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Review

A large outdoor radial maze for comparative studies in birds and mammals

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Abstract

For a comparative neurobiological analysis of spatial learning and memory, a large outdoor eight-arm radial maze was constructed which permits behavioral assessment of many avian and mammalian species both from the laboratory or the wild, using the same metric space and session schedules. It consists of a central part of 250 cm diameter, and has arms of 650 cm length, 170 cm height and 80 cm width. In order to determine appropriate training schedules for comparison of different species, we tested four mammalian and two avian species during 9–15 sessions: 18 albino rats (*Rattus norvegicus*), nine outdoors and nine in a conventional small indoor maze; six guinea pigs (*Cavia porcellus*); six rabbits (*Oryctolagus cuniculus*); five hedgehogs (*Erinaceus europaeus*); seven hooded crows (*Corvus corone cornix*) and six chickens (*Gallus domesticus*). Rats learned fast in both mazes yet significantly better in the large one. Good-to-excellent learning was also observed in juvenile rabbits and wild-caught crows, although the latter tended to avoid arms in the vicinity of the observer. Hedgehogs and chickens did not show significant learning as a group, but some individuals appeared to learn the task. Guinea pigs remained continuously passive and could not be trained. Thus, in spite of species-specific demands for reward, adaptation and pre-training, this type of radial maze permits to directly compare a wide variety of species. Such comparability is essential for an analysis of underlying neurobiological mechanisms. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Ecology; Rat; Crow (*Corvus corone cornix*); Chicken; Hedgehog; Rabbit; Guinea pig; Learning; Spatial working memory

Contents

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1. Introduction

1.1. Background

In the context of a research line focussing on ecological brain research, we are studying within- and between species variation of hippocampal size and circuitry with the aim of finding relations to species-specific or individual variations of behavioral talents [42]. As much of this neuroanatomical research takes place in a field station in Western Russia, we were faced with the problem of establishing a behavioral test permitting to compare directly spatial learning and memory in a wide variety of wild or domesticated species, both birds and mammals. The most widely used test for assessing hippocampal function is the Morris water maze. We have employed it successfully for comparisons of wild vole species transferred to the laboratory [60]. However, it has obvious limitations for studying species larger than rats, particularly birds, and is generally ill-suited for use in a field station without tap water supply. Thus, to our knowledge, there has been only one Morris maze study to assess the impact of celestial cues in an outdoor setting [35].

1.2. The radial maze

The device most suitable for the intended purpose appears to be the eight-arm radial maze as popularized 20 years ago by Olton and co-workers [52,55]. Typically, experimental subjects are placed on a central platform from which they have to collect invisible baits placed at the end of the arms. The most extensively studied species, the rat (*Rattus norvegicus*), quickly adopts a win–shift foraging strategy, avoiding double entries. On the other hand, learning win–stay strategies by revisiting given arms, appears to be more difficult for rats [54]. At least in rats, correct performance appears to depend primarily on memorizing extramaze cues [74], while olfactory cues help to improve choice accuracy in darkness [40]. Because of the ease by which the task is learnt by rats, the eight-arm radial maze soon became a standard apparatus for the analysis of normal and deficient spatial memory and learning, double entries being taken as evidence for impaired spatial working memory (for reviews see Refs. [19,62]). Modifications of the initial procedure by dividing arms in four never baited places and four places holding baits [29] permitted the distinction of spatial working memory errors (double entries into baited places) versus spatial reference memory errors (entering never baited arms), while learning with the aid of intramaze cues was possible by inserting differentially textured floor plates [30]. Another type of analysis focuses on the recognition and memorization of ordered items or places [37].

1.3. The radial maze in mammalian neurobiology

In mammalian neurobiology, the classical win–shift task was found to depend critically on the integrity of the rat hippocampus and its afferent or efferent projections [28,32,45,56]. Likewise, hippocampal lesions disrupted performance in the standard radial maze task in mice [3,64]. While initial studies reported no working memory deficits after lesions of extrahippocampal systems including the amygdala, frontal cortex, posterolateral neocortex and caudate nucleus [6], methodologically more refined studies revealed impairments of the reference memory component after lesions of the cholinergic nucleus basalis [16,49], septum [27] and striatum [58]. Damage to the dorsal striatum impaired selectively acquisition of the spatial win–stay task, while damage of the lateral amygdala impaired acquisition of an intramaze cue task but spared learning of the spatial tasks versions [46]. Strain-dependency of amygdala lesion effects was reported for C57/BL/6 (impaired radial maze performance) versus DBA/2 mice showing no impairment [4,64] and for CD1 mice in which amygdala lesions produced reference memory errors and modified the patterns of arm choices [3]. Lesions of the higher-order association cortex in rats (prefrontal, perirhinal and parietal association cortex) were also affecting radial maze learning and performance to various degrees [15,33,38,44,71].

Finally, and of importance for this report, correlative studies of the hippocampal intra/infrapyramidal mossy fiber projection (IIP-MF) in mice and rats showed that larger IIP–MF bundles were generally associated with a reduction of spatial working and reference memory errors, but bore no clear relation to performance in learning intramaze cues [12,13,26,67–70]. On the other hand, using a different type of radial maze and another set of mouse strains, Roullet & Lassalle [65] could not confirm these findings. Taken together, the neurobiological data indicate that performance in a radial maze task is sensitive to genetic differences and experimentally caused malfunction within a cortico-subcortical network including the hippocampal formation and

adjacent neocortical association areas, that is, in the neuronal machinery underlying cognitive processing in higher vertebrates [43].

1.4. Comparative studies with radial mazes in mammals and birds

The radial maze paradigm has also been used succesfully with other species. In mammals, radial maze learning was demonstrated and analyzed in gerbils (*Meriones unguiculatus*, [75]), and hamsters (*Mesocricetus auratus*, [18]). Radial maze learning was also demonstrated for a marsupial, the short-tailed opossum (*Monodelphis domestica*) [39]. In humans (*Homo sapiens*), a standard eight-arm radial maze with short arms (1.2 m) was used to study spatial memory of children and college students [1] and a larger outdoor maze with 2.4 m arm length to assess ontogeny of place learning in children [57].

The use of radial maze for evaluation of spatial memory in birds proved to be less easy as it usually required changes of apparatus and procedures. Ring doves (*Strepsotelia risorius*) have been found to perform accurately after extensive training in a variant of radial maze task with 14 short arms emanating from a large center area [76]. Similarly, savannah sparrows (*Amaurospiza sanwichensis*) performed accurately when tested outdoors in structured 8-arm radial maze [48]. The first studies of radial maze performance in pigeons (*Columba livia*) initially report poor learning [8]. After extensive pre-training and reduction of interaction with the experimenter, pigeons were shown to learn the task effectively [47,63]. These pigeon studies raised the issue of compatibility of species-specific foraging strategies and labyrinthine structure (see also Ref. [72]) and they also led to the development of various radial maze analogs for birds.

1.5. Radial maze analogs

Generally, such analogs consist of equidistantly placed feeders that can be accessed through open space without passage through arms. Such radial maze analoges have been frequently used to study performance, response strategy and retention interval effects in corvid species: Clark's nutcrackers (*Nucifraga columbiana*), pinyon jays (*Gymnorhinus cyanocephalus*), scrub jays (*Aphelocoma coerulescens*)and Mexican jays (*Aphelocoma ultramarina*). Balda & Kamil [5] found that Clark's nutcrackers performed well in an open-field analog of the radial maze and this level of performance was better than that obtained in radial maze analogs with pigeons [72,73]. The most intensely food storing species, Clark's nutcracker, acquired the radial-maze analog task more rapidly and to a higher level than the less specialized Mexican and scrub jays [34]. Using delayed win–shift and win–stay tasks revealed better performance in the win–shift group of Clark's nutcrackers [51]. Likewise, spatial memory of four tit species (*Paridae*) was studied successfully in an open-field analog of a radial

maze [25]. Indoor and outdoor radial maze analogs have also been used to assess brain lesion effects in homing pigeons in order to complement findings of homing studies [22], to analyze the role of the sun compass for local spatial learning [7], and to study the effects of lesions of the hippocampus and area parahippocampalis [11].

Radial maze analogs were also used for the study of human spatial learning and memory. Some of them were as simple as 17 cardboard flaps arranged radially around a center point [50]. Also, Glassman et al. [23] tested humans with a 17-arm radial maze and, in a follow up experiment, with a 13-arm giant radial maze with a diameter of 15.2 m, simply painted on a lawn. On the other extreme, Elmes [17] used a very small radial stylus maze (12 arms, 7.5 cm arm length and 5 cm in diameter of central circle). Other symbolic radial maze analogs for humans include the 'Kiel Locomotor Maze' to assess spatial memory and orientation in children [41] and the so-called 'Nine-box maze' to test patients with damage to the hippocampal formation [2]. Radial maze analogs of the circular type have been used to test preschool infants for working and reference memory, by requesting them to search for chocolate from identically labeled locations in unknown or familiar rooms [20,21].

1.6. The need for a multispecies radial maze

The radial maze is certainly a useful test apparatus in order to assess psychological or neurobiological correlates of cognition in many species. If the goal is to compare neurobiological mechanisms across species, for example the relative size and circuitry variants of the hippocampus across species, the main problem remains to find an apparatus which permits fairly standardized testing across many species, as it is impossible to build an optimized radial maze version providing cross-comparable data for every species.

Thus, we decided to construct a multispecies radial maze of large dimensions for two reasons. The first is that the typical laboratory devices are not only inappropriate for larger species, but may be in fact inappropriate even for rats and mice. The origin of the trend for small mazes is probably opportunistic, namely limited space in the laboratory. While Olton's original maze for rats in Baltimore was fairly large (with arms of about 2.5 m length, own observation), subsequent prototypes for rats became considerably smaller, typically with a diameter of the central part between 30 and 60 cm, arm lengths between 60 and 90 cm and arm widths between 9 and 12 cm [31,36,55,59,66,78]. One problem with such dimensions is that the distinction between a radial arm maze and a set of radially arranged feeders becomes a matter of debate, although the core idea behind the radial maze is ecological, namely an optimized foraging strategy. It would seem doubtful that animals which have feeding opportunities accessible within the range of their normal spontaneous activity should have much incentive to optimize their locomotor costs (unless one assumes that the preferred activity level of an animal
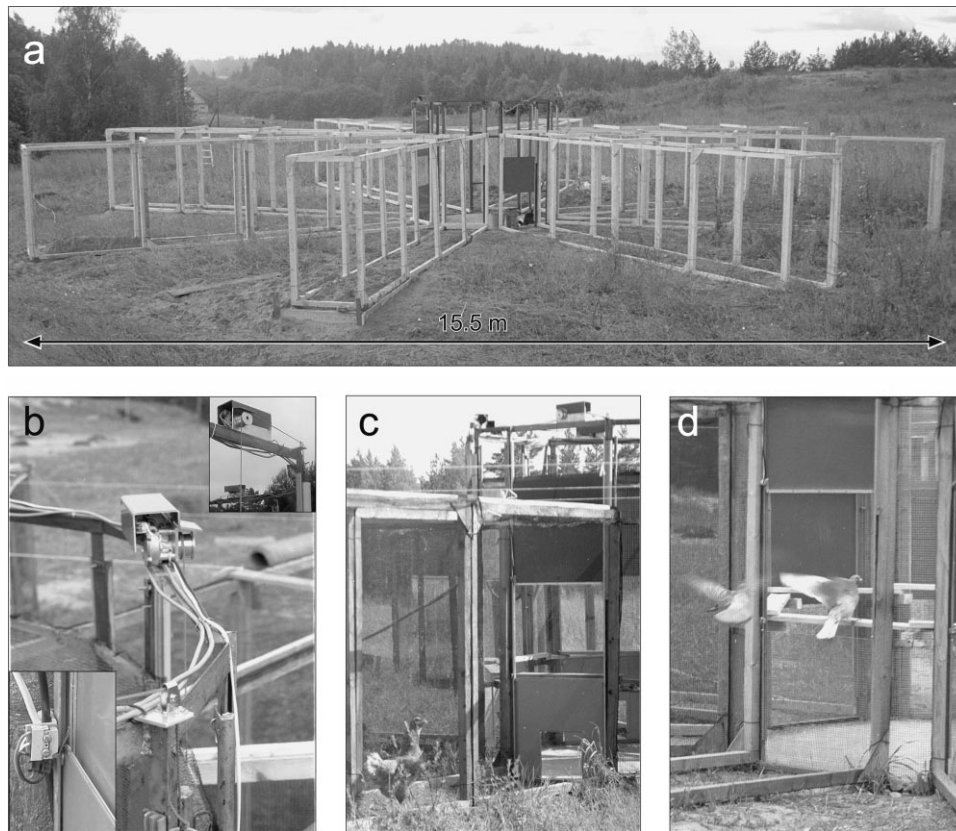
Fig. 1. Overall view and constructional details: (a) View of the entire maze after set-up of modular frames, (b) DC motor with pulley system. Note the double U-profile holding the sliding gates, (c) Maze arm with chicken. Middle panel and attached lower gate in bottom panel are lifted, (d) exploration of the maze by pigeons. Note the circular shelf system permitting inspection of arms by walking along the perimeter of the central part. In this set-up, the bottom panel consists of wire mesh and has no additional openings.

is zero). In fact, it has been shown that short arms tend to decrease choice accuracy significantly [10,11]. The other problem is that the decision for a given dimension of a radial maze is based on isometric calculations related to the body size of the species. Thus, many radial mazes for mice have arm length between 15 and 20 cm. However, it is equally conceivable that the important aspect for a small-sized animal is not the actual distance but the time needed to reach the feeding site. As mice move with speeds of 25 cm/s even without particular motivation, it is again difficult to see the immediate benefit of path optimization.

The other reason is that traditional small radial mazes may be comfortable for burrow dwelling animals such as many small rodents, but obviously inappropriate for any larger or more active species. Thus, in order to provide an equal testing ground for many small-to-middle sized birds and mammals, we preferred a construction as large as possible that would permit internal modifications and miniaturization if deemed necessary. The choice of an outdoor construction was then dictated by the dimensions of the maze.

In this paper, we describe some of the salient constructional features permitting the testing of many species. A comparison of the same rat strain indoors and outdoors is used to test the validity of the device in assessing typical radial maze learning. This is followed by an analysis of the learning behavior of some species never tested in radial maze learning before.

2. Methods

2.1. Design of the radial maze

The maze is located in the biological field station 'Chisti Lec' near Pozhnia in the western Russian province of Tvier. The maze was constructed on a flat ground consisting of sandy soil with little vegetation near a primitive animal house of the field station and thus remained familiar to birds such as pigeons and crows kept in the aviaries of the animal house. The core of the maze consisted of a metallic construction including eight door frames of 220 cm height (Figs. 1 and 2). The frames were soldered together and anchored permanently in an octogonal floor made of concrete (diameter 250 cm). The remaining parts consisted of modular elements including gates, panels, motors, cabling, and wooden frames covered with a net of sturdy black plastic (mesh diameter 10 mm, such as used for
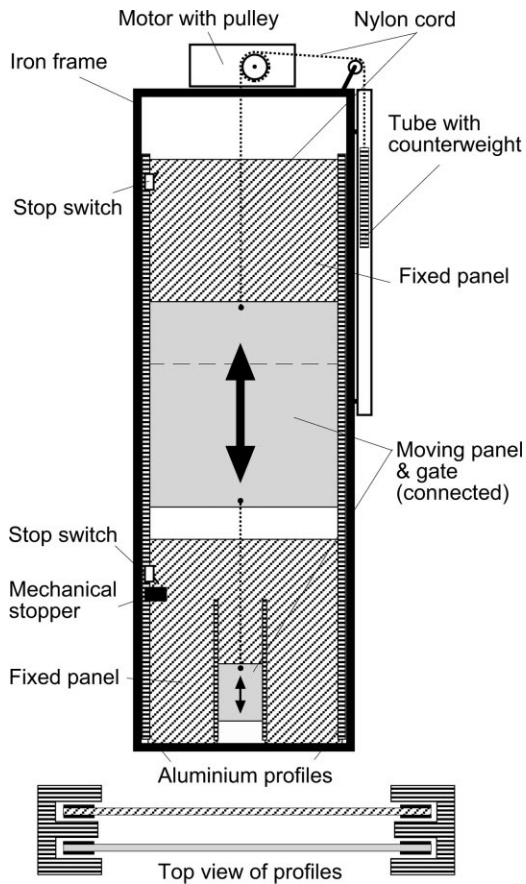
Fig. 2. Scheme of modular frame with sliding gates.

protecting crops and trees against ice rain). This black net provided good visibility across the panels. The modular elements were assembled in late spring (Fig. 1(a)) and disassembled for storage in mid September as outdoor testing becomes impossible in Russia during Fall and Winter.

The walls of the central part where formed primarily by the eight gates consisting of three slightly overlapping panels (66×66 cm, Fig. 2). The two upper panels were made of sturdy gray PVC of 3 mm thickness. The lowest panel was either made from wire mesh or PVC, depending on species (Fig. 1(b),(d)), and contained an opening of 25×30 cm bordered by metallic guides for a small door plate (Fig. 2). Opaque doors were chosen to provide a form of shelter for animals disliking to be exposed totally to the environment. The remaining vertical space in between the gate assemblies was closed with wooden frames covered with wire mesh (170 cm height, 18 cm width, Fig. 1(b),(d)). This enabled the animals to observe the surroundings from a hidden position. One of these small frames contained a detachable inlet permitting to place animals inside the maze. The top of the central part was closed at the level of 170 cm with a wooden frame covered with plastic wire mesh.

Each arm was formed by eight modular frames covered with wire mesh, kept together with metallic wire. Total length of the arms was 650 cm, the width 80 cm and the height 170 cm. Thus, the total diameter of the whole maze was 15.5 m. The arms were fixed against each other by nylon strings that were solidly anchored in the ground to provide protection against wind and storms. The end of each arm contained a detachable wire mesh frame of 170×80 cm permitting the experimenter to enter an arm, and from there, through the gates, the central part. Baits were usually placed in small white ceramic bowls placed themselves in a plastic tray shielding the bait from sight.

The most important constructional feature for use with different species was the arrangement of the confinement gates. Panels were inserted into a double-U profile of aluminium attached to the iron frame (Fig. 1(c), Fig. (2)). The top and bottom panel were inserted into the same groove and were fixed by screws at a given height. The mobile middle panel was inserted into the second groove, and overlapped for about 5 cm with the fixed panels. It was connected to a nylon string wrapped three times around a pulley of a geared DC motor located above the doors (24 V, SWF, Model 0270 SWMK), the string being connected to a counterweight gliding up and down in a plastic tube attached to the frame (Fig. 1(c) and Fig. 2). For terrestrial species or birds preferring to walk, the gate in the bottom panel was attached to the middle panel with a string. Activating the engine by a remote switch pulled the middle panel with the attached small bottom gate upwards (speed about 20 cm/s) until it met an upper electric stop switch fixed to the aluminium guide (inlet Fig. 1(b), Fig. 2). Reversing the remote control switch caused the engine to turn in the reverse direction, enabling passive closure of the gates by their own weight with about the same speed. A second stop switch (Fig. 2) terminated motor activity, further passive downward movement of the middle panel being blocked by a mechanical stopper inserted into the guiding groove. Every door could be controlled independently by means of a remote control unit located in an observer tent 8 m away from the nearest arm. A diagram of the circuitry between control panels, DC motors and stop switches is available on request from the corresponding author.

This arrangement provided some unique features. Firstly, it permitted various combinations of opening doors for different species. Moving the middle panel only was useful for flying birds. Connecting it with a smaller gate covering the bottom panel permitted access to the arms for both mammals and birds, and turned out to be the most convenient arrangement as crows and pigeons often preferred to fly into the arms but returned by walking. The use of pulley system with wrapped strings prevented motor burnout due to jamming of the panels. In such (rare) cases, the motor simply continued to turn until the operator corrected the problem. Also, the downward gliding of the panels was passive. This allowed animals inadvertently squeezed by the panel or gate to wriggle themselves free. An important feature for use with birds was a circular wooden shelf of 10 cm width fixed at a height of 76 cm above ground. It was situated 10 cm behind the moving gates
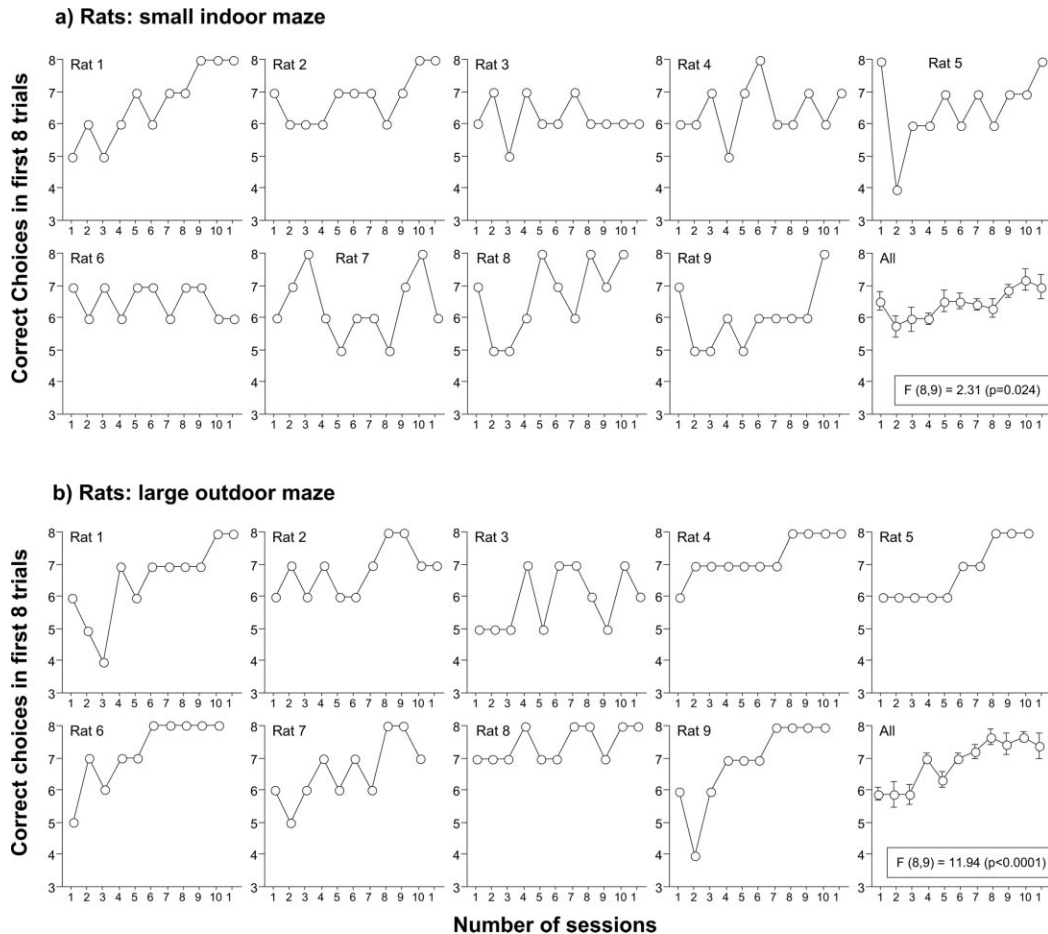
Fig. 3. Calibration of the large radial maze by testing the same rat strain indoors: (a) and outdoors (b). Plots give the individual scores of correct choices over 11 days. Note the more regular and more stable performance in the outdoor settings. Summary data for all animals show means and S.E.M.

and permitted birds to walk along the doors before choosing an opening (Fig. 1(d)).

2.2. General procedures, measurements and statistics

All species were tested according to the following common criteria: a session lasted until an animal had visited all bait sites, or had made 15 visits, or until 35 min had elapsed. With the exception of the first session (for details see under species), the subjects remained confined between trials in the central part for a duration of 10–30 s. The position of the experimenter with the control unit was always constant, the minimal distance being 8 m from the nearest arm. In most cases, he/she remained hidden in a tent with perspex windows. Performance of the animal was noted on standard sheets recording the order of choices, position of the observer, consumption of bait and duration of a session. From this, the following variables were calculated: the number of correct choices out of the first eight choices (learning score), the total number of visits, the number of double entries (errors) till visits of all arms or maximally 15 trials, the number of consumed baits, and the angle between sequentially chosen arms. The latter measure

permits to recognize choice algorithms not associated with remembrance of visited arms. Occurrence of learning was verified using one-way analysis of variance for repeated measures in a given species, possible species differences were tested by using a two-way ANOVA design with species and repeated scores as factors. Learning scores have a maximum of eight correct choices out the first eight trials; scores between 4 and 6 corresponding to chance level. Error scores are more variable (ranging mostly from 0 to 10) as they reflect both the number of correct choices and the errors in order to complete eight visits.

Species-specific variations of adaptation and pre-training will be provided separately for each species in the Results Section. All animals were treated according to the legal requirements of the University of Zürich and guidelines of the Swiss National Academy of Science.

3. Results

3.1. Albino rats (Rattus norvegicus)

This study served to calibrate the large maze by comparing

the learning of the same rat strain in both a conventional small indoor radial maze and in the large outdoor maze. The subjects were 18 experimentally naive, male outbred Wistar albino rats 4–5 months of age at the beginning of experiments. The rats were from a colony bred at Moscow State University for five generations, the original stock being maintained at Stolbovaya breeding company (Moscow). They lived in groups of 4–5 in standard rat cages ($53 \times 32 \times 19$ cm) under a natural light schedule (light on from 8 a.m. to 8 p.m.), and received commercial food pellets and vegetables. They were divided into two groups. One group was transferred from Moscow to the field station, and was kept there in the animal house for 3 weeks before the begin of training. The other one was tested in Moscow in a small radial maze similar to the one used by Schenk and Grobéty [66]. In brief, it contained a central platform of 30 cm diameter located in an octogonal tower of 45 cm height, made of translucent perspex plates. The eight arms of 60 cm length were formed by perspex tunnels (12 cm wide and high). Eight manually activated gates were used to confine animals in the central platform between trials. The bait consisted of 2 ml of diluted (1:3) sweetened condensed milk placed in a cup attached to the end of the arms. The laboratory contained numerous landmarks such as posters, tables, curtained windows, and was illuminated by two 100-W bulbs at the ceiling 4 m above. The experimenter sat in a distance of 1.5 m.

Both groups of rats were food deprived for 24 h before pre-training. Afterwards, we tried to keep their body weight at about 90% of the initial weight by supplementing a reduced amount of standard food after sessions. Experiments took place in Summer 1997. The rats were adapted to drink milk from the cups during 4 days, being placed first pair-wise and then individually in an empty rat cage for 30 min. For the animals in the field station, the rat cages were dusted with the soil from the radial maze, and the adaptation procedure was done outdoors to accustom the albino animals to daylight and sunshine. None of the groups were allowed to explore the mazes before testing. During the first day of testing, all arms remained open and no confinement procedure was used. In order to facilitate return to the central platform, a few drops of condensed milk were splattered within the central platforms of the small or large maze during the first and second session. From Session 2 on, a trial started with opening all eight gates simultaneously. After having advanced for half an arm length in the small maze (and 1.5 m in the large maze), the gate behind the rat was closed, as well as the seven other gates. When the rat visited the bait place (with or without consumption of reward), the gate was re-opened until the animal returned to central compartment. Then the gate was closed again. After 10 s of confinement, a new trial started with opening all gates. Such confinement procedures are known to block effectively chaining strategies based on successive visits of adjacent arms. Most rats were tested for 11 sessions, six sessions per week. For technical reasons, a few animals

were tested for ten sessions only. They can be identified on the individual data plots in Fig. 3.

The data from the small radial maze illustrate a typical learning sequence of laboratory rats. During the first session without confinement, four rats out of nine started with a score of seven or eight correct responses, indicating a genuine win–shift strategy (without systematical visits of adjacent arms), whereas the scores of the others remained at chance level. Following introduction of the confinement procedure, choice accuracy dropped in the those animals with high initial scores (e.g., rat 5, 8 and 9 in Fig. 3(a)). Afterwards, the number of correct choices increased with sessions, several rats showing occasionally perfect scores (eight correct choices out of first eight choices). However, considerable individual variability in choice accuracy persisted. Thus, the overall improvement between Sessions 1 to 10 (which include a complete data set for all animals) was only moderately significant ($F_{8,9}$: 2.31, $p = 0.024$). The performance level at the end (average of Sessions 8–10) was 6.81 ± 0.19 correct choices, the nine rats totaling ten perfect sessions during day 2 and 10.

During the first session in the outdoor radial maze, the choice behavior of all rats except one (rat 8) appeared to be random (Fig. 3(b)). The introduction of the confinement procedure with Session 2 entailed more errors in three rats (animals 1, 7 and 9 in Fig. 3(b)). Starting with Session 4, however, most rats attained choice scores of seven correct responses. Further on, they remained stable at this level or improved. Statistical analysis revealed a highly significant change of performance during 10 days of training ($F_{8,9}$: 11.94, $p < 0.0001$), the nine rats attaining an average performance level of 7.59 correct response during the Sessions 8–10, and showing a total of 21 perfect sessions. Analysis of choice angles did not reveal any systematic preference for a defined angle, nor did the analysis of errors reveal preferences for certain arms.

A comparison of the learning curves obtained in the two mazes (see also Fig. 3 (a),(b)) showed significantly better acquisition of the rats in the large outdoor maze (maze factor: $F_{1,16} = 4.57$, $p = 0.048$; session factor: $F_{16,9} = 8.67$, $p < 0.0001$; interaction sessions by maze factor: $F_{1,9,16} = 2.86$, $p = 0.004$). This interaction was mainly due to the less stable performance of the rats in the small maze. In fact, comparison of the performance during Sessions 8–10 (see above) showed significantly higher scores in the outdoor rats as revealed by t-test ($p = 0.014$). Also, the number of perfect sessions shown by the rats in the large maze was almost twice as high as compared to the observed in the small radial maze.

In the large outdoor maze, the rats often made quick exploratory moves into an open arm and appeared to take a decision after about 1.5 m, beyond which point rats never returned without having moved on to the bait. After having made a decision, most rats ran quickly to the reward cup, covering the distance in about 3–4 s. Consumption of the bait took about one minute. Afterwards, they returned

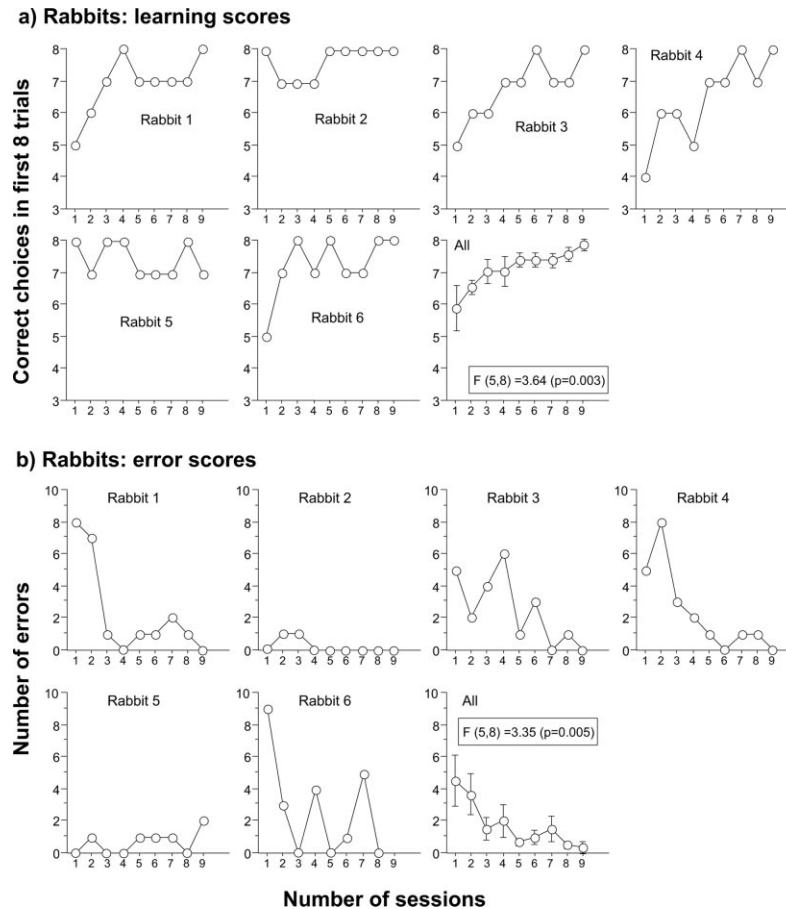**a) Rabbits: learning scores**

b) Rabbits: error scores

Fig. 4. Excellent radial maze learning of six juvenile rabbits: (a) Individual correct choices during the first eight trials of a session, (b) corresponding error scores. The maximal error score is 14 as there were a maximal of 15 choices before terminating the session. Note differential choice strategies of the rabbits at the begin (some win–stay, some win–shift) and the adoption of a win–shift strategy by all rabbits. Summary data for all animals show means and S.E.M.

slowly, and investigated both distal and proximal ends of the arms by rearing and object sniffing. Occasionally, they also showed bouts of grooming. The onset of the confining procedure starting with Session 2 entailed some hesitation in coming back which was quickly overcome.

3.2. Rabbits (Oryctolagus cuniculus) and Guinea pigs (Cavia porcellus)

These animals were tested in August 1998. Six juvenile black rabbits (average weight 750 g) were purchased at the 'Ptichii Rinok' animal market in Moscow, together with six juvenile short-haired guinea pigs of differential coat color (average weight 250 g). Both groups, rabbits and guinea pigs, appeared to be littermates. They had not reached sexual maturity at the age of testing and determination of sex was uncertain. They were transferred to the field station and housed there together for 2 weeks in an enclosure of 2×2 m containing sawdust, hay and paper boxes. Both species adapted well, the guinea pigs being active and interacting frequently with rabbits. Prior to testing, food supply was reduced and only pellets and grains were fed.

Pre-training took place during 3 days. The animals were caught and released as group into the radial maze, for 2 days both guinea pigs and rabbits together. Fresh green leaves of a variety preferred by the animals were placed in the arms and some of it in the central part. The animals were then left to explore the maze and consume the leaves for about 40 min. The rabbits appeared to enjoy the new environment and were soon moving or even running playfully through the arms. The guinea pigs refused any motor activity and remained motionless in a corner of the central part. They were pre-trained for an additional day without the rabbits, scattering more leaves in the vicinity of the animals and in the arms to lure them into moving, at no avail. Because of time constraints, further attempts to adapt the guinea pigs were abandoned. One may note that they continued to behave actively as soon as they were brought back to their habitual environment. The rabbits were then tested for nine sessions, mostly in intervals of 24 h, sometimes with breaks of 48 h because of constant rain.

As the rabbits seemed not to be impressed by moving gates, the first training sessions included already a confinement of 30 s duration. This species showed interesting choice patterns. Two rabbits (animals 2 and 5, Fig. 4) started
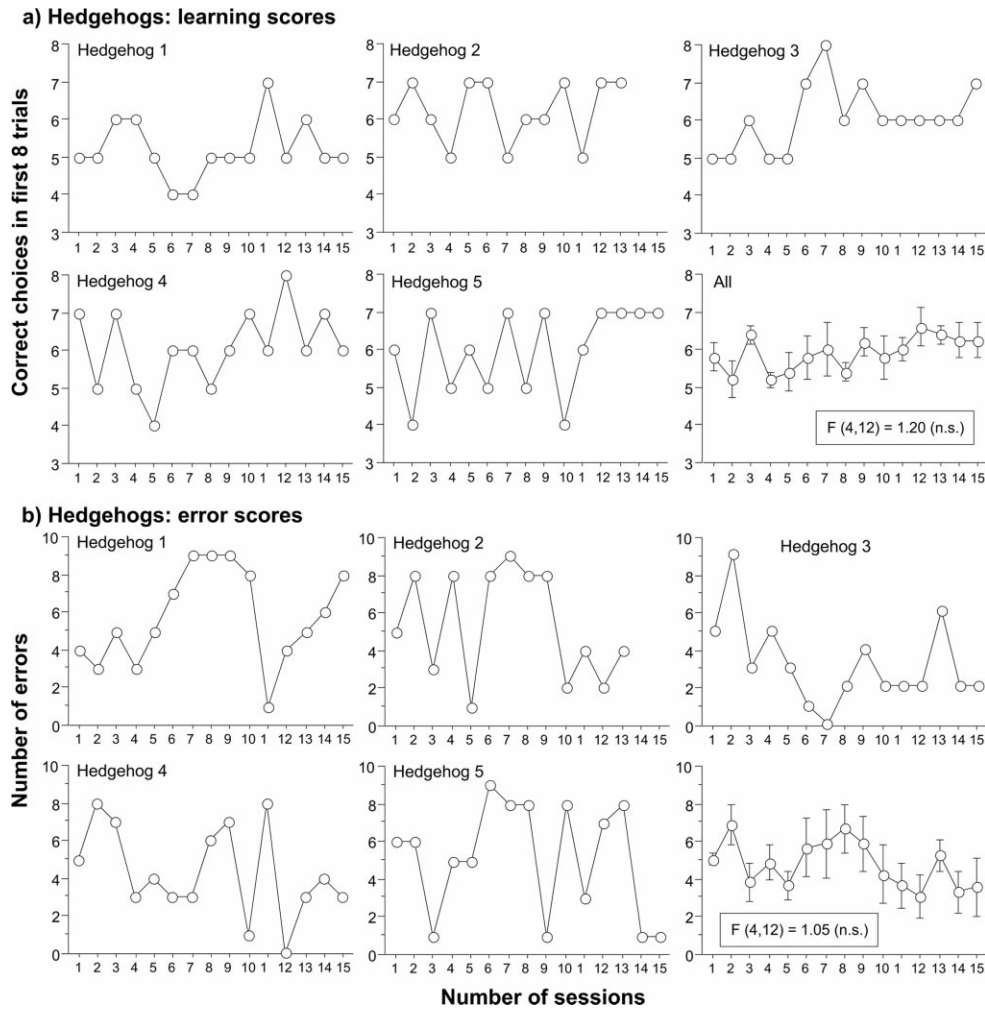
Fig. 5. Fluctuating radial maze learning in a group of five hedgehogs: (a) Individual correct choices during the first eight trials of a session, (b) corresponding error scores. Most animals appeared to solve the task occasionally (e.g., animals 3 and 4), but performance remained unpredictable. Summary data for all animals show means and S.E.M.

with a perfect sequence of eight correct choices and maintained a high choice accuracy throughout training, totaling an average score of 7.67, and 7.44, respectively, through all sessions. The others adopted initially an win–stay strategy characterized by many repeated entries and thus high error scores. Latest after Session 4, all rabbits had switched to a win–shift strategy and finished the training sessions with an group average of 7.83 out of a maximum of eight (Fig. 4(b)). This was also reflected in a highly significant learning effect as revealed by ANOVA ($F_{5,8}$: 3.64, $p = 0.003$).

As most other species, the rabbits moved to the bait (about 3 g of fresh green leaves) relatively quickly, but then spend a good deal of time in searching, exploring and nibbling the sparse grass in the arms before returning to the central compartment. One of these grass-nibblers was then chased back to the final compartment, but after re-opening of the gates, he immediately returned to this place, finished eating the grass, returned to the central part and chose the next arm correctly. Their spatial short-time

memory seemed also quite resistant to stress, as one animal, after returning from its seventh choice, got squeezed by the confinement door. It wriggled free and chose the last arm correctly.

3.3. Hedgehogs (Erinaceus europaeus)

Five adult hedgehogs (weight between 480 and 880 g) were tested during Summer 1999. Three were purchased at 'Ptichii Rinok' animal market in Moscow, one had been captured in Moscow and was kept at Moscow State University, and one was obtained from local farm boys. Three were females, two males, sex being determined by placing them in a bowl of water which forced them to unroll. During experiments, they were kept in standard rat cages where they spent most of the daytime sleeping. During 10 days, they were fed a diet of sliced and cooked chicken meat or raw liver, delivered in the same white cups as used in the radial maze. Prior to testing they were food deprived for 24 h. After sessions, they were fed a food supplement and
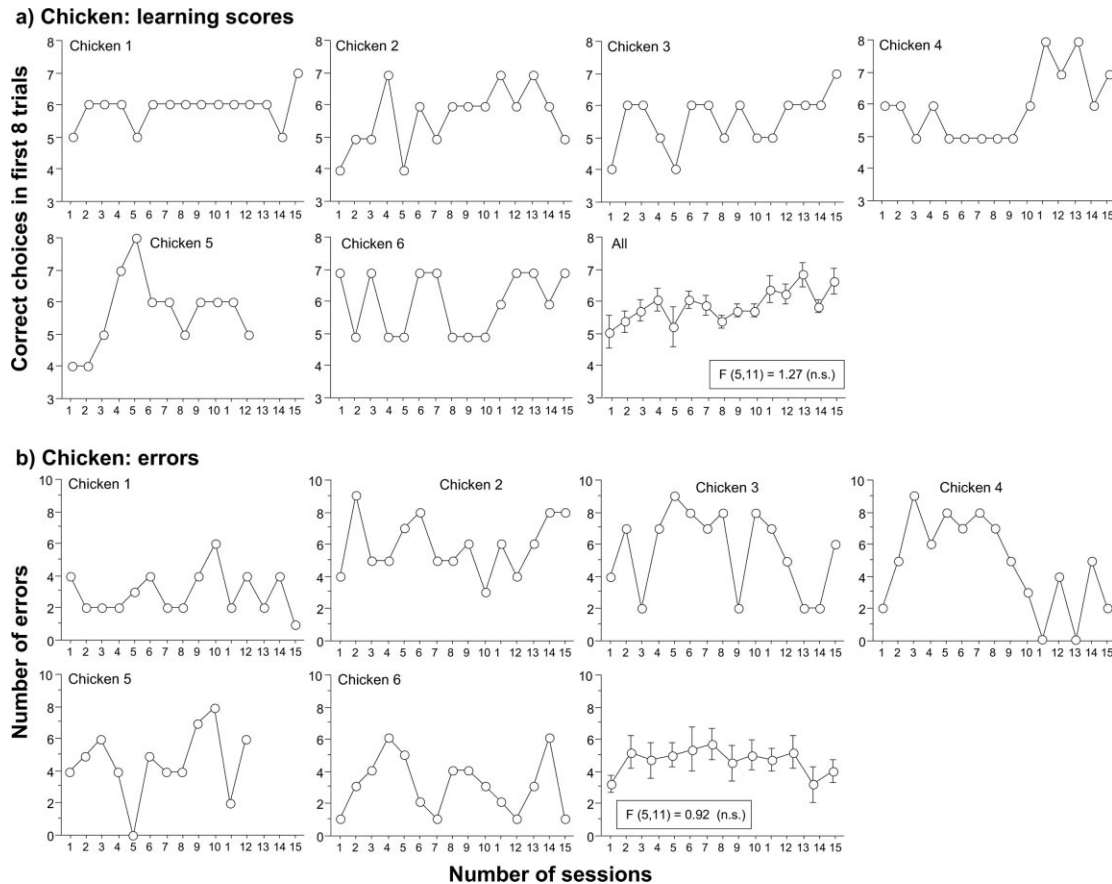
Fig. 6. Fluctuating radial maze learning in a group of six chickens: (a) Individual correct choices during the first eight trials of a session, (b) corresponding error scores. Summary data for all animals show means and S.E.M. As in hedgehogs, most of the animals seem to solve the task occasionally.

then kept food-deprived till the next session, except for days without training due to bad weather conditions or failures of electric power supply. Testing started after 9 p.m. and continued till dawn at about 11.30 p.m. They were pre-adapted to the radial maze only once. The first session was without confinement. The Sessions 2–15 included a confinement period of 10 s. One animal could only be tested for 13 sessions as it became ill.

The hedgehogs were less efficient radial maze learners. Their mean learning scores showed a weak yet not significant improvement with time ($F_{4,12}$: 1.20, n.s; trials 1–13 only for a obtaining a full data set). Analysis of both learning scores and accompanying errors (Fig. 5) showed that the pattern of errors fluctuated unpredictably from day to day ($F_{4,12}$: 1.05, n.s.). For example, hedgehog 2 showed several sessions with a learning score of seven correct choices (out of eight) which suggested correct solving of the task. However, on day 5, he solved the task with committing only one additional error before having visited all eight arms. The other day, he visited again seven arms without errors, but committed then eight additional errors without finding the remaining baited arm. During Sessions 12 and 13, he showed once more seven consecutive correct choices, but it took again two 2 and 4 additional trials before finding the last baited arm. Two hedgehogs (animals 3 and 4)

showed once a perfect session with eight consecutive correct choices that was followed, however, by several sessions with less success.

The only animal showing a fairly typical learning curve was hedgehog 3, but also this animal needed, at the end of training, still about 10 trials to visit all arms. Thus, the general problem of the hedgehogs appeared to be individually inappropriate search strategies and difficulties in remembering the position of the last unvisited arm. There was no systematic patrolling of adjacent arms, nor did they prefer or avoid certain arms.

The hedgehogs were surprisingly active. After having been placed in the central platform, most animals started to move as soon as the experimenter had left and patrolled the arms. During the first session, two hedgehogs tried to escape from the maze, one by biting the meshwork, the other by digging along a wooden frame. They abandoned their attempts soon, however. The animals moved in most cases quite rapidly to the end of the arms. After consumption of the bait, they returned more slowly, but not as exploratory as the rats.

3.4. Chickens (Gallus domesticus)

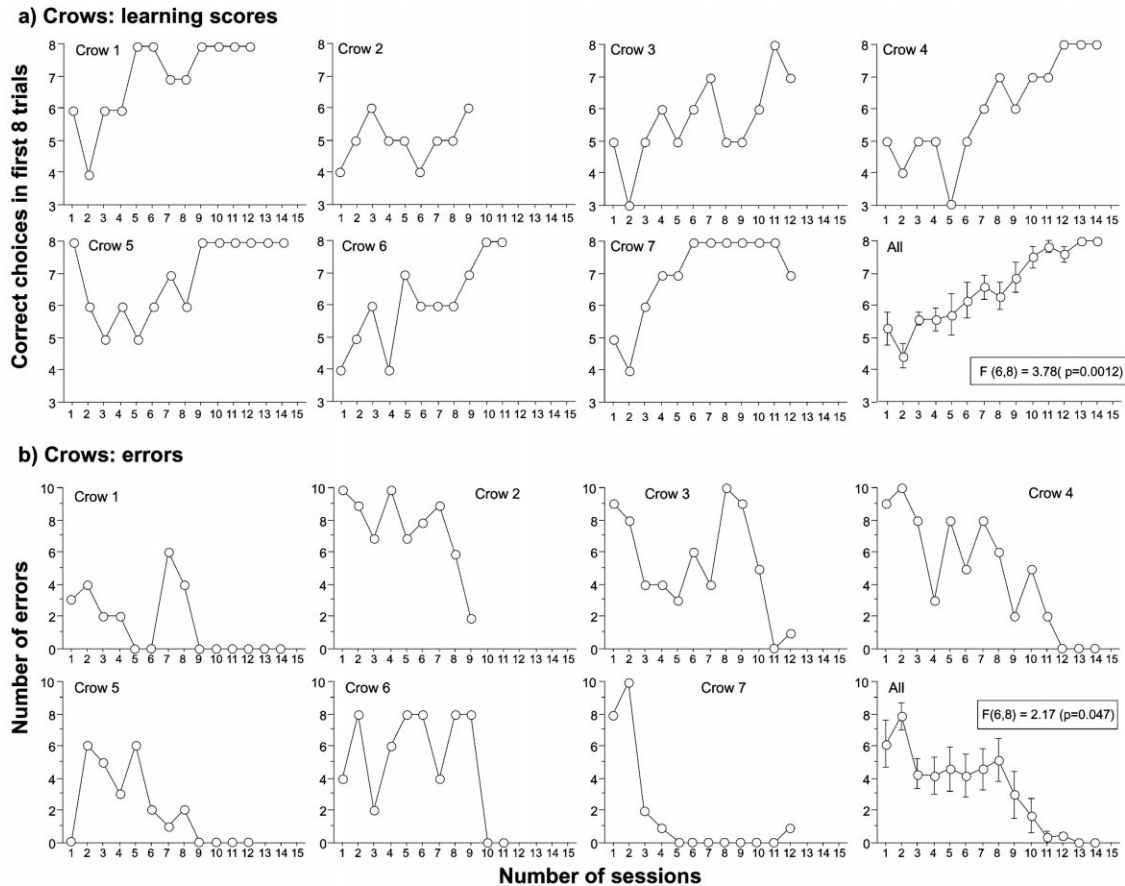This species was tested in a pilot study because of their

Fig. 7. Excellent radial maze learning in seven wild-caught crows: (a) Individual correct choices during the first eight trials of a session, (b) corresponding error scores. Summary data for all animals show means and S.E.M. Note many almost perfect sessions in crows 1, 4, 5 and 7. Errors were due to fear reactions and avoidance of arms close to the tent of the observer.

purported mental dullness [61]. Six hens of an approximate age of 3 months (weight between 800 and 1200 g) were purchased at 'Ptichii Rinok' animal market in Moscow. Three of them were from the Plymouth Rock race, the breed of the others was unknown. They were kept for the experiments in an compartment of 2×2 m in the animal house and fed there once daily a portion of commercial food from the same cups as used in the radial maze. The bait consisted of two parts of cooked pasta (vermicelli of 2 cm length resembling worms), and one part of millet-seed. Experiments took place in Summer 2000. The adaptation period included food deprivation for 24 h, followed by a group release into the radial maze with all arms open and baited. They were then trained for 15 sessions, receiving a reduced food supplement (80%) after training. The first session was done without confinement, the others included a confinement period of 10 s. Five hens completed all sessions, one was removed from training after Session 12 because of suspected illness. The ANOVA for 12 days of training revealed no significant improvement of learning scores during this time ($F_{5,11}$: 1.27, n.s; see also Fig. 6(a)), and there was no significant trend for reduction of errors. Nonetheless, some chicken appeared to learn the task

slowly, e.g., animals 2 and 4. A detailed analysis of learning and error scores (Fig. 6) showed that the errors of the chicken were not due to a strategy of repeated entries into the same arm (win stay). Rather, they appeared to visit the arms in random order which is reflected in scores of five to six correct choices, e.g. by animals 1 and 3. Afterwards, they showed no pronounced choice accuracy and error scores fluctuated unpredictably ($F_{5,11}$: 0.92, n.s.).

The chickens were active in the radial maze, although their walking to the bait appeared less goal-directed than in rats, for example. Interestingly, however, they did not spend much time in exploring the arms during their return. Rather, they ran quickly back to the central platform. Analysis of the error scores also revealed a slight bias to enter more frequently arms closer to the observer.

3.5. Crows (Corvus corone cornix)

The experimental animals consisted of eight adult wild-born hooded crows that had been caught in 1998 and 1997, and kept with other crows in an aviary at Moscow State University. Animals were identified by foot rings. Prior to the experiments, they were
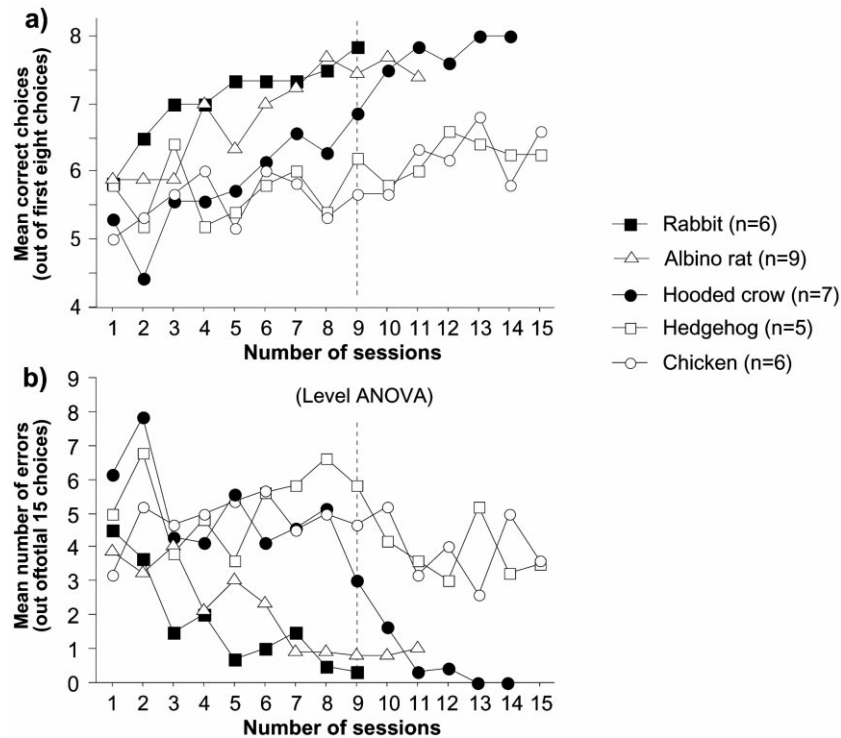
Fig. 8. Comparative analysis of radial maze learning in two avian and three mammalian species. Analysis of variance included Sessions 1–9 indicated by dotted line: (a) Mean correct choices during the first eight trials of a session, (b) corresponding mean error scores. For error bars of different species, see Figs. 3–7. For results of the ANOVA see text. Note the clear separation of species in good and poor learners.

transferred to the field station and kept there together in an aviary with in- and outdoor compartments from where they could see the large radial maze. During pre-training and experimental sessions, the animals were deprived of protein food, trying to keep them at an approximate body weight of 85% as compared to free-feeding conditions by providing mixed cereals only. Proteins in form of eggs, fish or meat were supplemented after sessions. Experiments took place in Summer 1998.

For pre-training, mealworms (the later bait) were offered first in the usual white ceramic cups placed in the aviary. During the next 3 days, the crows were caught with a catcher, wrapped into dark cloth and released in groups of 3–4 into the radial maze. Then the gates were opened and the birds allow to explore the arms and central part during 30–40 min. Each arm contained two feeder cups baited with mealworms, one placed proximally to the central part, the other at the distal end. Some mealworms were also scattered on the floor of the central part. After the daily habituation period (and also after the training sessions), the arm entrance doors were closed in order to keep the birds in one of the arms where they could be caught more easily than in the central part, and the birds were transferred back to the aviary. One crow panicked constantly and had to be discarded for further habituation and training. Due to time constraints and other technical reasons, not all birds could be trained for the same period. The number of

sessions by the individual birds up to a maximum of 14 sessions is indicated in Fig. 7.

During the first day of training, no confinement procedure was used, all arms remaining constantly open. The bait consisted of six mealworms per arm; at the begin of the session, a few worms were also left in the central part. On the second day, a confinement of 10 s after return of the crow was begun. Four of the birds (Nrs. 1, 4, 5, and 7) got accustomed to this, but three others (Nrs. 2, 3, and 6) were very sensitive to sight and noise of the moving doors and always escaped into adjacent arms before the gates were closed. For these birds, confinement between choices was abandoned. However, a certain noise level was kept by lowering and opening the gates while they were consuming a bait. A final analysis of choice angles and other variables did not reveal any statistically significant difference between these crows and the birds undergoing systematic confinement.

Quantitative analysis (Fig. 7) showed a significant improvement of the average learning scores of the crows till Session 9 ($F_{6,8}$: 3.96, $p = 0.009$). During this period, the crows committed a relatively high number of errors, the reduction in errors during the first nine sessions being only marginally significant ($F_{6,8}$: 2.15, $p = 0.047$). Analysis of errors showed that they were not caused by win–stay choice strategies but by avoiding the four arms in proximity of the tent housing the experimenter. The crows improved their learning scores rapidly, however, and four birds

showed a remarkably constant optimal performance. For example, crows 5 and 7 showed six consecutive perfect sessions. Also, the six crows available for testing at Session 11 showed all maximal learning scores. Given such final performance levels, it is obvious that the large variability in performance, due to slow learning of several crows during the first sessions, was caused by their extreme alertness and anxiety.

In fact, the crows were always highly nervous and attentive to any movement of the experimenter. Thus, the experimenter had to stay for the whole duration of a session in a closed tent housing the control unit and had to observe the behavior through a plastic window. Also, no other person was allowed to approach the radial maze during training. All birds disliked being handled and, while being held or wrapped, fiercely and forcefully pinched any object within reach. Once in the radial maze, the crows walked along the circular shelf before taking a decision which arm to choose. Then they flew down and walked quickly to consume the bait. However, because of their distrust against the movable gates, they took a long time to return and often waited close to the entry for considerable time. Many of them walked in through the bottom gates, but some individuals preferred the top gates to return.

3.6. Species comparisons

A comparative analysis of learning and error scores is given in Fig. 8 which shows the curves for the maximal number of sessions, regardless of the number of animals available at the end of training. For statistical analysis, only sessions one to nine could be compared, as these contained a complete data set for every species.

Comparison of the learning scores revealed an overall highly significant effect of training sessions ($F_{4,8}$: 10.88, $p < 0.0001$) and of species differences ($F_{4,28}$: 10.77, $p < 0.0001$). There was also a significant interaction of species by session ($p = 0.03$), reflecting non-parallel improvement of learning scores. Scheffé post hoc comparisons showed that there was a statistically undistinguishable group with higher learning scores (rabbits and albino rats). The less efficiently learning species (hedgehogs and chickens) and the initially troubled crows were statistically equal. They all scored significantly inferior when compared to either rabbits or albino rats (chicken vs rabbits: $p = 0.0014$; chicken vs rats: $p = 0.01$; hedgehogs vs rabbits: $p = 0.007$; hedgehogs vs rats: $p = 0.05$; crows vs rabbits: $p = 0.041$). With ongoing training, however, the superiority of the crows in comparison to these two species became evident (Fig. 8(a)).

Comparison of the error scores revealed a highly significant reduction errors with ongoing training ($F_{4,8}$: 4.39, $p < 0.0001$) and a highly significant species effect ($F_{4,28}$: 8.37, $p < 0.0001$). There was again a strong interaction species by session, reflecting the persistence of errors in chickens and hedgehogs ($p = 0.005$). Pair-wise post hoc

comparisons showed that an error prone group comprising of chickens, hedgehogs and crows could not be discriminated according to errors committed during sessions 1–9, while rats and rabbits could also not be separated. Owing to the larger variability of the error scores, a somewhat different pattern of differences was found for the other comparisons. Chickens were significantly different from rabbits ($p = 0.022$) but only marginally significantly from rats ($p = 0.057$). Hedgehogs were significantly different from both rats and rabbits (hedgehogs vs rabbits: $p = 0.009$; hedgehogs vs rats: $p = 0.022$). Also, the crows could be discriminated on the basis of their errors (at this point of training) from both rabbits and rats (crows vs rabbits: $p = 0.013$; crows vs rats: $p = 0.03$), although the error scores of the crows remaining in training became quickly reduced to almost zero (Fig. 8(b)).

4. Discussion

4.1. General comments

The data from these studies show that an outdoor eight-arm giant radial maze is well suited to analyze the radial maze learning of many different species comparatively. Firstly, because it revealed decent to excellent learning in spite of vastly different levels of stress and needs for adaptation in wild-caught animals, and secondly, because the common set-up allowed to analyze the errors causing species differences. The latter is of particular importance for comparative studies, because all radial mazes (including this one) have one default or virtue, depending on viewpoint. As it is based on an ability found in practically all species, it is suitable to demonstrate the presence of spatial working memory. On the other hand, its power to recognize group differences in basic spatial working memory is limited. This is because there is some variable performance even in well performing animals. Given the narrow range of performance scores and the traditional ceiling at maximally eight responses, any increased variability in one of the groups tends to reduce significance levels. Thus, an additional analysis of errors is mandatory [77], and this is only possible if the errors can be observed in a common apparatus.

4.2. Comparative aspects

To our knowledge, this report demonstrates for the first time classical radial maze learning of rabbits, crows. It also suggests that chickens and hedgehogs might also be capable to learn it. As the scope of this preliminary studies was methodological, we had no intention to quantify species differences more thoroughly. From a qualitative point of view, however, there were clearly many interesting differences deserving detailed investigation.

The data from the rats show that our large radial maze revealed results comparable to small laboratory set-ups. In

fact, the rat showed significantly better learning and stable performance in the outdoor maze. These data confirm the observations that arm length of the maze might be a factor determining choice accuracy [9,10]. However, the difference might have been caused by other factors in the testing environment. The results also show that the traditional good performance of rats in laboratory devices is not dependent on a burrow type environment, as the rats showed high scores of correct choices after 9–11 sessions as typically found in laboratory studies, e.g. [53,55]. Lastly, our results show the astonishing adaptability of this species by attaining good performance despite of being handicapped as albinos under the bright sun. It will thus be of interest to compare laboratory *Rattus norvegicus* with the black rats (*Rattus rattus*) found traditionally on the territory of the field station.

An unexpected finding was the excellent learning of the rabbits. Pending replication with other and perhaps older animals, it would seem that this species has a natural endowment for radial maze learning. Given the traditional role of rabbits as experimental animals in neurophysiology, it would seem that this species represents an excellent candidate to study activity of hippocampal place cells in naturalistic set-ups. They behave, with little training, as good or better as rats, but are large enough to carry easily a telemetrical set-up for single cell recording.

Given the low level of encephalization in hedgehogs, the relatively poor radial maze learning was not that surprising. It would seem that a larger sample size will almost certainly reveal significant improvement of learning scores over time as this was already evident in some individuals. However, there might also be ecological constraints accounting for the modest performance. Hedgehogs typically roam a large territory for a variety of food. Hence, remembering places of previous food consumption is perhaps not particularly relevant for this species.

The refusal of guinea pigs to move in the radial maze came as no surprise, as we have been unable to use that species for any classical laboratory task including open-field activity, two-way avoidance learning and Morris maze learning. The excessive freezing of guinea pigs, which grows more pronounced with age, obviously prevents testing of the animals in any other than their habitual environment.

Similar constraints may account for the moderate or missing improvement in chicken. This species also wanders repeatedly across a larger territory with widely scattered and different sources of food. Nonetheless, their inferiority in the radial maze as compared to crows suggests some mental limitations in learning and performance. This issue is being followed up in future studies.

We consider the crows as the best performers, because they were wild caught animals and considerably stressed. Yet, cognitive capacities reflect to a large extent the ability to perform accurately even under adverse conditions. Despite their nervousness, the crows gave the impression of truly having grasped the task and performing at will. Our results confirm the good performance other corvid species [5,34]. One may note that the hooded crow also caches food occasionally [24], but it remains to be seen whether the good radial maze learning is specifically correlated with the ability to remember food caches. Clearly, the position of the experimenter was a biasing factor which makes the use of video observation commendable for this species.

4.3. Methodological perspectives

The main methodological goal in constructing a large radial maze was the need for a common apparatus permitting comparative neurobiological analysis of spatial learning across many different species. This goal has been attained. It would seem difficult to imagine another learning device which permits to screen comparatively, for example, magpies with hedgehogs, or geese with foxes, to name only a few species. It is equally suitable to analyze radial maze learning between members belonging to the same genus, such as mustelidae, squirrels, or corvids, which makes it particularly suitable for a correlative neurobiological analysis. The only restriction are very large or small species. Because large-brained species are ill-suited for a neurobiological analysis, they have never been in our focus. The unsuitability for very small species is a more serious problem, as small rodents and other small mammals are optimal for neuroanatomical comparisons. Since the main problem is the observability of small animals, this could be technically overcome by inserting smaller channels and placing video cameras for surveillance. However, we have chosen to solve this problem by constructing radial maze analogs, consisting of equidistantly placed computer-controlled feeders delivering food selectively to transponder-tagged mice or small rodents in their natural habitat [14].

An additional and unplanned methodological benefit of a large radial maze is its unmatched flexibility for modifications that can be inserted because of the generous space. Thus, we have already demonstrated that shortening the arm length has a significant effect on choice accuracy of pigeons (Pleskacheva et al., forthcoming). For example, one could test the capacity of social learning by keeping observers watching the demonstrator animal, make the task more demanding by inserting additional spatial or non-spatial tasks at the end of the arms, or use the maze for assessing both spatial and temporal learning. Another interesting field of application would seem to study the spatial learning according to celestial cues as already demonstrated for pigeons [7].

Taken together, we believe that this type of large maze could have far more applications than used or proposed here and might be profitably constructed on any territory of an

university, preferably under a barn, as working in the rain is the only disadvantage we are aware of.

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