rodriguez and Afonso, 1993; Santin et al., 1996; Schwarting and Borta, 2005). Furthermore, rats exhibited better learning performance when trained to select the arm ipsilateral to their preferred side as compared to the contralateral arm (Andrade et al., 2001). With respect to farm animals, in a study on the effects of prenatal undernutrition on cognitive flexibility in sheep, Erhard et al. (2004) found that in a T-maze, undernutrition resulted in a shift of spontaneous right-side preferences to neutrality in males and to a left-side preference in females.

In studies on maze learning, the results can be influenced by changes in the animals' motivation to run the maze, which are related to the incentive value of the reward (Gaskill et al., 2011). When food or water is used as the reward, animals typically have to be resource-deprived to a certain level throughout the experiment. However, animals still become satiated after a number of successful runs and may become unmotivated to act correctly (Mason et al., 1998) or start to perform so-called 'off-task behaviours' (Gaskill et al., 2011). In social species, social incentives can be used to motivate subjects to learn the maze. It seems likely that in social animals, the motivation to rejoin pen-mates after separation is resistant to satiation.

The aims of the present study were to analyse dwarf goats' ability to learn a Y-maze and to test for the impact of lateralisation on initial and reversal learning. We sought to determine whether the goats could establish a learning strategy and thereby reduce their learning effort across several reversals. We used a partly automated Y-maze to train the goats. Recall of the maze was tested after three months. As well, the goats were tested with 10 arm reversals.

2. Animals and methods

2.1. Animals and housing

The study was conducted from June 2008 to February 2009 at the Leibniz Institute for Farm Animal Biology (FBN, Dummerstorf, Germany). The experimental animals were 29 female Nigerian dwarf goats (*C. hircus*) from a line bred at the FBN. Goats were kept first in three and later in two experimental groups of up to 10 animals in adjacent indoor pens (12 m^2) separated by a visual barrier. Initial grouping was performed at a mean age of 93 d (±2 d), six weeks before the maze training started. Each pen provided straw as litter, a wooden two-level rack to climb on, a hayrack, and a round-feeder. Hay was offered ad libitum. Food concentrate was offered twice a day at a total amount of 300 g/d/animal. An automatic drinker was placed in each pen. Goats were maintained under a photoperiod of 12 L:12 D, with lights turned on at 6 a.m. All procedures involving animal handling and treatment were approved by the Committee for Animal Use and Care of the Ministry of Agriculture of Mecklenburg-Vorpommern, Germany.

2.2. Design and functioning of the Y-maze

The design of the Y-maze and its dimensions are presented in Fig. 1. Goats were run through the maze as follows. An experimental group was brought into the waiting pen (12 m^2, with straw as litter), and then individual goats were taken out of the pen and gently driven to go down a race to enter the start box. The start box was fully closed but large enough to enable an individual to move around. The goat stayed in the start box for 20 s before a guillotine door was lifted to allow entrance into the maze. After the goat left the start box, the guillotine door was quietly closed. In cases in which the goat did not leave the start box within 30 s, it was gently pushed out into the maze. Once the goat had selected an alley, it interrupted the associated light beam and caused the door blocking the opposite alley to close automatically. When the goat chose the correct alley, it could leave the maze through another door at the end of the alley and return to its pen-mates in the waiting pen. This door was made from acrylic glass with an additional opaque cover that was not lifted until the goat in the maze had chosen an alley and crossed the light beam. This manoeuvre was intended to prevent the goats in the waiting pen from gathering in front of the correct alley and influencing the responses of the goats inside the maze. When the goat chose the wrong alley (door closed), it was held in the maze for 60 s. In case it interrupted the contralateral light beam during this period, the door that blocked the opposite alley was also closed, and the goat could only move around in the entrance area. After one minute, the goat was gently driven back into the start box, where it was held for a further 30 s before it was allowed to walk freely back down the race to rejoin its pen-mates. Such runs were recorded as a wrong choice. No forced correction run followed. During each run, the goats had olfactory and acoustical, but not visual, contact with its companions in the waiting pen.

2.3. Assessment of general motor laterality

To assess general motor laterality independent of learning, we analysed whether single goats consistently stepped into the maze with the left or right leg. The level of the start box was 10 cm above that of the maze. All goats paused for a moment after the guillotine door was lifted before entering the maze. We used video recording to determine the leading leg with which each goat entered the maze. Preferences for the left or the right leg were analysed only for individual goats that voluntarily left the start box. Analyses were done separately across all runs during the initial training and the reversal learning.

2.4. Adaptation and initial training

All goats completed two runs per day, one in the morning and one in the afternoon, from Monday to Friday, throughout all phases of the experiment. The order in which groups and individuals were tested was randomised for each run. The pause between the two daily runs varied for individual goats between three and four hours. To allow the animals to adapt to the maze, each goat completed two