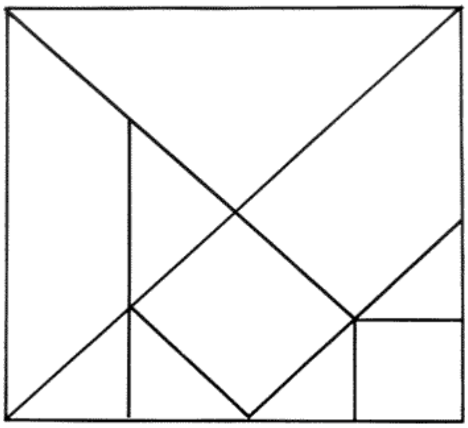
PhD THESIS

SPATIAL CHOICES OF ANIMALS BASED ON ABSTRACT VISUAL STIMULI: CONFIGURATION OR SHAPE?



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CONTENT

INTRODUCTION

Spatial cognition as a model for study of learning, memory and problem solving has a long history in neurosciences. This cognitive ability is used for several reasons. Firstly, the ability to form the inner representation of a space, to orient in an environment, to perceive positions of prominent objects and of other animals is essential for all mammals and birds. Thus it is natural for animals to perform such behavior even in experimental conditions. Secondly, it is possible to compare spatial cognition of different species in similar tasks. And thirdly, there are strong indices of the possible neuroanatomical substrate and mechanism underlying spatial cognition.

There are different strategies of navigation in an environment, which could be distinguished by different criterions.

They differ in the **frames of reference** in which the observer operates, i.e. whether the co-ordinates are centered in a subject (**egocentric orientation**) or whether the co-ordinates encode only the relations between objects and dominants in the environment and they are not dependent on observer (**geocentric orientation**).

The navigational strategies also differ by the type of cues that are used for navigation. In **allothetic orientation** the subject employs external landmarks, which may be not only visual stimuli, but also the stimuli of other sensory modalities.

The inner information about self-motion in space, which came from statokinetic system or from proprioreceptors, are used in **idiothetic orientation** (path integration). Path integration is the ability to determine the subject's position by integrating subject's velocity with respect to time.

Interaction between different strategies can reduce navigational errors (Collett and Graham, 2004).

In spatial cognition research various experimental tasks based on different navigational ability are used, but a few principal methods can be distinguished:

- An animal freely moving through an environment (T-maze, open arena, Morris water maze, etc.)

- A passively moving animal (animal on a rotating arena)
- An animal discriminating configuration of a real or of a virtual scene
- An animal performing spatial choices (orienting) in a real environment according to abstract stimuli (stimuli not connected with this environment)

The animals often demonstrate the ability to form representation of the geometric properties of the surrounding environment and of the configuration of the objects in this environment.

We developed new behavioral tests to study the cognitive ability to perceive configuration of visual stimuli and to perform spatial choices in a real space according to these abstract stimuli not directly connected with the response space.

We tried to determine whether the animals could interpret inner spatial configuration of these visual stimuli or whether they perceive them simply as geometrical patterns and associate appropriate spatial responses with particular patterns.

Contrary to most studies concerning the ability of animals to represent geometric features of environment, we tested the ability of animals to perceive the configuration of stimuli in one "spatial frame" and to transfer this ability to another "spatial frame". The animals had to demonstrate the ability to abstract geometric relations of presented stimuli.

As model organisms we used hooded rats (*Rattus norvegicus*) and macaque monkeys (*Macaca mulatta*).

In order to show the potential of animals to solve this task, I review the experiments concerning the ability to represent geometric features of environment and to abstract geometrical rules.

COGNITIVE MAP

To orient in the environment, to perceive positions of prominent objects and of others animals – predators, preys or mating partners – animals have to form inner neural representation of space.

The concept of a "cognitive map" – inner representation of the environment, where an animal is moving - was first formulated by Tolman in 1932 (reviewed in Tolman, 1948). In his classic experiment, Tolman trained rats to find a goal through an indirect route. Then he blocked this route, but the rats had the opportunity to reach the goal through a direct route or through number of false routes. The rats chose the direct way more often than by chance, what suggested that they knew in which direction the goal was, even though they had never walked through this route.

However, because of predominant behaviorism paradigm, the concept of cognitive map was not generally accepted until 60ties, when the cognitivism became one of the dominant forces in psychology.

The theory of cognitive map was also supported by the discovery of hippocampal neurons with place-selective activity called "place cells" (O'Keefe and Dostrovsky, 1971; O'Keefe and Nadel, 1978). These cells, with later discovered "head-direction cells" and entorhinal "grid cells", may serve as a basis of the neuronal representation of space.

The cognitive map according to O'Keefe and Nadel is a memory for allothetic landmarks, an inner map, which enables animals and humans to create shortcuts and routes through of environment, even in the locations, which the subject have never visited before.

However, such concept brings some difficulties (Roberts, 2001). Although some evidence suggested that animals could form novel shortcuts, there exists a controversy. Bennett (1996) proposed that there could be any alternative explanations for novel shortcuts: (1) an animal could be familiar with the environment and thus the shortcut was not novel. In experiments with wild animals it is difficult to prove that animals have never used the shortcut before; (2) an animal could use a prominent familiar landmark closed to the goal; (3) an animal could use not allothetic but idiothetic information (path integration).

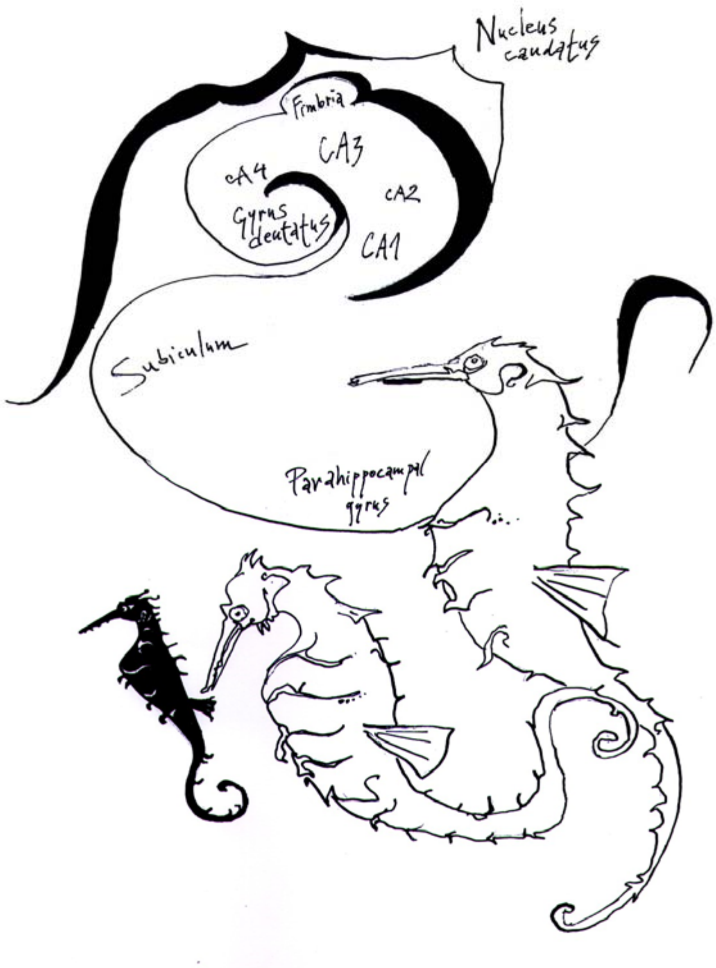
As this specific term provokes controversy, the existence of cognitive map in larger sense is undisputed (Mackintosh, 2002).

Gallistel defined cognitive map as “a record in the central nervous system of macroscopic geometric relations among surfaces in the environment used to plan movements through the environment” (Gallistel, 1991).

Such representation of space could be based both (1) on allothetic external landmarks of all modalities and (2) on internal information about movement came from proprioreceptors and muscles (path integration).

It seems that the brain structure pivotal for forming such representation is hippocampus, or its homologue (O’Keefe and Nadel, 1978; Redish and Touretzky, 1997; Jeffery, 2003).

HIPPOCAMPUS



O’Keefe and Nadel supposed that the rat hippocampus primarily serves for spatial representation, whereas Eichenbaum and colleagus assume that the hippocampal spatial function is just a special case of more general non-spatial function (Eichenbaum, 1999; Shapiro and Eichenbaum, 1999; Eichenbaum et al., 1999).

It seems that hippocampus is involved in spatial cognition, particularly in encoding of the configuration of distal stimuli, but its computational capacities could also serve for other purposes.

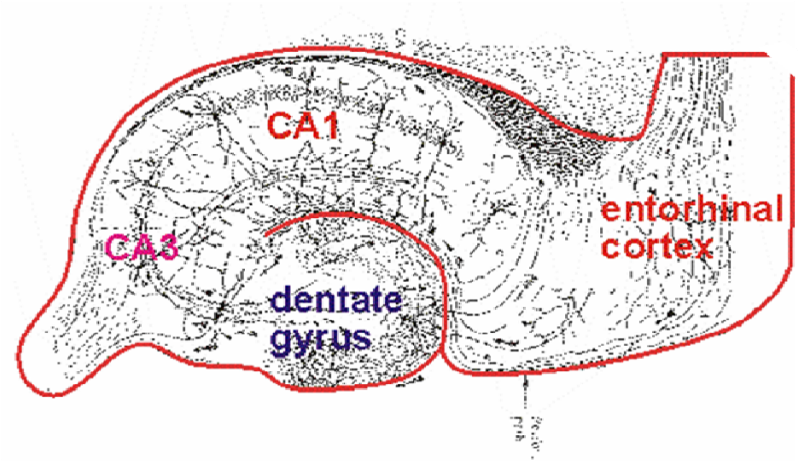


Fig.1: Scheme of the rat hippocampus and adjacent entorhinal cortext. (Adopted from web page of University of Birmingham, division of Neuroscience)

Hippocampus is a part of archicortex, functionally belonging to the limbic system. In mammalian brain it is situated inside the medial temporal lobe.

The hippocampal formation of mammals consisted of dentate gyrus, the Cornu Amonis – fields CA1-CA3 (and CA4, called hilus) and the subiculum (Fig.1).

The connections within the hippocampus generally follow the laminar structure and they are unidirectional. They form well-characterized closed loops predominantly rising from the adjacent entorhinal cortex (EC).

Hippocampus receives a main input through the perforant path from entorhinal cortex and a number of subcortical inputs. The perforant path comes mainly from layer II and III of EC with minor part from deeper layers IV and V. The axons from layers II and IV project to the granule cells of dentate gyrus, whereas the axons from layers III and V project to the pyramidal cells of the CA3 and the subiculum.

The neurons of CA3 also receive the input from the gyrus dentatus through the mossy fibres, which forms their main input. CA3 neurons combine both inputs from gyrus dentatus and entorhinal cortex and project to CA1 region through the Schaffer collaterals.

Region CA1 receives inputs from the CA3, layer III of EC and from the thalamus (nucleus reuniens). The axons from CA1 project to subiculum, where it is combined with the input from layer III of EC.

The pathway from subiculum to the entorhinal cortex is the main output from the hippocampus. (O'Keefe and Nadel, 1978)

In the hippocampus and adjacent areas, there are neurons closely related to the ability to form the inner representation of space. These cell mechanisms were widely studied especially in rodent hippocampus, although the neurons with spatially selective activity were also showed in non-rodent species (Rolls, 1999; Rolls et al., 1999; Georges-Francois, 1999)

Place cells are pyramidal cells found both in region CA3 and CA1 of the hippocampus in rats and mice. Place cells are characterized by location-selective firing – it means that a given place cell is active only when the animal is in a particular part of the environment called "place field". Each place in fixed environment has a stable field that persists for a long time period, but one cell can have two or more fields. It is possible that the computation of position from population activity could increase the accuracy. (Muller, 1996)

In open environments, the place cells are not directionally selective, but the same place cell could be directionally specific under other circumstances (for example in an arm of 8-arm maze) (Muller, 1994).

Place cells are not uniquely determined only by visual cues, it was shown that after removal of prominent landmark, the fields could remain intact (Muller and Kubie, 1987).

Recently, experiments suggested that the place cells do not encode only spatial information and they could also react to non-spatial variables. This challenged a pure mapping theory.

Head direction cells complement spatial information. They were found in postsubiculum, but also in the parts of thalamus reciprocally connected with the postsubiculum. Head direction cell is strongly active when the rat's head points at a preferred direction (relatively narrow angle in the horizontal plane) and the firing rate decreases as a deviation from preferred direction (clockwise or counterclockwise) increases.

The peak of firing rate varies among particular head direction cells but it is characteristic for a given cell in all conditions.

The preferred direction for a particular cell is the same everywhere in the environment, thus the population of cells serve as a compass. (Muller et al., 1996)

Grid cells are directionally oriented, topographically organized cells found in medial entorhinal cortex. These cells are active when the animal is being in the position coincides with any vertex of a regular grid of equilateral triangles overlaid an environment. Grid spacing, orientation and field size are topographically organized, with spacing and field size increased from the dorsal to the ventral part of entorhinal cortex. The grid structure persists even after removal of allothetic cues. (Hafting et al., 2005)

The deeper layers of entorhinal cortex involve conjunctive grid cells and head-directional cells. The integration of directional and positional information could form a metric representation of animal's location. (Sargolini et al., 2006)

There are number of structural differences between avian and mammalin hippocampus. The avian hippocampus consists of the hippocampus (H) and the area parahippocampalis (APH) situated on the dorsal surface of the brain along the midline (Fig.2). In the avian hippocampus there are no clearly discernible structures as cornu Ammonis, dentate gyrus or subiculum and there is absence of a distinct laminar organization (Siegel et al., 2005).

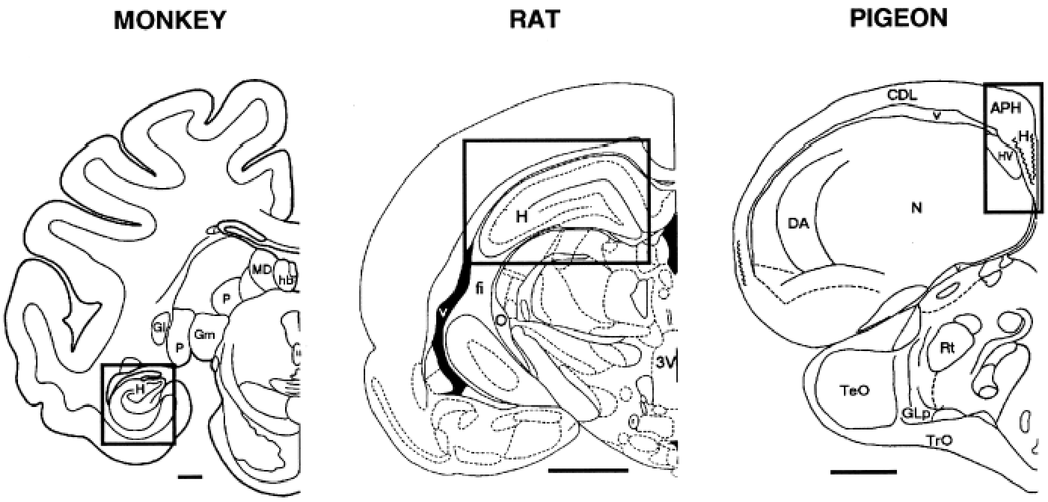


Fig.2: Coronal sections demonstrating the relative position of the hippocampus (in the frame) in the monkey, rat and pigeon. The scale represents a distance of 2 mm. (The figure is adopted from Colombo and Broadbent, 2000).

Despite the anatomical differences, there are evidence supporting the homology between the hippocampus of birds and mammals: (1) Avian hippocampus develops in ontogenesis from the same part of the medial pallidum as the mammalian hippocampus does; (2) The patterns of input and output connections are similar; (3) There are similar neurotransmitters and neuropeptides in the avian and mammalian hippocampus; (4) Both hippocampi demonstrate LTP plasticity; (5) The lesions of both mammalian and avian hippocampus impair similar tasks, mainly those requiring the spatial cognition. (Colombo and Broadbent, 2000).

The studies not only demonstrated the dependence of avian spatial behavior on hippocampal formation (Colombo and Broadbent, 2000), but also revealed that subset of single cells recorded in the hippocampus of freely moving birds showed space-specific changes in firing rate (Siegel et al., 2005; Hough and Bingman, 2004).

Siegel and colleagues found location-correlated single-unit activity of hippocampal cells in homing pigeons (*Columba livia*) freely moving in the "plus maze".

These cells showed clear spatial specificity, but some differences between avian cells and place cells in the rodent hippocampus were revealed. On contrast to rodent place cells, which usually encode only one or two locations, avian cells were active in multiple regions. The spatial-selective activity of pigeon hipocampal cells was significant, but in comparison with rodent hippocampal cells, it was only moderate and often had transient characteristics. The rodent place cells demonstrate higher level of spatial coherency and specificity than the observed pigeon cells.

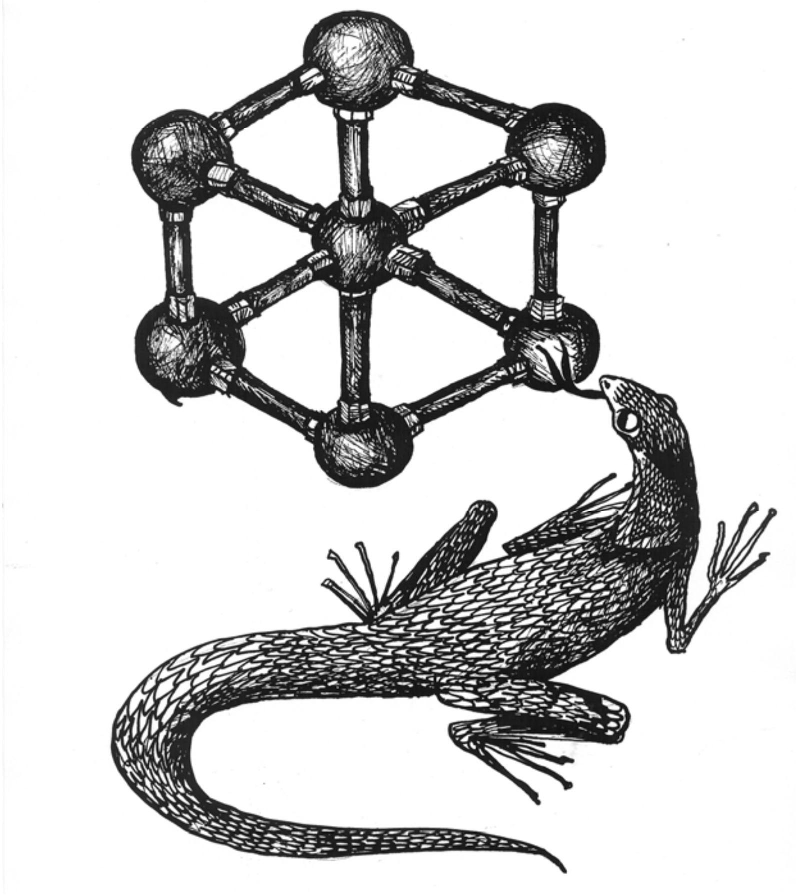
The authors proposed that lower spatial coherency and transient characteristics of avian hippocampal cells could reflect high correlation of these cells also with non-spatial (behavioral, motivational, contextual) parameters. Indeed, there was subpopulation of cells changing their activity according to whether the birds were in the maze or not. Other cells increased their activity at the end of the maze arms (where the reward was obtained) what also supported context-dependent activity.

It is also possible that the avian cells remapped during session, however it would suggest that the cells were eminently sensitive to contextual changes, because there was no intended environmental manipulation in the experiment.

Hough and Bingman (2004) distinguished three categories of space-selective cells in avian hippocampus: (1) *Location cells* showing higher firing rate in specific locations of the arena. The location cells showed strong interaction with non-spatial features and lower coherence than the place cells of rodent hippocampus; (2) *Path cells* displaying higher activity as the bird was moving through the arena between goal locations; (3) *Arena-off cells* that were more active when a pigeon was in a baseline, out of the experimental arena. These cells could reflect not only space, but also the motivational or contextual setting.

The experiments demonstrated that in the avian hippocampus there are cells showing spatial selectivity, but that they are different from place cells in mammalian hippocampus.

GEOMETRY OF THE SPACE



There are suggestions that the animals encode the space in Euclidean (metric) system. Euclidean geometry has been exposited as an axiomatic system, in which all theorems are derived from a finite number of axioms. In the first book of the *Elements*, Euclid gives five postulates (axioms):

1. Any two points can be joined by a straight line.
2. Any straight line segment can be extended indefinitely in a straight line.
3. Given any straight line segment, a circle can be drawn having the segment as radius and one endpoint as center.
4. All right angles are congruent.
5. Parallel postulate. If two lines are drawn which intersect a third in such a way that the sum of the inner angles on one side is less than two right angles, then the two lines inevitably must intersect each other on that side if extended far enough.

The axioms defining the Euclidean geometry determine which geometrical features of environment could be encoded and which one resulted from features already represented. For example: we could specify equidistance relations between the points (and thus their possible parallelism). The hierarchic arrangement of geometrical features enables for example to obtain information about parallelism, when a distance of lines is known, but not conversely. (Gallistel, 1990)

Shape is largely defined by the distances between and along surfaces or lines and by the angles they form. To represent the shape, animals should perceive and represent in some way metric properties of the space, at least some behaviorally important relations between objects, points and surfaces in its environment, but not necessarily the full set of Euclidean relations. (Gallistel, 1990)

The geometrical object in Euclidean space could be transformed in some way. In Cartesian coordinates, a **translation** of the shape means moving of every point by a fixed distance in the same direction. It can also be interpreted as the addition of a constant vector to every point, or as shifting the origin of the coordinate system.

Rotation is a type of transformation from one system of coordinates to another system of coordinates such that distance between any two points do not change under the transformation. The rotation about the origin of a Cartesian coordinate frame is given by the formulas:

$$x' = \cos\Theta\, x + \sin\Theta\, y$$
$$y' = -\sin\Theta\, x + \cos\Theta\, y,$$

where Θ is the angle of rotation.

Displacement transformation is a combination of a translation and a rotation. It is computed by the formulas:

$$x' = \cos\Theta\, x + \sin\Theta\, y + m$$
$$y' = -\sin\Theta\, x + \cos\Theta\, y + n,$$

where Θ is the angle of rotation; and m, n are parameters of translation. Displacement transformations are special cases of affine transformation.

None of mentioned transformation changes any of geometric parameters. They only change the position of shape (or the beginning of coordinate system) and/or the orientation of that shape.

On contrast, **affine transformation** changes the shape of the object. It is a combination of stretches and reductions along one or more axes computed by the formulas:

$$x' = a_1x + b_1y + c_1$$
$$y' = a_2x + b_2y + c_2.$$

Values a, b, c are arbitrary constants.

However, some categories are invariant under this transformation. Affine transformation does not change collinearity or categories of linear section, but it alters unique metric relations as distances or angles between points.

Another type of transformation is a **reflection**. Reflection alters right/left orientation, but preserves metric relations.

REPRESENTATION OF THE GEOMETRY OF THE SPACE

CONFIGURATION OF MULTIPLE LANDMARKS

Both mammals and birds can represent not only visual appearance of prominent landmarks and to use them as beacons directly marking a goal, but they can represent also their mutual configuration or the global shape of the environment in which they move and their own position within this space. This means that animals are able to identify a landmark not only by its appearance but also by its spatial relations to other landmarks (i.e. "the apex of square array"); or that they can use global geometry of the space (i.e. "in the center of the arena") (Biegler et al., 1997).

The ability of rats to use multiple landmarks to locate a goal is widely used as standard behavioral test in Morris water maze. Morris (1981) demonstrated that rats were able to find in a circular water pool a submerged platform, which was not marked directly. Rats used for navigation a configuration of extramaze cues.

Later experiments showed that this ability is highly dependent on hippocampus (Morris et al., 1982; Pearce et al., 1998). Pearce and colleagues showed that the hippocampal lesion impaired the ability of rats to learn multiple landmarks, but it did not affect the navigation based on a heading vector.

Whishaw and Tomie (1997) proved that hippocampal rats could locate a platform in water maze, but that they were impaired in the ability to learn its new positions. This suggests that hippocampal lesion impairs spatial reversal learning.

Kamil and Cheng demonstrated the ability of Clark's nutcrackers (*Nucifraga columbiana*) to use multiple landmarks for orientation. They showed that nutcrackers are able to search precisely with using the metric relationship between a goal and multiple landmarks. Clark's nutcrackers are food-storing birds and thus that their survival and reproduction depend highly on stored pine seeds. They could cache tens of thousands of seeds in thousands of locations, and their retrieval demands exceptional memory capability (Balda and Kamil, 1992).

In many situations birds locate a particular place by a beacon or by a cue near this place and thus directly marking it, but nutcrackers frequently cache in the middle of open meadows with only few local landmarks. This strategy could serve as a defense against cache-robbing by rodents. Thus many cache sites are located quite far from large landmarks. Because small local landmarks could be easily affected for example by seasonal changes, birds prefer to use geometry of distal landmarks and a goal to locate the goal site. (Kamil and Cheng, 2001)

In experiment of Vander Wall (1982) the birds were trained to locate a position of a goal with using multiple landmarks. When some landmarks in aviary were shifted, the birds searched in the position between the shifted and non-shifted locations in the environment. This also implies the use of at least two distinct landmarks.

Spetch et al. (1992) demonstrated the ability of pigeons to use multiple landmarks presented on a computer screen for locating a goal. Vertical surface of touch screen provided two-dimensional spatial arena and computer-generated stimuli displayed in different locations served as landmarks. Pecking in the particular position was rewarded. The landmark configuration was shifted vertically or horizontally. The results proved that pigeons are able precisely locate an unmarked goal in a two-dimensional vertical arena and that these results are comparable in many aspects with results found in open-field search tasks.

Although there are many evidences that birds are able to use configuration of multiple landmarks, in some situations birds prefer to use single landmark directly marking the goal location. This means, that the landmark which is very close to the goal location, could overshadow other landmarks (Spetch, 1995, Gould-Beierle and Kamil, 1999).

It has been suggested that natural selection could favor redundancy of multiple landmarks as an adaptation against change in landmarks in environment. While it is reasonable hypothesis, it is difficult to test.

Many evidence indicate that animals can encode and use metric properties of distance and direction. Locating of a goal thus could be separated into two processes: the first process is judgment about direction and the second process is judgment about distance.

Kamil and Jones (2000) trained the nutcrackers to search for a goal according to two landmarks with varying distances among them. The seed was buried at a third point. The directional relation between the goal and the landmarks was maintained constant, but the distance between the goal and the landmarks varied as the distance between the landmarks increased.

Other experiments indicate that directional information is more significant when the distance between a goal and a landmark is relatively large. Kamil and Jones (1997) separated search errors into distance and directional components: error along an axis defined as a line between the landmark and a goal would estimate distance error; error perpendicular to that line would be directional error. Kamil and Jones showed that with increasing distance between landmarks the distance errors increased more rapidly than the directions errors. Kamil and Jones (2000) obtained similar results when they trained two groups of nutcrackers to find the third point defined by two landmarks. For one group a goal-landmark distance varied and bearings were constant and for the second group the goal was buried at the same distance from each landmark and goal-landmark bearings varied. The group with changing distance and constant bearing was more successful and learned to solve the problem more rapidly than the second group. Thus, under these conditions, the directional information (bearings) provided a more useful cue to locate a goal than the distance information.

Experiments mentioned above demonstrated that multiple landmarks make it possible to design a representation of mutual position of a goal and multiple distal landmarks and that directional information is under such conditions more valid than information about distance.

When more than one landmark is used, there are many ways how to encode the goal location: it can be defined as an intersection of two bearings, an intersection of bearing from one landmark and a distance from the second landmark (circle with radius approximately equal to goal-landmark distance).

The birds could use two types of bearings - absolute bearings (when absolute compass direction from goal to landmarks is used) and relative bearings (the angle subtended by two landmarks viewed from the target location is used; it can be used efficiently with three or more landmarks).

Simultaneous use of multiple redundant landmarks could decrease errors in estimating of a direction and a distance both with use of absolute and relative bearings.

In case of absolute bearings, when absolute compass is applied, this strategy could reduce both constant error and error specific for each landmark (Kamil and Cheng, 2001). If there are three or more goal-landmark bearings with constant error in output of the compass, the bearings do not intersect in one zone and form the area of uncertainty. In case of constant errors, the subject would search in the center of the "uncertainty" zone. This area would decrease with growing number of landmarks.

Relative bearing could be defined as the difference between two absolute bearings. There must be more than two landmarks or additional information from absolute bearings or from distance measurement to use relative bearings for locating a particular position. An advantage of relative bearings could be that this method is not sensitive to a constant error in estimating bearing. There are evidence that birds are able to use relative bearings as cues and that using of redundant landmarks specifies the searching (Kamil and Cheng, 2001).

As was summarized, animals prove their ability to generate geometric representation of the environment based on multiple landmarks. It means that they could represent a mutual configuration of multiple landmarks or determine distances and directions between landmarks and a goal.

It seems that there are both commonalities and differences across species in strategies of landmark use. Some aspects of landmark use (such as preference for near landmarks) appear to be highly general across species from invertebrates to humans. However, some differences have been revealed.

The manipulations with relations among landmarks could demonstrate such differences between species. The animals are trained with a goal hidden at a fixed location relative to an array of two or more identical landmarks. The array of landmarks is located in the environment with stable allothetic directional cues, but the landmark array and the goal are moved so that the landmarks have to be used to locate the goal.

The information provided by landmarks could be used in several ways: (1) One strategy is to represent the global configuration of the landmark array and to locate the goal in relation to this configuration. (2) The second strategy is to encode the distance and direction of the goal from individual landmarks in the array. (3) The third strategy is to use of a landmark as a beacon and to simply search near the landmark array. This strategy could be used only if the landmarks are situated very close to the goal and with increasing distance it becomes ineffective.

The transformation of landmark array (for example expanding) should reveal which of the specified strategies is used. (1) An animal using configuration strategy would search in the same relative position to the landmarks (for example at the center of the array). (2) An animal using an individual landmark would search in the same distance and the direction from individual landmarks as in training. (3) An animal using a beacon would search near the individual landmarks, but not necessary in appropriate direction or distance.

The expansion tests were carried out in many species, but only honeybees and humans showed spontaneously a pure configuration strategy (MacDonald et al., 2004). Adult humans performed configuration strategy in several tasks both in the real environment and in the task presented on the computer screen. Spetch et al. (1996) trained humans and pigeons to search for a hidden goal centered between four identical landmarks. The goal was always in a fixed relative position to an array of landmarks presented in a different placement on a computer screen.

After initial training, the landmark array was expanded in vertical or horizontal direction. Humans adjusted the distance from the landmarks to maintain the same bearings from landmarks and thus they searched at the center of array, whereas pigeons preserved the distance and direction to a single landmark, and thus the goal location was shifted from the center. The results of these experiments showed that both humans and pigeons were able to use configuration of stimuli for locating the goal, but only humans could perform complete transformation when the stimuli were changed.

Similar results were obtained from the comparable experiments in a real space (Spetch et al., 1997) – pigeons were trained to search on the laboratory floor and humans searched on a table or on an outdoor field. The goal was centered in a fixed position between four landmarks situated in square array.

When the distance between landmarks was increased, humans searched in the center of the array, whereas pigeons preserved searching in the same distance and direction from single landmarks as in the initial training. These experiments suggested that humans and pigeons differ in using landmark configuration.

Other experiments with touch-screen devices carried out in humans and pigeons (Spetch et al., 1998) showed that humans and pigeons rely on different stimuli when locating the goal. Pigeons and adult humans were trained to search an unmarked goal in digitized images of an outdoor scene presented on a touch-screen monitor. On the scene there were three landmarks near the goal and a visually rich background. Removal of the landmarks or background revealed that pigeons' searching was controlled by both proximal landmarks and distal background cues, whereas humans were controlled only by proximal landmarks.

MacDonald and colleagues (MacDonald et al., 2004) compared how common marmosets (*Callithrix jacchus jacchus*), human children and human adults use landmarks to locate a goal. The subjects were trained to find a goal hidden in one of the discrete places at the center of four identical landmarks. The training was followed by expansion test, when the landmarks expanded to the corners of the experimental enclosure, whereas the goal stayed at the center.

In the training phase the marmoset monkeys readily learned to find a hidden goal (a cup with a mealworm) placed randomly in an enclosure and closely surrounded by four landmarks. However, in the expansion test, the marmoset monkeys did not use a "center rule", but searched near the landmarks. It seems that they used a combination of a "beacon rule" and vector from individual landmarks. But in the case of using the vector, they probably had to determine the identity of particular landmark from the landmark array.

Human children of age 5-6 years (younger group) and 7-9 years (older group) were tested on a similar task (only a goal differed from experiments with marmoset monkeys - there was a chocolate candy instead of mealworm hidden in a cup). Children of both groups learnt to find the goal in training phase, but similarly as monkeys, they searched near the landmarks on the expansion test. However, unlike the monkeys, the children did not search for the goal in the position that could indicate that they can learn vector from the landmark to the goal and they used strategy purely based on beacons.

Following experiments revealed that only the human adults in equivalent experiments used the “center strategy” even when the landmarks were adjacent to the goal.

The experiments of MacDonald et al. (2004) in marmoset monkeys and human children and experiments of Spetch et al. (1996, 1997) in pigeons and humans demonstrated that subjects of different species showed lack of spontaneous tendency to use configuration of multiple landmarks and did not abstract “central rule” to search a goal in expansion test.

Similarly, experiments with birds (Spetch, 1995) showed that under some circumstances single landmark could overshadow other landmarks when it is in close proximity to the goal. In this case the subjects could prefer to use a single landmark as a beacon rather than to use a configuration of landmark matrix.

Collett et al. (1986) trained gerbils (*Meriones unguiculatus*) to locate a goal in specific relations with multiple landmarks. Gerbils prove the ability to find a goal even when the room light was turned off, what implies that they already planned a trajectory to the goal before the room was darkened. This means that they form internal representation based on information about distances and bearings among the landmarks and a goal.

However, when the gerbils were tested with an array of landmark either with several landmarks removed or the whole array expanded, they searched in the positions computed from the single landmark. For instance, when they were tested with two landmarks in doubled distance, they searched in two positions at the correct distance and correct direction from each of the landmarks.

On contrast, Kamil and Jones (1997) proved that Clark’s nutcrackers were able to learn geometric relations among landmarks, when they were trained to locate a goal in the halfway between two landmarks with varying distance.

This finding was replicated in comparative study (Jones et al., 2002) with three avian species: a seed-caching corvids (Clark’s nutcrackers; *Nucifraga columbiana*), a non-seed-caching corvids (jackdaws; *Corvus monedula*), and a non-seed-caching columbids (pigeons; *Columba livia*). All three species learnt to find a goal in the task, when inter-landmarks distance varied, even it took longer time in jackdaws. Both nutcrackers and pigeons showed good transfer in the sessions with novel inter-landmarks distances, which were not used during the training, but the results from jackdaws were inconclusive. The nutcrackers demonstrated the best results in this task. However, the differences between species seemed to be more quantitative than qualitative.

The results of reviewed experiments clearly proved that both mammals and birds are able to use multiple landmarks to locate a position of a goal. This implies that animals form inner representation of mutual configuration of multiple objects in an environment. However, the results were ambiguous in the tasks when animals should deduce abstract geometric rules (for example "find a center").

One possible interpretation is that there are phylogenic differences in cognitive capacity between species, which limit their ability to perform the task. This difference evolved under different ecological demands. Nevertheless, it seems more probable, that performance (at least in some cases) was influenced by important differences in training procedure.

In experiments of Spetch, McDonald, and Collett the subjects were trained with stable landmark-configuration and then tested with totally novel configuration. During this training phase both coding - (1) geometric ("finding a center") and (2) with using of single landmark – were in principle correct. On contrast, in experiments of Kamil and Jones the subjects were trained with changing configuration, thus they were really trained to learn abstract geometric rule.

GLOBAL SHAPE OF THE ENVIRONMENT

Animals demonstrate not only the ability to form a representation of mutual relations and configuration of multiple landmarks, but also the ability to represent global geometry of the surrounding environment (Cheng, 2005).

Cheng (1986) developed a paradigm concerning the geometric and non-geometric cues controlling rats' behavior. He showed that rats could represent geometry of the surrounding space. In Cheng's experiment rats were trained to find food in a corner of a rectangular enclosure. The location of a goal was partly specified by the global shape of the environment and partly specified by the non-geometric cues (brightness of walls and the patterns and odors in its corners).

When the rats had mastered the task, they were removed from the enclosure and completely disoriented. After the disorientation procedure, the rats were returned to the enclosure to search for the food. To find the goal, the rats had to re-establish its own allocentric position.

The positions in which the rats searched after disorientation made it possible to assess the strategy used by the rats during reorientation.

The results of experiments showed that rats had responded mainly in the correct position and also in the rotationally equivalent position. The rotationally equivalent location was the location situated diagonally; e.g. the geometrical cues were the same on the both locations – for examples the long wall on the left and the short wall on the right. (Fig.3)

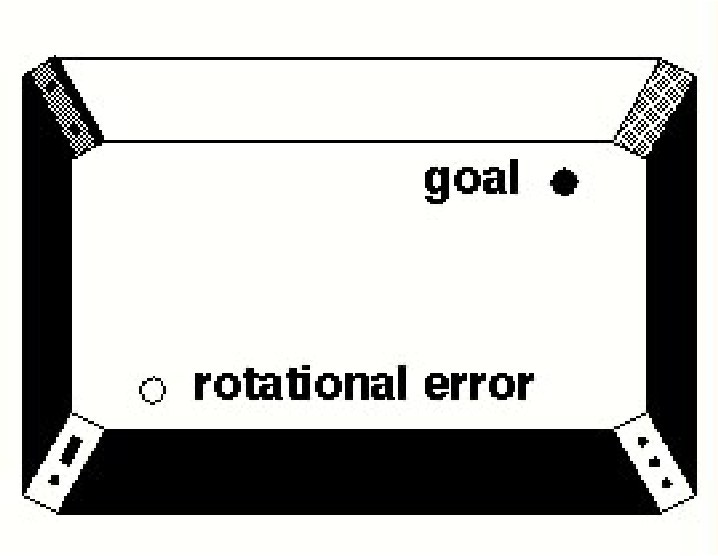


Fig.3: The scheme of experimental box used by Cheng. The panels in the corners were differentiated by visual appearance and by odor. The rotational error marked the locations geometrically identical with the position of goal, only rotated by 180°, and differing by local cues. (Figure from Cheng, 1986)

Rats performed high rate searching in the diagonal position in spite of presence of many local marked cues (both visual and odor). These findings suggest that rats in these conditions reoriented by using environmental shape and ignored non-geometrical cues.

The conclusion that the rats were able to use geometrical cues was confirmed by experiments of Margules and Gallistel (1988), when non-geometric cues were not available at all, and rats searched in the two geometrically appropriate positions with equal frequency.

Analogous results obtained Biegler and Morris (1993) who trained rats to find food in a square enclosure. After disorientation procedure the rats were not able to find the correct location even when it was marked by distinguishable non-geometric cues.

Importance of geometric information for reorientation could be adaptive in nature, where the macroscopic shape of environment provides stable information, whereas particular beacons could often vary, for example by seasonal changes.

Hermer and Spelke (1994, 1996) carried out a series of experiments with experimental paradigm previously developed by Cheng (1986). They used this experimental design to test cognition of children and adult humans.

Both children and adults were supposed to search for an object hidden in one of the corners of a rectangular room. They would see as the object was hidden and than they were disoriented.

Firstly, they were tested in a rectangular room with all walls white and with no distinguishable non-geometric cues. Both children and adults could reorient themselves in these conditions according to the shape of environment – similarly as the rats in Cheng's experiments, they searched preferably in the correct corner and in the corner geometrically identical.

When the subjects received in similar training also a non-geometric cue (bright blue piece of fabric attached to one of the shorter wall), the adults integrated both geometric and non-geometric information to reorient in the room – they searched only at the correct location.

It was interesting that when they were interviewed, most of adults were aware of non-geometric cue as a mechanism underlying their behavior, but only one mentioned spontaneously the shape of environment. It could suggest that (at least under such conditions) the encoding of the shape of the environment is not as conscious process as those involving non-geometric cues.

On contrast, children (ranging in age from 18 to 24 months) failed to use non-geometric cues at all, and similarly as rats they maintained searching both in correct and rotated locations.

The failure was probably not caused by a lack of motivation, attention or understanding the task, because the children successfully used the geometric cues. To test the motivation the authors used different non-geometrical cues, which were supposed to be for children more interesting (large toy track and large toy bear). However, even under these conditions the children could not use non-geometric information for reorientation in the room.

In the following test, children searched for an object hidden inside one of two triangular boxes identical in shape but differing in color, texture and pattern. The children were divided into two groups: (1) the first group was disoriented between hiding an object and the test, similarly as in previous conditions ("reorientation task"), (2) in the second group, the children's eyes were covered between hiding and the test, and the child did not undergo disorientation procedure. Instead of it, only the boxes were moved ("find-the-object task").

If the children had a general problem to attend or remember the non-geometric cues, both groups should fail. On contrast, if the children had a problem to reorient themselves in the environment according to non-geometric information, then only the first group should fail. The results indeed showed that only "disoriented" group failed to reorient in the task and used only geometric cues. On contrast, the children who were not disoriented could represent and remember non-geometric properties. Obviously, the children could use non-geometric cues to find removed object, but they did not use these cues to reorient themselves in the stable environment. The following test proved that the failure was not caused only by a distraction during disorientation procedure.

In the next task both groups of children (involving disorientation process and without disorientation) were tested in the two different conditions. In the room were two boxes differing in colors, the toy was hidden in one of them. On concordant trials the boxes were shifted diagonally (rotation transformation of the room), thus the geometric and non-geometric information were concordant. On conflict trials the boxes were moved directly across the room to the far but adjacent corners, thus the geometrical and non-geometrical information were in conflict. Both disoriented and oriented children searched at the correct location in concordant task. On conflict trials, in which geometric and non-geometric information specified different locations, disoriented subjects searched according to the geometric cues (shape of the room), whereas oriented subjects searched according to the non-geometric cues (color and the pattern of the boxes).

These results were confirmed by experiments of Lourenco and colleagues (Lourenco and Huttenlocher, 2006; Lourenco et al., 2005) who tested 18- to 25-month-old children in two disorientation tasks involving either subject- or space-rotation. The performance was significantly better in the space-movement task. It suggested that performance was better from inside the space than from outside.

The results of Hermer and Spelke's experiments indicate that there exists in children a task-specific system for reorientation and re-establishing the sense of position and heading. This suggests that distinct processes could underlie performance in space and object memory tasks.

Hermer and Spelke suggested that children are predisposed to use geometric information to reorient themselves in a closed environment. They proposed that children's reorientation depends on "geometric module", what is task-specified and encapsulated cognitive ability to represent the geometric properties of the environment. According to the results of the experiments, humans share the mechanism to re-establish their position and heading with other mammals. The term "module" came from Fodor's proposition (1983), that the brain contains domain-specific systems for particular function.

In contrast to children, adults performed better and they were able to compose geometric and non-geometric information. There could be two possible explanations: (1) the reorientation process could become more flexible and enable integration of both spatial and non-spatial cues, or (2) the original geometric processes could persist over development, but new process could appear.

Hermer-Vazquez et al. (1999) used dual-task paradigm to investigate which processes could interfere with reorientation mechanism. Subjects could reorient themselves precisely when they did not perform secondary task, whereas they had similar results as children and adult rats when they were engaged in verbal shadowing of continuous speech. When the subjects were exposed to nonverbal shadowing (continuous rhythm), they reorient similarly as non-shadowing subject. This suggests that interference effect was not caused by general limits of working memory or attention but by processes more specific to language. The verbally shadowing subjects successfully learnt both geometric and non-geometric cues, but they failed to combine these cues together to find a position of an object.

The authors thus proposed that the ability to combine such information into integrated representation depends on natural language.

Later, Hermer-Vazquez et al. (2001) studied the developmental changes in children, which result in more complex and flexible adult-like performance in reorientation task. They suggested that the behavior (dependence on geometric cues versus ability to combine geometric and non-geometric cues) changes between 5 and 7 years. They revealed that languages production abilities correlate with more flexible reorientation and with more flexible searching in moving object search task.

In combination with previous findings, authors suggest that language skills play a key role in the ability to construct novel representations flexibly.

However, recent data from primates suggest that language is not essential to integrate geometric and non-geometric information to form complex representation of an environment. Gouteux et al. (2001) trained Rhesus monkeys (*Macaca mulata*) to find a food reward in a rectangular room with distinctive non-geometrical cues. The results showed that the monkeys were able not only to use global geometry of the room to reorient, but that they used also non-geometric information (colored wall).

Learmonth et al. (2001) replicated the experiments of Hermer and Spelke (1994, 1996) and changed some parameters to find out whether a theory of "geometric module" is really plausible. Hermer and Spelke used landmarks that could not been perceived as immovable, whereas Learmonth and colleagues used landmarks that were invariant (door, big bookcase). The children mastered the task when two landmarks were used, but also the task with only one landmark. In such situation, children had to use "left-right" information.

In both cases, the children visited significantly more often correct corner than the corner geometrically identical. These results proved that under certain circumstances even children under the age of 2 years could use local landmarks as well as geometric information to re-orient themselves and to find a hidden object.

The correct using of left-right orientation and non-geometric cues before the language skills developed in children also demonstrated the independence of ability to combine geometrical and non-geometrical cues on languages skills.

The main difference was that Learmonth and colleagues used landmarks, which children perceived as invariant and permanent. By contrast, in Hermer and Spelke's studies the landmarks were movable and sometimes the children could even play with them. Laermonth et al. also used the bigger experimental room (12 x 8 feets) then previously Hermer and Spelke (6 x 4 feets).

It seems that the size of the room can also affect the children's performance: the children were able to combine geometrical and non-geometrical information to reorient themselves in large but not in small spaces.

Similar results were obtained also in experiments with animals. Vallortigara et al. (2005) tested chickens in the re-orientation task in a small or large rectangular enclosure containing also non-geometric cues. They found that the chicks were able to combine geometric and non-geometric information to reorient themselves in both the large and the small enclosure. They were also able to reorient immediately after displacement from a large to a small enclosure and vice versa, what suggested that they used the relative metrics of the environment. However, when the chicks were tested after affine transformation of environment (transformation, which altered the geometric relations between the goal and the shape of the environment), the chickens made more errors based on geometric information in the small than in the large enclosure.

In the following experiments Sovrano and Vallortigara (2006) trained young chickens to find food in a corner of a small or a large rectangular enclosure with a distinctive landmark (a blue wall). The chickens were disoriented and tested after displacement of the cue to an adjacent wall. In the large enclosure, chickens chose the corner that maintain the correct arrangement of the non-geometric cue with respect to geometric sense (i.e. right-left position), whereas in the small enclosure, they chose the corner that maintained the correct metrical arrangement of the walls with respect to sense.

Sovrano et al. (2005) demonstrated the ability of fish to reorient both in a small and a large enclosure even immediately after dislocation from a large space to a small and vice versa. However, fish made relatively more errors according to geometric information when they were moved from a small to a large space, and relatively more errors according to non-geometric information when they were moved from a large to a small space.

Consecutively (Sovrano et al., 2006), the fish were trained to reorient and find a corner in a rectangular tank with one blue wall. After the landmark was replaced to an adjacent wall, the fish in the large enclosure preferred the two corners with the non-geometric landmark and also tended to choose the one that maintained the correct arrangement of the non-geometric cue with respect to geometric sense. On contrast, in the small enclosure, the fish chose both the corners with non-geometric cues and also the corner without feature, but maintaining the correct geometric sense.

Sovrano et al. (2002) repeatedly proved the ability of fish (*Xenotoca eiseni*) to reorient in tasks similar to those presented to rats (Cheng, 1986) and humans (Hermer and Spelke, 1994, 1996). In ability to combine geometric and non-geometric information, fish under certain conditions even surpassed rats and children. This demonstrated that this ability is evolutionary ancient and that it depends more on environmental demands and on ecological adaptation of particular specie than on phylogenetic complexity.

The previous experiments demonstrated the ability of various species to perceive geometric relation of closed environment (experimental enclosure of room).

In the following text I will review a series of experiments testing the ability of mammals and birds to abstract geometric characteristics of the close enclosure. In these experiments a shape or a size of the close environment were manipulated.

Tommasi at al. (1997) trained chickens *(Gallus gallus domesticus)* to find a food hidden under sawdust in the center of a closed enclosure. After the training phase, the birds were tested in the enclosures of different shapes or sizes.

They were tested in a circular, triangular (both equilateral and isosceles) and rectangular-shaped arena.

During training the chickens learnt properly to find food in the center of the square-shaped enclosure. They maintained this behavior also when they were placed in a circular or equilateral triangle-shaped arena. In the isosceles triangle-shaped arena the three possible mathematical centers could be computed (the geometric center, the gravity center of the vertices, the intersection of bisectors). The results indicated that the chickens searched preferably in the gravity center.

In all mentioned cases, the birds clearly searched in a limited central area. However, when they were tested in the rectangular-shaped arena (obtained by doubling the original square-shaped arena), the chickens performed more diffuse searching. The searching was concentrated along the main axis, with three focuses. Birds searched (1) around the centers of one of two (left or right) square-halves, corresponding with the original enclosure, or (2) around the true geometrical center of the rectangular arena (Fig.4).

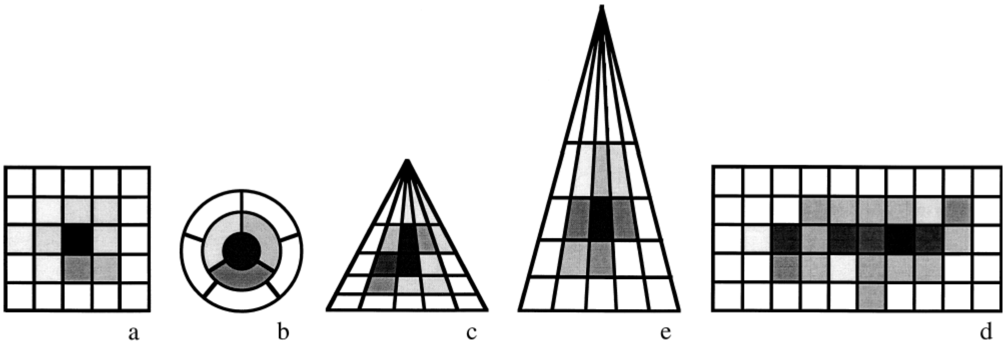


Fig.4: Results of the shape-transformation experiment. First, the chickens were trained to search a center in a square-shaped arena (a) and then they were tested in the enclosures of different shapes (b-d). The darker a cell, the more searching chickens performed in that area. Chickens performed good transfer to all testing enclosures, except to the rectangular-shaped arena. (Figure adopted from Tommasi et al., 1997)

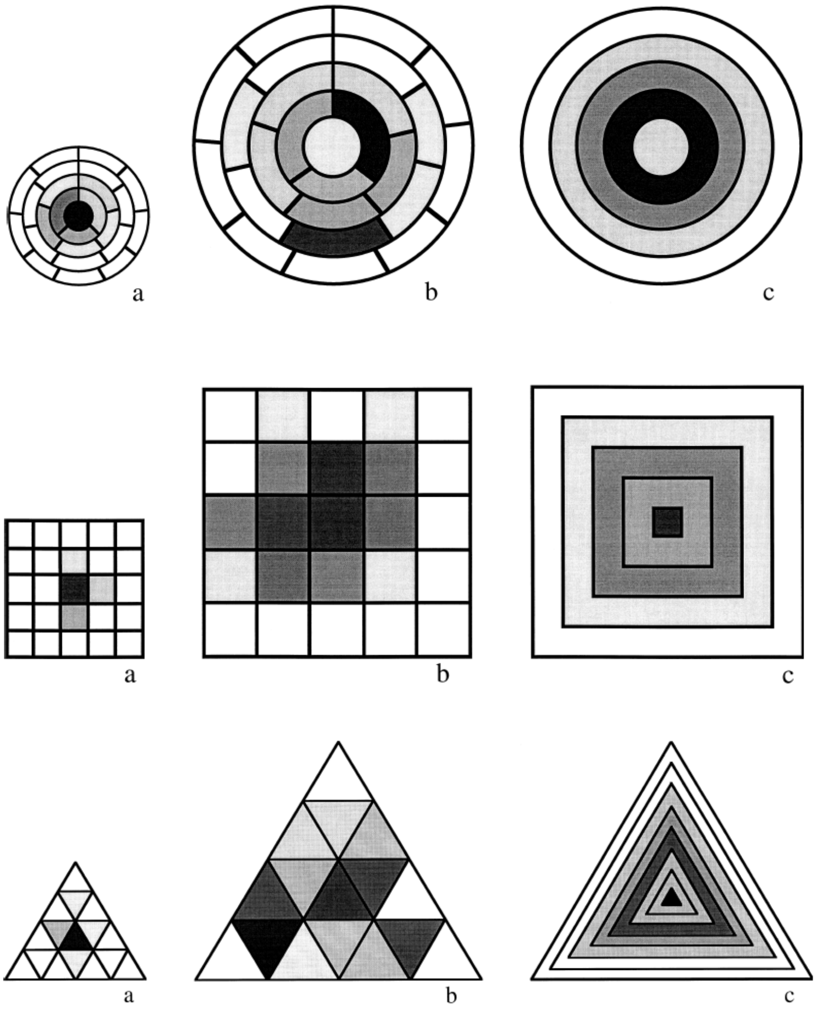


Fig.5: Results of the size-transformation experiment. When searching in the larger circular arena, the chicks searched at a distance from the walls, which was midway between the centers of the smaller (training) and of the larger (testing) enclosures. In both the square-shaped and triangular enclosure the birds searched partly in the center of the testing arena, partly in the distance from the walls corresponding to that of the center of the smaller (training) arena. (Figures adopted from Tommasi et al., 1997)

It seems that size-transformation was for chickens more confusing. When the birds were trained in a square- or triangle-shaped enclosure and then they were tested in the arena of the same shape but larger size, they searched at two different distances from the wall of the arena. One corresponded to the correct distance between the wall and the center in the small original enclosure; the other corresponded to the true center of the actual test arena.

On the other hand, when chickens had to search in the center of the enlarged circular arena, they searched in the wide area ranging from perimeters to center. When the animals' choices were counted in concentric annuli of the same width, it appeared that they searched mainly at a distance midway between the radius of the original small (training) and of the large (testing) enclosure.

In the square-shaped arena the chickens in the testing phase searched in two locations: partly in the center of the large (testing) arena, partly in the distance from the walls that corresponded to the distance between walls and the center of the smaller (training) arena. Similar results were obtained also in the triangular arena. (Fig.5)

The results proved that the chickens were able to use distances from the walls to localize the center. Results of the shape-transfer test suggested that birds could abstract information about geometric characteristics of the environment. The size-transfer experiments indicated that the chicks during the training learnt both the absolute and relative distances between the center and the walls. Apparently, identifiable cues as corners were required to compute the center, because the birds could not localize it in the enlarged circular arena.

In the following experiment Tommasi and Vallortigara (2000) tested chickens' ability to find a center in enclosures of similar shape but either a larger or a smaller than was the training enclosure.

When tested in the larger arena, the chickens searched in the two locations: (1) in the center of the novel testing arena and also (2) in the distinct area localized in a circle region in distance from the wall same as the distance from the walls to the center previously learned in the training arena (Fig.6).

When the chickens were tested in the arena smaller than was the training one, the searching was concentrated only in the central arena. The mean distances from the center did not differ between searching in the larger training and the smaller testing arena (Fig.7).

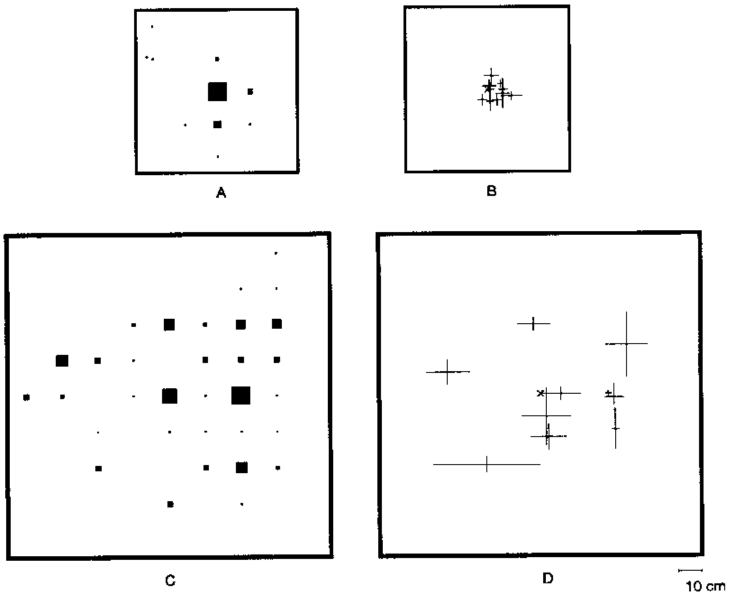


Fig.6: Results of the size-transformation test. The chickens were trained in the smaller arena and then tested in the large one. In graphs A and C the larger squares represent the more searching behavior in that location. In graph B and D each cross represents the location of peak searching for each individual with associated variability (SEM). The chicks in the testing session searched at the two locations: (1) center of the large arena and (2) location at the distance the same as was the distance between the walls and the center in the small training arena. (Figure adopted from Tommasi and Vallortigara 2000)

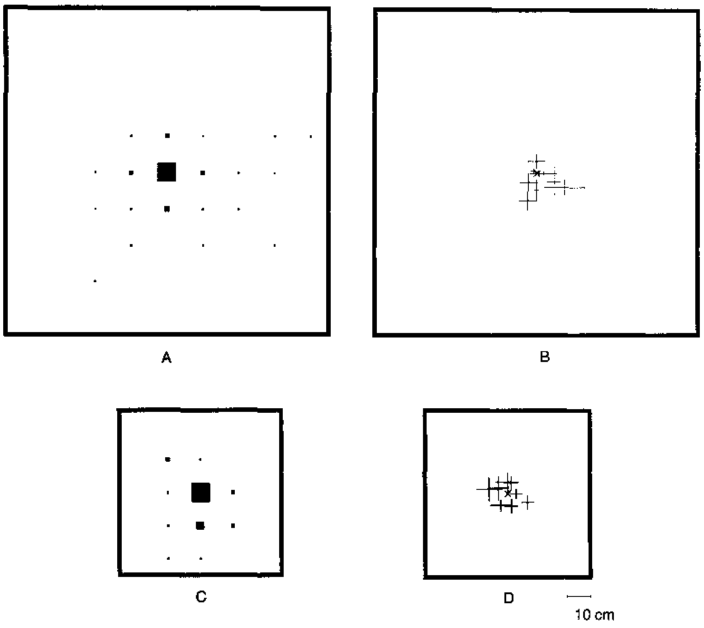


Fig.7: Results of the size-transformation test. The chickens were trained in the large arena and then tested in the smaller one. In graphs A and C the larger squares represent the more searching behavior in that location. In graph B and D each cross represents the location of peak searching for each individual with associated variability (SEM). The chicks in the test session searched precisely at the center of the novel arena. (Figure adopted from Tommasi and Vallortigara 2000)

In the described tasks no local non-geometric visual landmarks were available during the training to locate central position in the arena. Thus the chickens were forced to rely on the geometrical arrangements of the walls. In the following experiments researchers provided additional visual cues to find out whether the chicks would encode both the geometry of the space and non-geometric information.

Tommasi and Vallortigara (2001) studied whether encoding of geometric information (relative and absolute distances) and the encoding of prominent landmarks were identically represented and used by the two cerebral hemispheres of birds or whether the hemispheres are functionally different. These experiments should reveal the role of cerebral hemispheres in localization of the center of an enclosure in size-transformation test and in searching based (1) on geometric information (relational properties between distances in the enclosure) and (2) on local visual cues.

Because of special brain organization, birds offer an important model for the study of visual specialization: in birds' brain, there is decussation at the optic chiasma, thus the primary visual projections go mostly to contralateral hemisphere. It means that temporary eye patching caused that what is seen by left (or right) eye is processed by the contralateral right (or left) hemisphere (Rogers, 1995).

The chicks were first trained to locate binocularly a center in a square-shaped enclosure and then they were tested in the same enclosure with only one eye used. The results revealed that the chicks were able to precisely localize a center and that the inputs from both left and right eye seemed to be identically sufficient for neural system processing the geometric information.

The chickens were also tested in the size-transformation test, when they were trained in the enclosure of the standard size and than tested in either enlarged or reduced arena. The results confirmed previous findings that binocular chickens searched in the enlarged arena partly in the central position, partly at a distance from the center to the walls same as that in the training enclosure. On the other hand, when the chicks were tested using only left eye (input to the right hemisphere), they searched mainly in the central area, whereas when they were tested with only right eye open (input to the left hemisphere), chicks' searched pattern was distributed more peripherally.

When the chickens were tested binocularly in the smaller enclosure, they searched in the center and the same results were obtained when they were tested with only left eye in use. In contrast, when only their right eye was in use, search patterns were markedly scattered.

When the chicks were trained binocularly to localize the center of an enclosure in the presence of a centrally placed visual landmark, they encoded the geometry of the enclosure and thus they were able to localize the center binocularly even after removal of the landmark. When they were tested using only one eye (both left or right), chickens showed slightly wider dispersion but they still searched centrally. This dispersion could have been also caused by the disturbance during the manipulation during eye-patching.

However, when the chicks were binocularly trained with the landmark at the central position and then tested with only one eye in use and with the landmark shifted from the center to a corner of the enclosure, the differences between the brain hemispheres emerged. When the chickens were tested only with left eye opened they searched at the central position, even better than binocularly. In contrast, with only right eye in use, they searched exclusively near the local landmark. (Fig.8)

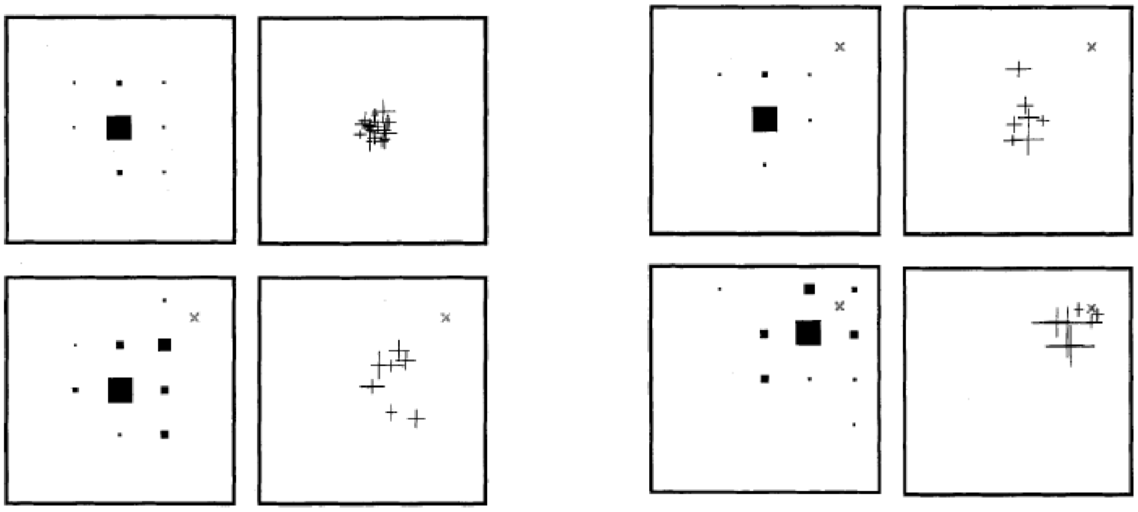


Fig.8: Results of the experiment with translocation of the visual landmark. Results of the last training session – the chick searched binocularly and the visual landmark was situated at the central position (first row, left). Results of the test sessions: the landmark removed to the corner (indicated by a gray cross) in binocular (second row, left), left-eyed (first row, right), and right-eyed (second row, right) birds. In graphs in the left columns the larger squares represent the more searching behavior in that location. In graphs in the right columns each cross represents the location of peak searching for each individual with associated variability (SEM). (Figure adopted from Tommasi and Vallortigara 2001)

The results of these experiments (Tommasi and Valllortigara, 2001) suggest that the chickens encode different aspects of the environment differently in the cerebral hemispheres: it seems that the left hemisphere favors the use of absolute distances, whereas the right hemisphere prefers the use of relative distances.

Tommasi and Vallortigara (2004) carried out other tests studying sexual differences in different aspects of encoding of space and of lateratisation of the brain.

The tests confirmed sex differences in lateralisation of cognitive functions. Sex effects did not seem to modify basic pattern of hemispheric specialization when the chicks should search using only one eye in the same arena as in the training. However, the differences appeared when the presented geometric and non-geometric information about environment were conflicted: After displacement of the central landmark to the corner, left-eyed females searched only in the center, whereas left-eyed males search both in the center and also close to the landmark. This suggests that right-hemispheric specialization to attend geometric information is stronger in females than in male birds. On the other hand, right-eyed males searched only close to the landmark, whereas right-eyed females seemed to search more dispersedly at the location between the center and a new position of the landmark. This indicates that left-hemispheric specialization to attend local cues is stronger in male chickens than in females.

The clear difference between male and female chicks in using information about environment emerged when the original landmark was removed from the center of the arena and replaced by a novel landmark of different color. Under these conditions right-eyed males searched closer to the original landmark in the wrong position, whereas right-eyed females searched at the center, close to the novel landmark.

These results could indicate that also the left hemisphere in female could have control over geometric information, whereas in males could exist stronger asymmetry between hemispheres. This is in congruence with some studies concerning the lateralisation of cognitive function carried out in human.

The results of the experiments (Tommasi and Vallortigara, 2001, 2004) confirmed the previous findings that right hemisphere predominantly attend to global, geometric information provided by an enclosure, whereas functions of left hemisphere mainly depend on local cues provided by landmarks.

Recently, similar results were also found in experiments (Vallortigara et al., 2004) designed similarly as those that carried out Hermer and Spelke (1994, 1996). Chickens were binocularly trained in a closed rectangular arena (providing geometric information) with distinguishable panels at the corners (providing non-geometric information). The chickens were passively disoriented between trials. When the chickens were tested after the removal panels, left-eyed chickens, contrary to right-eyed chicks, reoriented using the geometric information. When they were tested after change of geometric information (in a square-shaped cage), both right and left-eyed chickens reoriented according to non-geometric information provided by landmarks. The left-eyed chickens also reoriented better when they were previously trained binocularly only with geometric cues. Moreover, when geometric and non-geometric information were conflicted, left-eyed chickens relied more on geometric cues, whereas right-eyed chickens relied more on non-geometric cues.

The results imply the avian brain has separate mechanisms for processing of geometric and non-geometric aspects of the environment.

It seems that the asymmetry in processing of geometric information is localized mainly at the hippocampal level. Tommasi et al. (2003) trained chickens with unilateral or bilateral hippocampal lesion to find a center of a square shaped arena, with a landmark presented at the center during the training. The results showed that the chicks were able to localize a central position in an enclosure with landmark presented at the center even without the hippocampus.

When the chickens were tested after removal of the landmark, intact chickens still searched at the center. Chicks with bilateral lesions or with lesion of the right hippocampus were in absence of the local landmark totally disoriented. On the other hand, the chicks with lesion of the left hippocamus were completely unaffected – they searched at the center.

When tested with the landmark shifted from the center of the enclosure to the corner, intact chickens ignored the landmark and searched at the center, whereas chicks with bilateral lesion to the hippocampus searched near the landmark. The results of chickens with lesion to the right hippocampus were similar to those of chickens with bilateral lesion, whereas the chicks with lesion to the left hippocampus showed some memory of the central position. (Fig.9)

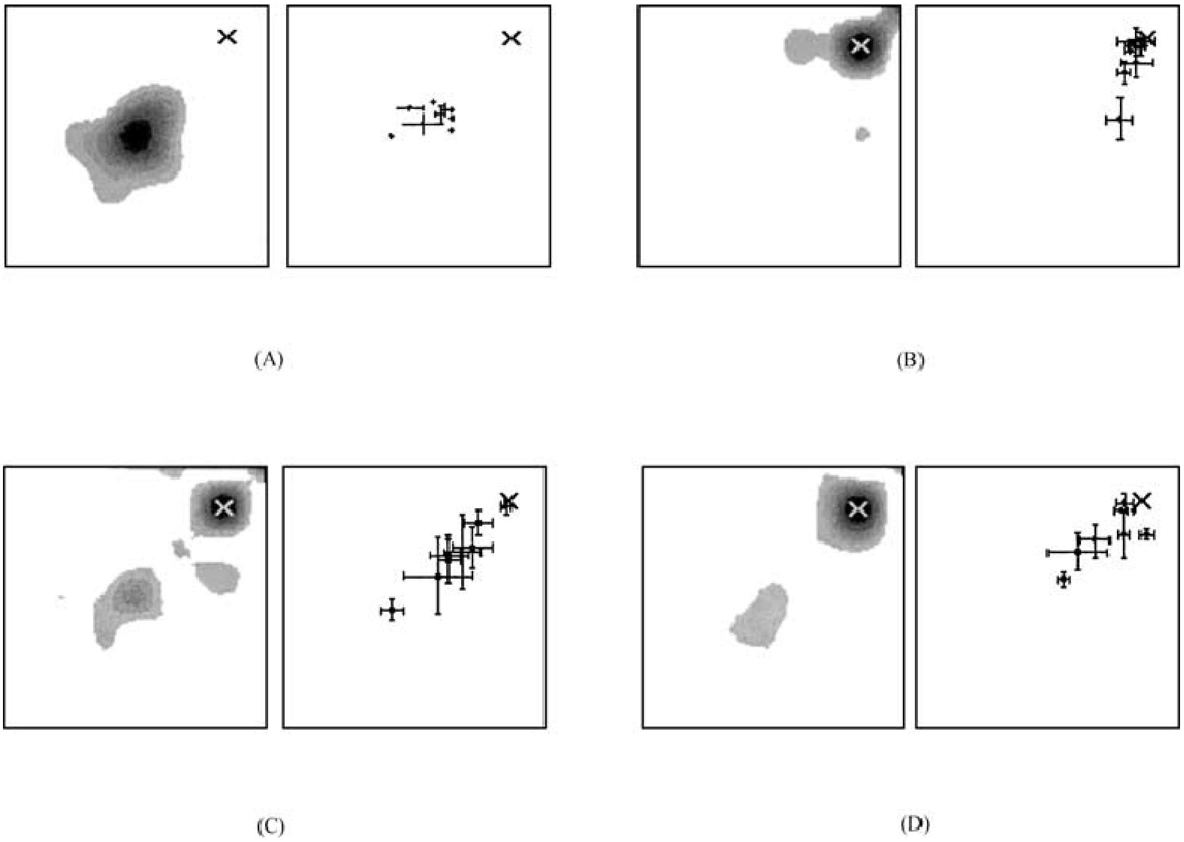


Fig.9: Results of searching after displacement of the local landmark. Intact chickens maintained searching at the center (A); chickens with bilateral lesion searched close to the shifted landmark (B); chickens with the unilateral left-side lesion showed less clear results, but they displayed some memory for the center (C); chickens with the unilateral right-side lesion preferred searching close to the landmark (D). (Figure adopted from Tommasiet al., 2003)

This experiment suggests that encoding of geometric features of the environment occurs in the right hippocampus, whereas the information about local cues seems to occur outside the hippocampus.

It is obvious that the birds demonstrated the ability to locate the central position of the enclosure based on the information about global geometry of this environment. Recently, Tommasi and Thinus-Blanc (2004) used similar tasks to assess this ability also in rats.

Rats were trained to search for food in a center of a square-shaped enclosure. The shape of the arena provided geometric information about environment. The rats were subsequently tested in enclosures of different shapes to test whether they were able to generalize geometric relationships of the environment.

During the training, the rats learnt to find precisely the center of the square-shaped arena. Despite the innate tendency of rats to spend a large amount of time near the walls (thigmotaxis), they performed rapid excursions to the center and than back.

When the rats were tested in a novel rectangular-shaped test enclosure, they were able to search correctly for the center and the similar results were obtained in an equilateral triangle-shaped enclosure. In an enlarged square-shaped enclosure the result was slightly different: rats searched mostly in the central region, but some rats searched also in the center of one of the four quadrants composing the large enclosure, which had the same size as the training arena. (Fig.10)

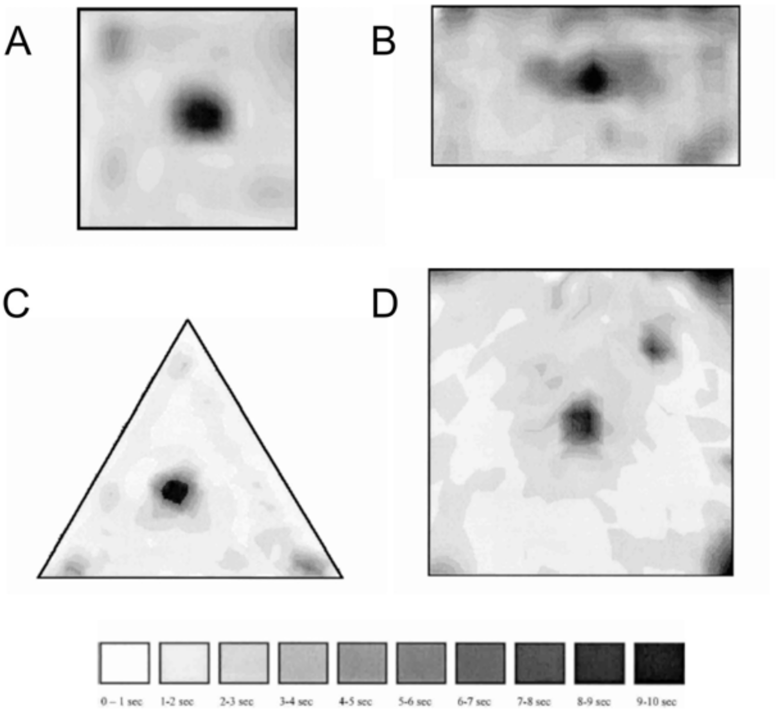


Fig.10: Overall distribution of the average time spent in the enclosure of different shapes: square-shaped training arena (A), rectangular arena (B), triangle arena (C), enlarged square-shaped arena (D). (Figures adopted from Tommasi and Thinus-Blanc, 2004)

These experiments suggest that rats are able to learn to localize the central position of an enclosure and transfer this ability to novel enclosures, which differed in the shape or in the size.

The comparison with analogous data from similar experiments with birds (Tommasi et al., 1997, Tommasi and Vallortigara, 2000) suggests stronger reliance on geometric cues in rats than in birds.

However, the chosen cognitive strategy (reliance on geometric or non-geometric information) could depend more on experimental design then on difference between species.

Looking for neuroanatomical substrate of the ability to orient according to the geometric features of the environment, Tommasi and Save (2005) trained the rats bilaterally lesioned to the hippocampus to search for a center in different enclosures.

At first, the rats were trained in a square-shaped enclosure and then they were tested whether they were able to transfer this ability to enclosures of different shapes. After this, half of the rats were bilaterally lesioned to the hippocampus and then the test was repeated.

The results demonstrated that even the rats with bilateral hippocampal lesion were able to find a center of the square-shaped arena after the training. However, they failed in the shape-transformation test, when they should transfer the ability to find the central position to the enclosures of different shapes. (Fig.11)

This suggests that the hippocampus plays a relevant role in orientation based on geometry of the environment.

This finding is also supported by the results of previous experiments of O'Keefe and Nadel (1996). They found that the environmental features as was size or shape of experimental enclosure could control place fields of hippocampal place cells of rats. The activity of place cells was recorded while the rats were foraging for food in four types of enclosures: a small square, a large square, a horizontal rectangle and a vertical rectangle.

It seems that the main determinant of shape and location of the place fields was the distance from two or more walls of the enclosure.

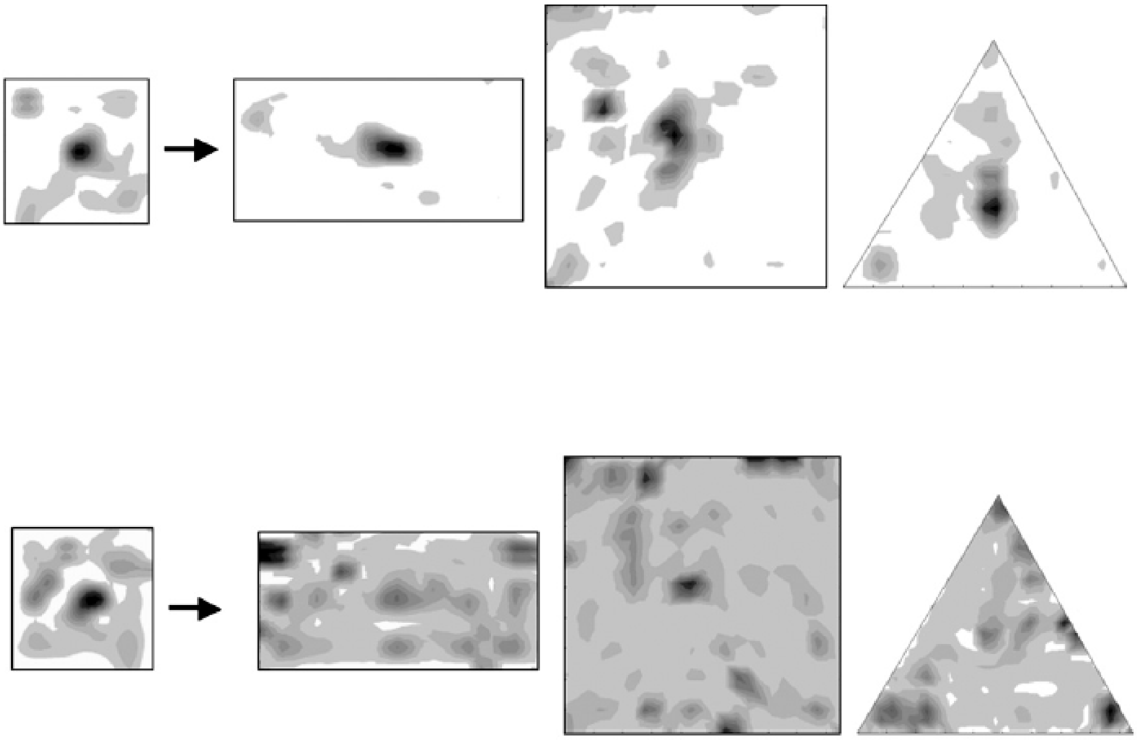


Fig.11: The first row shows the results of intact rats. The second row shows the result of rats with bilateral hippocampal lesion. The figures demonstrate that the lesioned rats did significantly worse than the control. They were able to find only the center in the square-shaped enclosure. (Figures from Tommasi and Save, 2005)

The results of reviewed experiments show that in an environment defined by an array of discrete landmarks localization of a center appears to be often controlled by distance and bearings from single landmarks; on the other hand, in an environment defined as a closed arena, the searching depended more on a global geometry of the arena.

These findings were also supported by Skov-Rackette and Shettleworth (2005), who trained rats in an arena with an array of objects. They showed that rats encode differently the object array and the shape of enclosure.

For orientation in a space animals used different strategies as dead reckoning, perception of single beacons or encoding relative positions and directions of multiple landmarks.

It depends on many factors which strategy would be preferred in particular situations: animal species, used training, configuration of environment, previous experience of subject or its ontogenetic stage.

However, it is obvious that under certain conditions animals proved ability to encode configuration of multiple objects and with appropriate training they are able to abstract geometric rules about space.

This ability is fundamental for our experiments – we trained animals to choose specific position in the real space according to the configuration of abstract stimuli. Therefore animals had to perceive the configuration of stimuli presented on the computer screen and then to transform the relations of virtual stimuli to the real space.

AIMS OF THE DISSERTATION

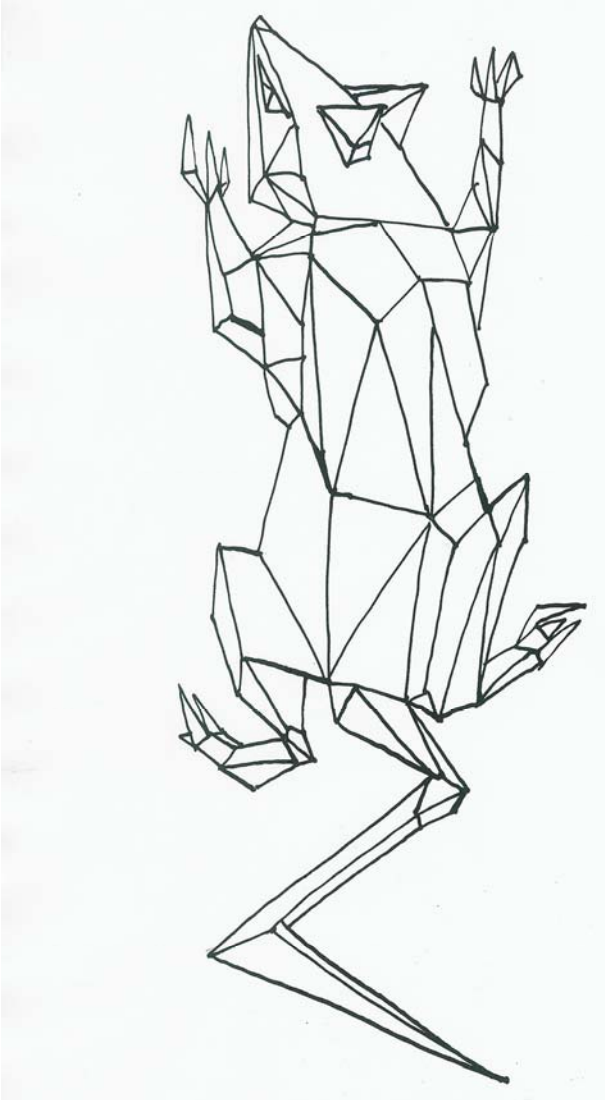
Spatial cognition is a widely studied subject for neurosciences, ethology, cognitive sciences and behavioral ecology. Recently, many researches concern animals' capacity to encode the geometry of the space, e.g. relative positions of multiple landmarks and a goal in a space or a global shape of an environment.

In my thesis I focus first on animals' ability to process configuration of visual stimuli presented on a computer screen. In further experiments I concentrate on the ability of animals to orient in one spatial frame (real response space) according to information from another spatial frame (computer screen).

The aims of my thesis were:

- To develop appropriate behavioral tests in which the operant behavior (either non-spatial or spatial) is controlled by visual stimuli presented on a computer screen.
- To find out whether rats are able to perceive and to discriminate configuration of visual stimuli presented on a computer screen.
- To study whether rats are able to make spatial choices in the real environment based on the abstract visual stimuli.
- To find out whether rats process configuration-stimuli as simple geometric patterns or whether they perceive their spatial/configuration component.
- To compare performance of these behavioral tasks in different animal species.

SUMMARY OF THE EXPERIMENTS



EXPERIMENT I

Operant behavior of the rat can be controlled by the configuration of objects in an animated scene displayed on a computer screen

In the first presented experiment (Nekovarova and Klement, 2006) we trained the rats to distinguish the visual stimuli displayed on a computer screen. We used modified Skinner box with open front wall. The box contained a lever and a feeder. In front of the box, there was a computer monitor for presenting the visual stimuli. The 36 cm wide and 90 cm deep gap between the box and the computer screen prevented the rats from escaping (Fig.12; A scheme of the experiment: Fig.1 in Nekovarova and Klement, 2006).

Lever pressing was rewarded by delivering of pellets into feeder only during the time-intervals when the “rewarded stimulus” was presented on the screen.

During the session, three time-intervals were alternated in a complex sequence: 20-sec and 40-sec “non-rewarded intervals” (lever pressing were not rewarded and “non-rewarded stimulus” was presented on the screen) and 10-sec “rewarded intervals” (lever pressing was rewarded and “rewarded stimulus was displayed).

The rats were trained in the three successive phases.

In the first phase of the experiment the first group of rats (group L; n = 5) was trained to discriminate between rewarded bright stimulus and a dark screen (brightness-discrimination task). The second group (group T; n= 5) was used as a control and the rats were trained with the same time schedule of reinforcement as the rats from the group L, but with no visual stimuli presented on the computer screen.

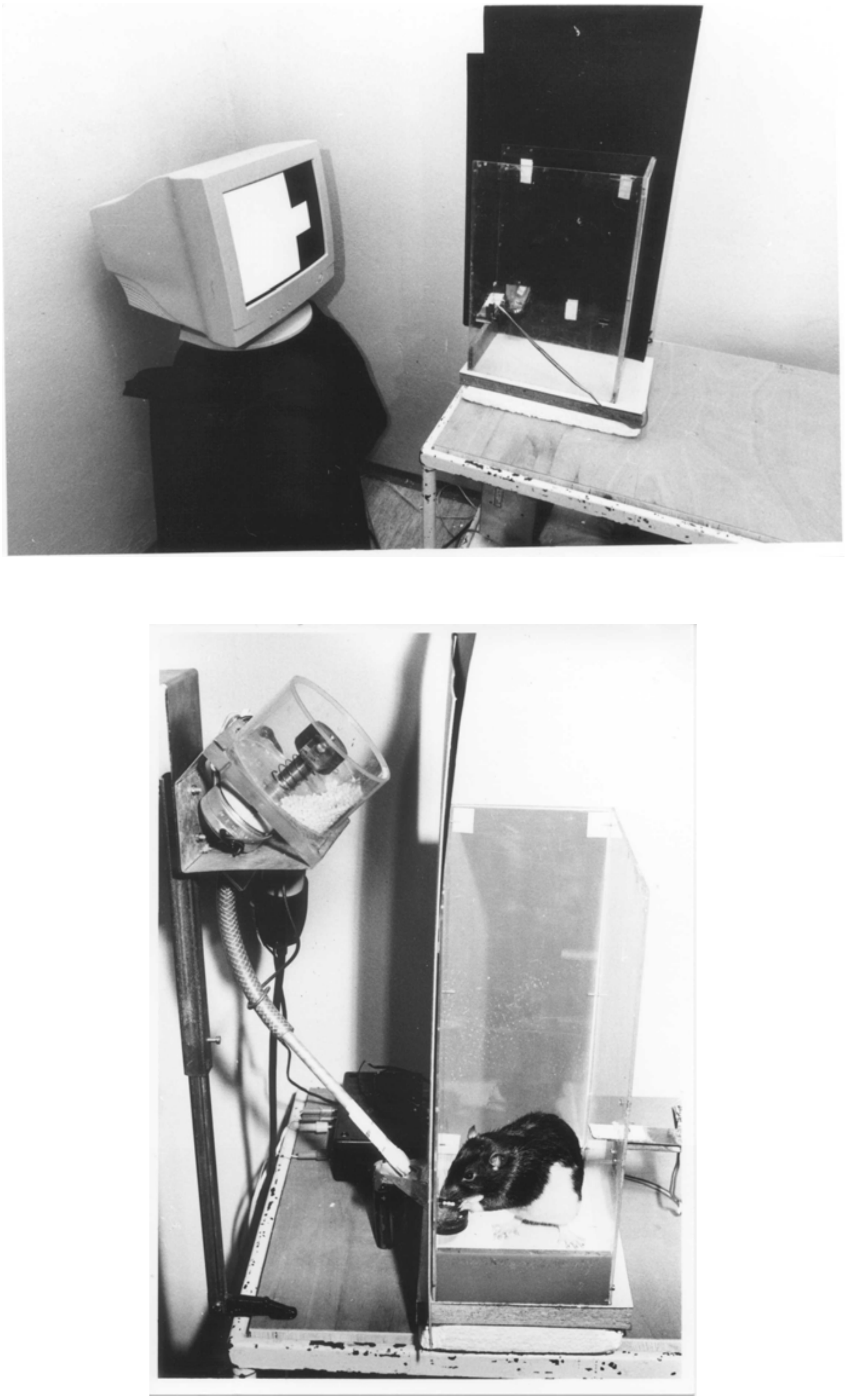


Fig.12: The apparatus used in Experiment 1 (Nekovarova and Klement, 2006). The apparatus consisted of a Skinner box with a lever and a feeder, and of a computer screen placed in front of the box. Correct operant responses were rewarded by delivery of pellets to the feeder.

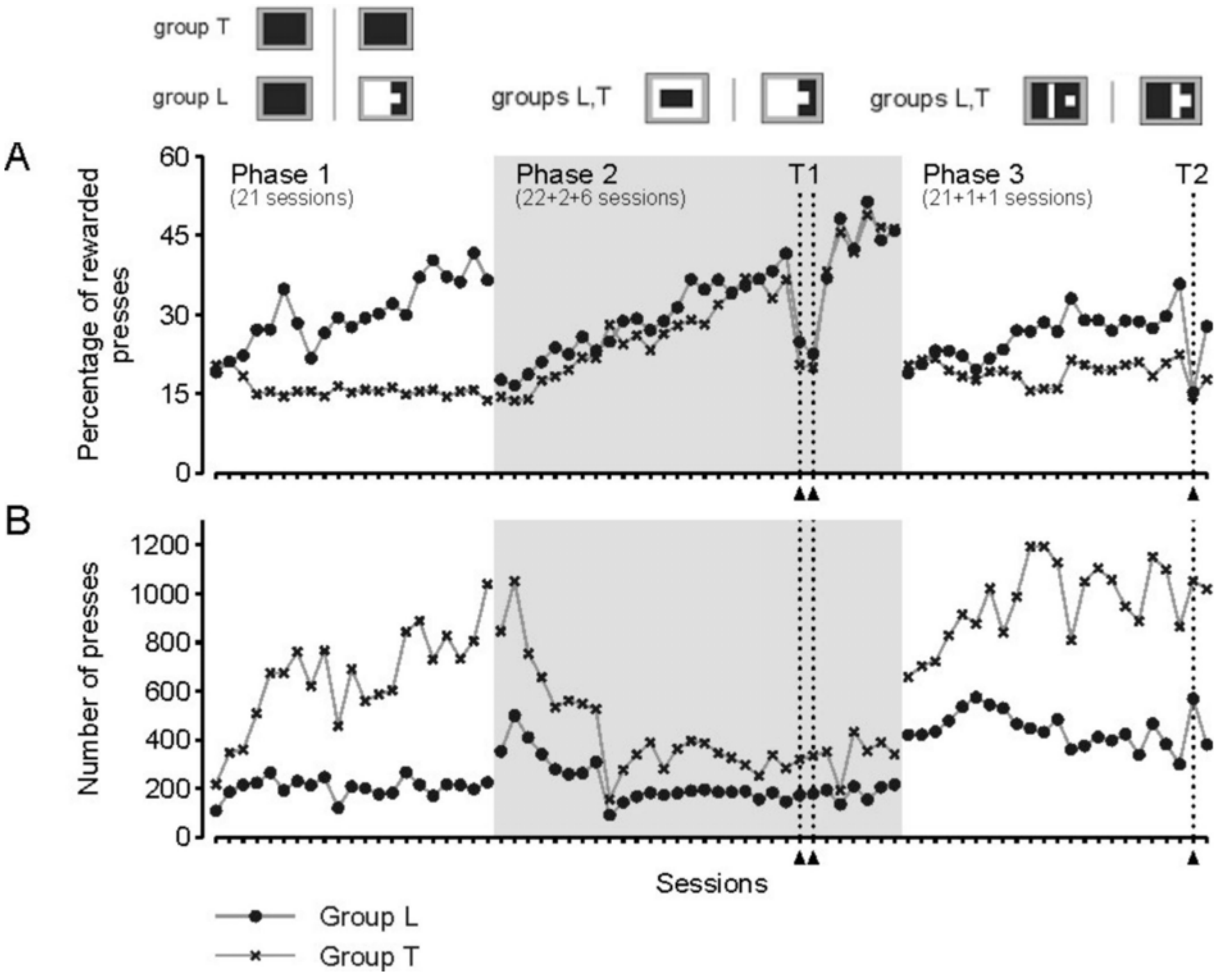


Fig.13: A: The percentage of the rewarded responses (efficiency - the ratio of correct responses to the number of all responses) per session.

B: The number of all responses per session during the whole experiment.

During the test sessions (T1, T2) the same novel stimulus was displayed during both non-rewarded and rewarded intervals. These sessions were used as a control whether the rats were able to use any other cues than visual information.

Pictures above the graphs show screenshots of rewarded (right) and non-rewarded (left) patterns in particular phases. In Phase 1 group L was trained to discriminate brightness, group T was trained to respond without any visual stimuli on the screen; in Phase 2 both groups of rats were trained to discriminate patterns, in Phase 3 both groups were trained to recognize mutual configuration of moving and stationary objects.

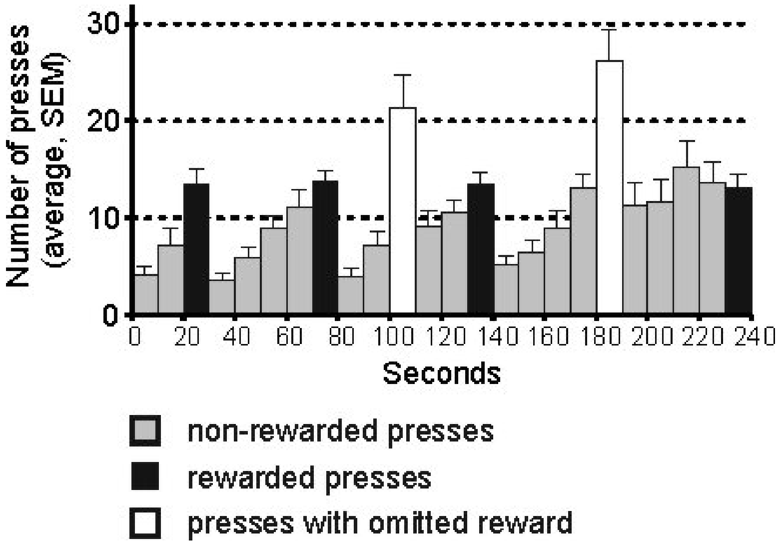


Fig.14: The histogram of lever pressing during the test session with modified rewarded intervals.

One session consisted of ten “hypercycles” (periodically repeating sequences of rewarded and non-rewarded time intervals). One hypercycle consisted of three 20-sec and three 40-sec non-rewarded time intervals (gray columns) and of six 10-sec rewarded time intervals (black columns).

In the test session, the rewarded stimulus was displayed during the appropriate rewarded intervals, but in two of them the lever pressing was not rewarded (white columns). The graph shows that the number of lever-presses during these modified intervals was significantly higher than in both non-rewarded and in standard rewarded intervals.

In the second phase of the experiment, both groups of rats were trained in the same way to discriminate between two different patterns of the same brightness presented on the computer screen. Control sessions, when no visual stimuli were displayed on the screen, were carried out at the end of Phase 2. These sessions could prove whether the rats’ operant responses depend on visual stimuli on the screen, or whether the rats used another cognitive strategy (for example timing).

In the third phase, both groups were trained with the same visual stimuli: there was a vertical strip moving across the computer screen and a stationary square in the right third of the screen. When the moving object touched the stationary square, it stopped and this configuration was rewarded. At the end of this phase a control session without visual stimuli displayed was carried out.

The result of the first phase showed that the first group (group L) using the visual stimuli gradually learnt to discriminate between the bright pattern and a dark screen. On contrast, the second group (group T) had no visual stimuli and thus the rats had to use only a time-discrimination strategy to solve the task.

The time schedule of the experiments did not allow the effective time strategy, thus the group T was significantly worse than group L and its efficiency (the ratio of correct and all responses) did not change during the whole Phase 1 (Fig.13).

There was also significant difference between groups in the number of all operant responses: group T emitted significantly higher number of lever presses than group L (Fig.13).

In Phase 2, when both groups were trained in the same way, the rats reached the similar level of efficiency. All rats learnt gradually to discriminate between two patterns presented on the computer screen. There was no difference between group L and T in efficiency, but the difference in the number of all presses remained.

In the control sessions, when no visual stimuli were displayed, the percentage of the correct responses decreased significantly to the level of random presses, same as the level of efficiency of group T in the first phase (control) (Fig.13).

The ability of rats to recognize patterns was also demonstrated in the control session at the end of Phase 2. In this session we modified rewarded time intervals. During these modified intervals, the rewarded stimulus was displayed on the screen, but the lever pressing during these intervals was not rewarded. The rats could possibly emit responses randomly or according to the timing strategy (variable interval schedule) and increased the number of responses after the first rewarded response. The results showed that the number of lever presses in the modified time-intervals were even higher than in the standard rewarded intervals. It proved that the operant behavior was controlled by the visual stimuli and not by the information about previous response (Fig.14).

During the third phase of experiment, when the vertical strip was moving across the screen, the percentage of rewarded responses decreased contrary to the previous phase. This was caused by a higher number of emitted responses during the non-rewarded time intervals, when the strip was approaching the stationary object (Fig.13).

The results of this experiment proved that rats were able to discriminate configuration of objects presented on the computer screen.

EXPERIMENT II

Spatial decisions in rats based on the geometry of computer-generated patterns

In the next experiment (Nekovarova and Bures, 2006) we tested whether the rats were able to make spatial decisions in a real space based on the abstract visual stimuli presented on a computer screen.

We used group of 5 rats. The rats were placed in a Skinner box placed in front of a computer monitor serving for presentation of visual stimuli. In the transparent front wall of the box there were four nosing holes arranged in a rectangular matrix. The nosing holes were equipped by a photoelectric device, which registered nose poking in a particular hole. There was a 7-cm gap between the monitor and the Skinner box, where the mechanical arms could raise one of two dippers from a water reservoir placed under the apparatus. (Fig15; A scheme of the apparatus: Fig.1-A,B in Nekovarova and Bures, 2006)

The visual stimuli were displayed on the computer screen and a rat chose one of the nosing holes according to a displayed stimulus. When the rat chose correct position, the dipper was raised to the level of chosen nosing hole and the rat could drink through the hole for 7 sec. Then the stimulus was displayed in a new-generated position. After an incorrect or no response, the stimulus disappeared and access to the nosing holes was blocked by closing of a transparent shifting barrier. After 4 sec the new stimulus was generated.

The displayed stimuli were designed as a representation of the response space - they had the same configuration as was the configuration of the nosing holes on the front wall. The stimuli consisted of a rectangle and four rings in its corners. A bright filled circle marked the position of the rewarded nosing hole, whereas the others three were represented by empty contours. (Fig. 1C in Nekovarova and Bures, 2006)

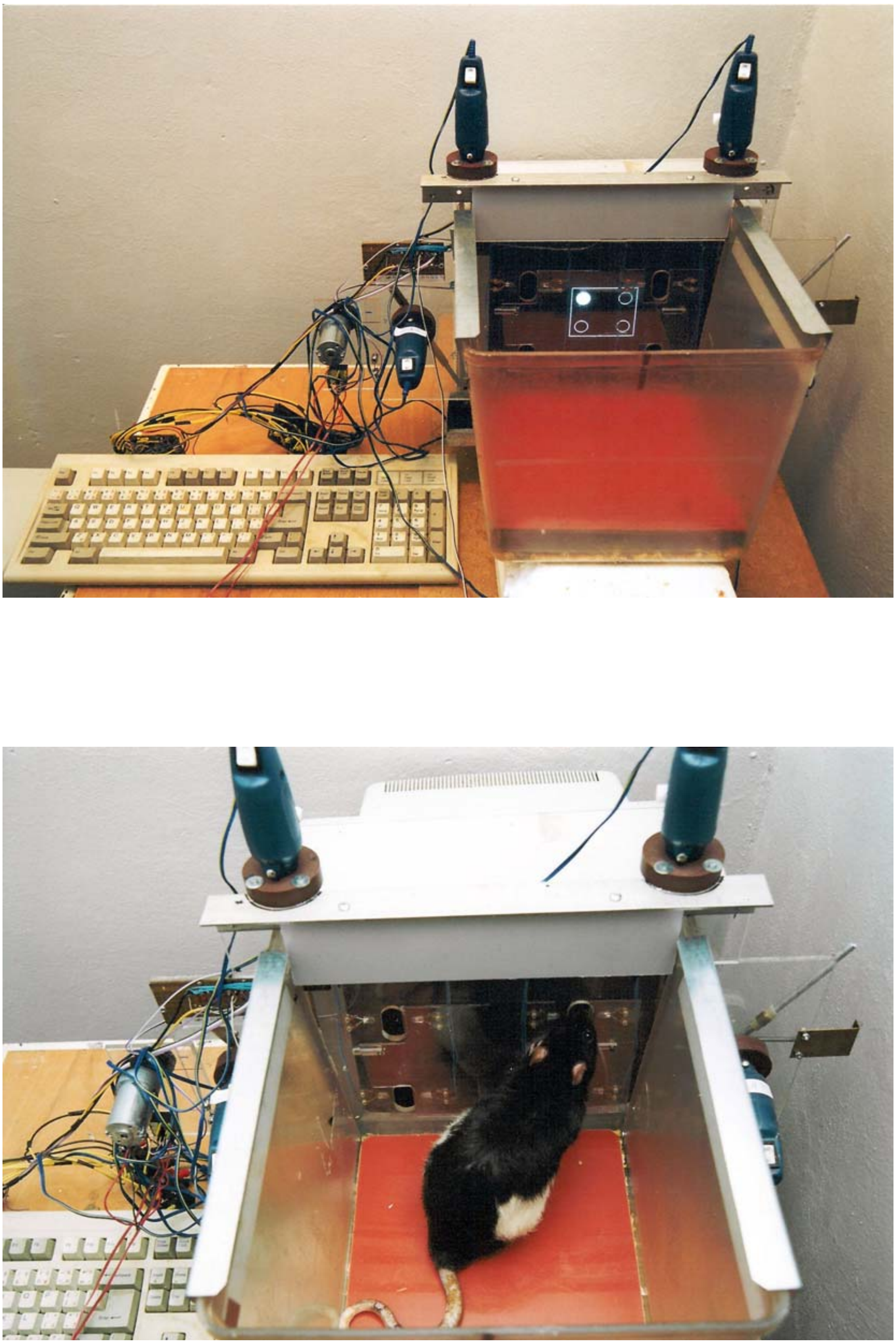


Fig.15: The apparatus used in Experiment II. The scheme of the apparatus: Fig. 1A,B in Nekovarova and Bures, 2006.

The rats were trained in four successive phases. In Phase 1 the visual stimuli were situated at the center of the screen and they had the same size as the response space, thus the bright circle representing the rewarded position overlapped with the appropriate nosing holes.

In Phase 2 and 3 the visual stimuli were reduced approximately to one third, but they remained at the center of the screen. In these phases the bright circle did not mark directly the rewarded nosing hole. Nevertheless, because the nosing hole the nearest to the bright circle was the rewarded one, the visual stimuli could be used simply as pointers.

In the last phase the visual stimuli were shifted to the right side of the screen, thus they overlapped with the nosing holes on the right and could not be used as a pointer anymore.

In each phase we carried out a control session, when the monitor was off and no visual stimuli were available, to test whether the rats oriented according to the visual stimuli or whether they could use other cues.

(stimuli shown on Fig. 1C in Nekovarova and Bures, 2006.)

The positions of the rewarded nosing hole were generated during Phase 1 and 2 in the given pseudo-random sequence of eight positions. In Phase 3 and 4, the position was generated fully randomly.

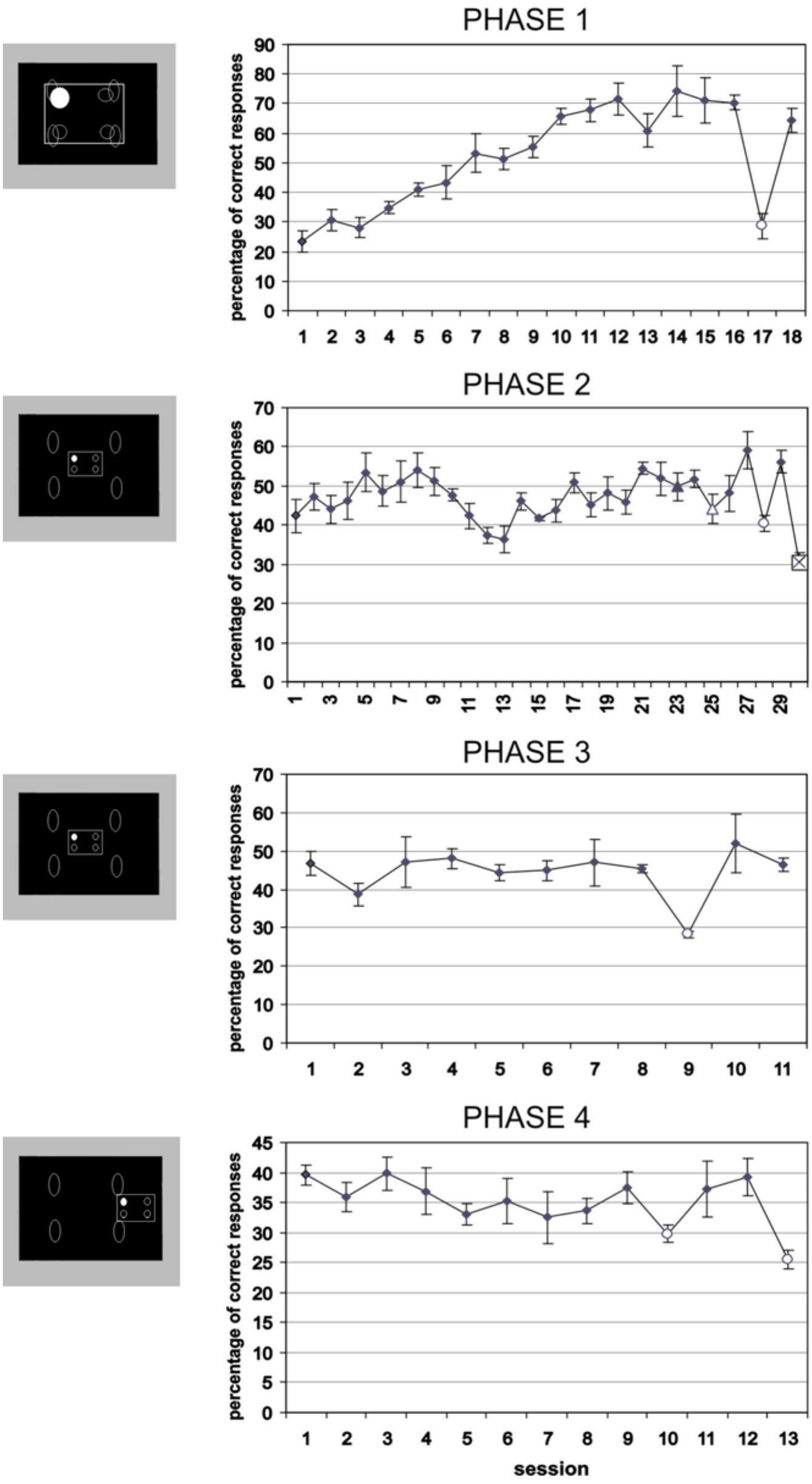


Fig.16: The percentage of the rewarded responses (efficiency; the ratio of the correct responses to the number of all responses) per session. The empty points marked the control sessions. In Phases 1, 3 and 4 they represented the control sessions with monitor off and no visual stimuli displayed. In Phase 2 no visual stimuli were presented in session 25, in session 28 the sequence of rewarded positions was changed and in the last session the sequence was changed and no stimuli were presented at once.

We analyzed the efficiency – ratio of the correct responses to the number of all responses per session – as a marker of rats' ability to recognize correct position of the particular nosing hole in the response space (Fig.16).

The results showed that the rats in Phase 1 gradually learnt to chose correct nosing hole. The rats were entirely dependent on the visual stimuli as was demonstrated by the sharp decrease of efficiency in the control session at the end of this phase.

After we reduced the visual stimuli in Phase 2, what made brightness-discrimination strategy inefficient, the efficiency decreased, but this decrease was not to the level of the random choice, as if that the rats had used only brightness discrimination strategy.

However, control session 25, when no visual stimuli were displayed on the screen, showed only slight decrease of efficiency. It was in contrast with the results of the previous phase and it indicated that after additional training the rats were able to use the given sequence as a cue for solving the task. To test whether they could also recognize the visual stimuli or whether they were entirely dependent on the sequence, we carried out the second control session. In this session the visual stimuli were presented on the screen as usual, but the sequence of rewarded positions was changed.

The sequence previously used in Phase 1 and 2 consisted of eight elements ("1-4-2-3-4-1-3-2"). Thus the particular position could be followed only by two of other positions (for example after the reward in position 1 could be rewarded only position 4 or 2) and the rats might potentially use it as a cue. The sequence used in the control session consisted of 16 elements ("2-3-4-4-1-3-2-4-2-1-1-4-3-3-1-2") and thus the each position could be followed by every other position, including itself.

The efficiency in this control session decreased only slightly, to the level significantly higher than was the level of random choice.

The efficiency decreased significantly only in the third control session, when the new sequence was used and no visual stimuli were presented on the computer screen

These results suggested that rats were able to use both the sequence and the visual stimuli as cues.

To eliminate the influence of the given sequence we repeated in Phase 3 the training with the displayed stimuli same as were in Phase 2, but the position of rewarded nosing hole was generated entirely randomly. After the change of the conditions, the efficiency did not decrease to the level of the random choice and remained at the same level as in the previous phase. The significant decrease of the efficiency in the control session with no visual stimuli displayed proved that rats depended fully on the visual stimuli on the screen. (Fig.16)

The question is why the rats at the end of Phase 1 depended evidently on the visual stimuli, whereas at the end of Phase 2 they could use also the sequence of the rewarded positions to solve the task. This could be because (1) the task in Phase 1 was quite easy, and thus the rats could solve it with brightness-discrimination strategy and they had no motivation to use any additional strategy; (2) the training in Phase 2 was quite long and thus rats could learn some rules about the sequence of positions of rewarded nosing holes.

Even if the rat in Phase 3 could not use the visual stimuli for brightness discrimination they could use them as a pointer to the closest nosing hole, which would be rewarded. Thus in following Phase 4 we moved the visual stimuli of the same size to the right side of the screen, so that they overlapped with the nosing holes. The nosing hole the nearest to the bright circle was not necessary the rewarded one anymore.

The efficiency in this phase was slightly lower than in Phase 3, what probably reflected the increasing complexity of the task. However, even though the decrease in the first session of Phase 4 differed significantly from the last sessions of Phase 3, it also differed significantly from the control session of Phase 3 with no visual stimuli displayed. It showed that the efficiency did not decrease to the level of random choices. The efficiency decreased only in the control sessions of Phase 4, when no visual stimuli were presented on the screen.

These results suggested that the rats were able to use abstract visual stimuli designed as a representation of the response space as a cue to make spatial choices in this space. However, we could not decide how the rats perceived the visual stimuli. They could (1) perceive the stimuli simply as four different geometrical patterns and associate them with four different positions of the nosing holes in the response space; or (2) they could encode the information about configuration/space included in the stimuli.

To resolve this question we carried out the following experiment.

EXPERIMENT III

Spatial choices of rats based on abstract visual information: Pattern- or configuration-discrimination?

In Experiment III (Nekovarova et al. 2006a) we replicated the training from previous Experiment II with one group of rats (group A; n = 7), but we used the second group of rats (group B; n = 6) as a control. We displayed configuration stimuli (similar as those from the previous experiment) to group A. These stimuli were designed as a representation of the response space and reflected the configuration of the nosing holes in this space. For control group B we used simple geometrical patterns, which evidently did not include any information about space/configuration.

One session consisted of 60 stimuli-presentations. One stimulus was presented on the screen in one moment, either the configuration stimulus (for rats from group A) or one of four geometrical patterns (for rats from group B).

We call the used visual stimuli “abstract” because except in Phase 1 they did not mark directly the correct positions of nosing holes in the real response space.

The apparatus was the same as in the previous experiment; only as a reward we used not water but two-percent sugar solution.

Rats were trained in the successive phases: first, the bright circle on the configuration stimuli and the geometrical patterns were displayed just behind the rewarded nosing hole, thus the visual stimuli displayed on the screen directly marked the rewarded nosing hole (Phase 1). Then the size of the configuration stimuli was reduced and both the configuration stimuli and the geometrical patterns were displayed at the center of the screen (Phase 2). In Phases 3 and 4 the stimuli remained of the same size as in Phase 2, but they were shifted either to the right (Phase 3) or to the left (Phase 4) side of the screen, thus they overlapped with the nosing holes. (Fig.1 in Nekovarova et al., 2006a)

The comparison of the learning and the efficiency of these two groups should reveal whether the rats could interpret spatial configuration of the abstract stimuli, or whether they perceive them simply as geometric patterns.

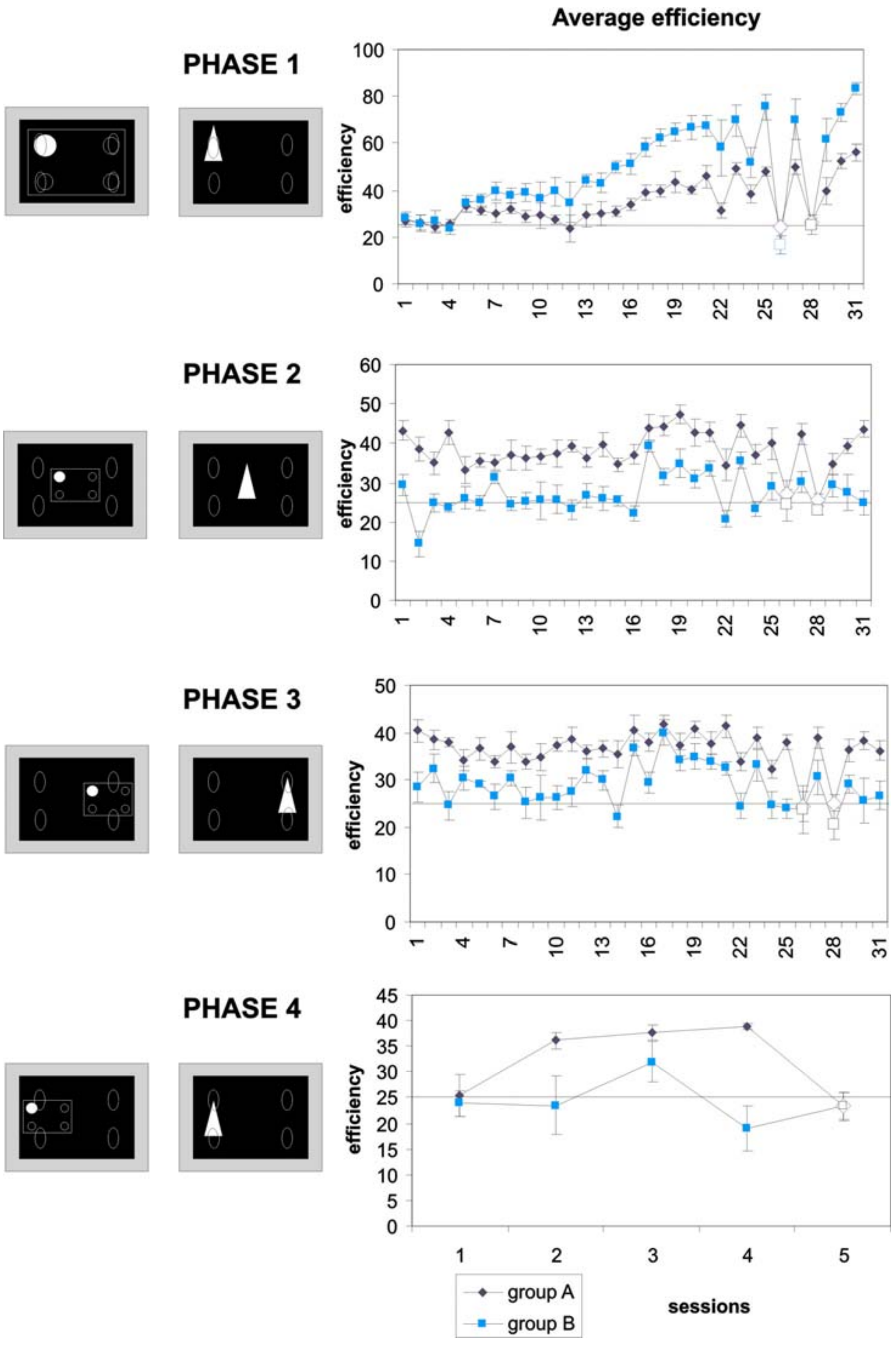


Fig.17: The percentage of the rewarded responses (efficiency; the ratio of the correct responses to the number of all responses) per session and the visual stimuli displayed in the particular phases for group A (left) and group B (right). The dark points represent the efficiency of group A, bright points of group B. The empty points marked the control sessions, when the monitor was off and no visual stimuli displayed.

During Phase 1 both groups gradually learnt to use visual stimuli to choose the rewarded nosing holes more frequently than at the random level. Group B was significantly better than group A. A control session at the end of training, when the efficiency sharply decreased, showed that the rats of both groups were fully dependent on the visual stimuli and did not use any other cue. (Fig.17)

After we changed the visual stimuli in Phase 2, the efficiency of both groups decreased significantly. However, it was important, that efficiency of group A did not decrease to the level regarded as a level of random choice (the first session of Phase 2 or the control session with no visual stimuli at the end of Phase 1).

The efficiency of group A was also significantly higher than the efficiency of group B. The efficiency of group B significantly decreased in the first session of Phase 2 to the level close to the level of random choice and it did not increase systematically during the whole Phase 2. The first session of Phase 2 differed neither from the session from the beginning of Phase 1 (naïve animals) nor from the control session of Phase 2 (no visual stimuli). (Fig.17; Fig.2 in Nekovarova et al., 2006c)

In Phase 3 the visual stimuli were shifted to the right side of the screen to overlap with the non-rewarded nosing holes. The results were similar as in Phase 2 – the percentage of the rewarded responses for group A decreased only slightly, and it was significantly higher than the efficiency in the control session in Phase 2 and in Phases 3 (no visual stimuli). In the first session of Phase 4 (stimuli shifted to the left side of the screen) the efficiency of group A markedly decreased but immediately in the second session it increased again to the level comparable to Phase 3.

Group B did not increase systematically its efficiency during the whole Phase 3 and it was significantly lower than the efficiency of group A. The efficiency in the control session did not differ from the standard sessions. The efficiency of group B did not increase even in Phase 4 and stayed on the level close to the random choice. (Fig.17)

The results of the experiment proved that rats were able to use abstract visual stimuli of some kind for spatial choices in the real environment. The results showed distinct difference between the groups using the different visual cues: (1) group A using the “spatial stimuli” reflecting the configuration of the real space and (2) group B which should have associated the simple geometrical stimuli with the appropriate spatial choice.

It suggested that the stimuli containing the configuration information allowed the rats to orient in the environment, whereas the rats failed to associate spatial response with the simple geometrical patterns without any spatial component.

The results showed that rats from group A were able to use some information about configuration even at the beginning of Phase 2, when the stimuli were changed for the first time, or that they were able to adopt the new strategy rapidly. In contrast, rats from group B seemed fully dependent on brightness discrimination strategy in Phase 1 and they were not able to relearn this task after this strategy had became inefficient. It suggested that they did not associate the visual stimuli with position in Phase 1. However, previous experiments (Eacott and Norman, 2004; Gilbert and Kesner, 2004) proved that rats were able to associate position and object (position x object memory), but this task corresponded only with Phase 1, whereas in following phases the task was more complicated.

EXPERIMENT IV.

Spatial choices of macaque monkeys based on abstract visual stimuli

After we carried out the series of experiments with rats, we studied whether monkeys could manage similar tasks. We studied how the macaque monkeys perceived abstract visual stimuli and whether the monkeys were able to make spatial choices according to these stimuli.

The experimental design was similar to experimental design in Experiment III.

The monkeys were put in a box placed in front of a monitor equipped with a touch-panel. The panel was placed directly on the screen and consisted of a transparent board with nine touch-holes equipped with a photoelectric device for registering the touch. The front wall of the box was opened, allowing the monkeys to view the screen and to touch the panel through a touch-hole. The monkeys were trained to choose one of the nine touch-holes on the panel (response space) corresponding to one of the four visual stimuli displayed subsequently on the screen. Correct responses were rewarded by sweet cereal pellets delivered to the monkey. (Fig.1-I in Nekovarova et al., 2006b; photo of the apparatus: Fig.18)

The first monkey (Subject A - Puck) was exposed to the visual stimuli designed as a representation of the response space: the configuration of the stimulus was the same as a configuration of the response space. The position of the rewarded touch-hole was indicated by a bright circle shown in relation with empty circles representing the other, non-rewarded touch-holes.

By contrast, the second monkey (Subject B - Attila) was trained to associate geometrical patterns or pictures (without any implicit spatial component) with the particular positions of the touch-holes. (Fig. 1-II and III in Nekovarova et al., 2006b).

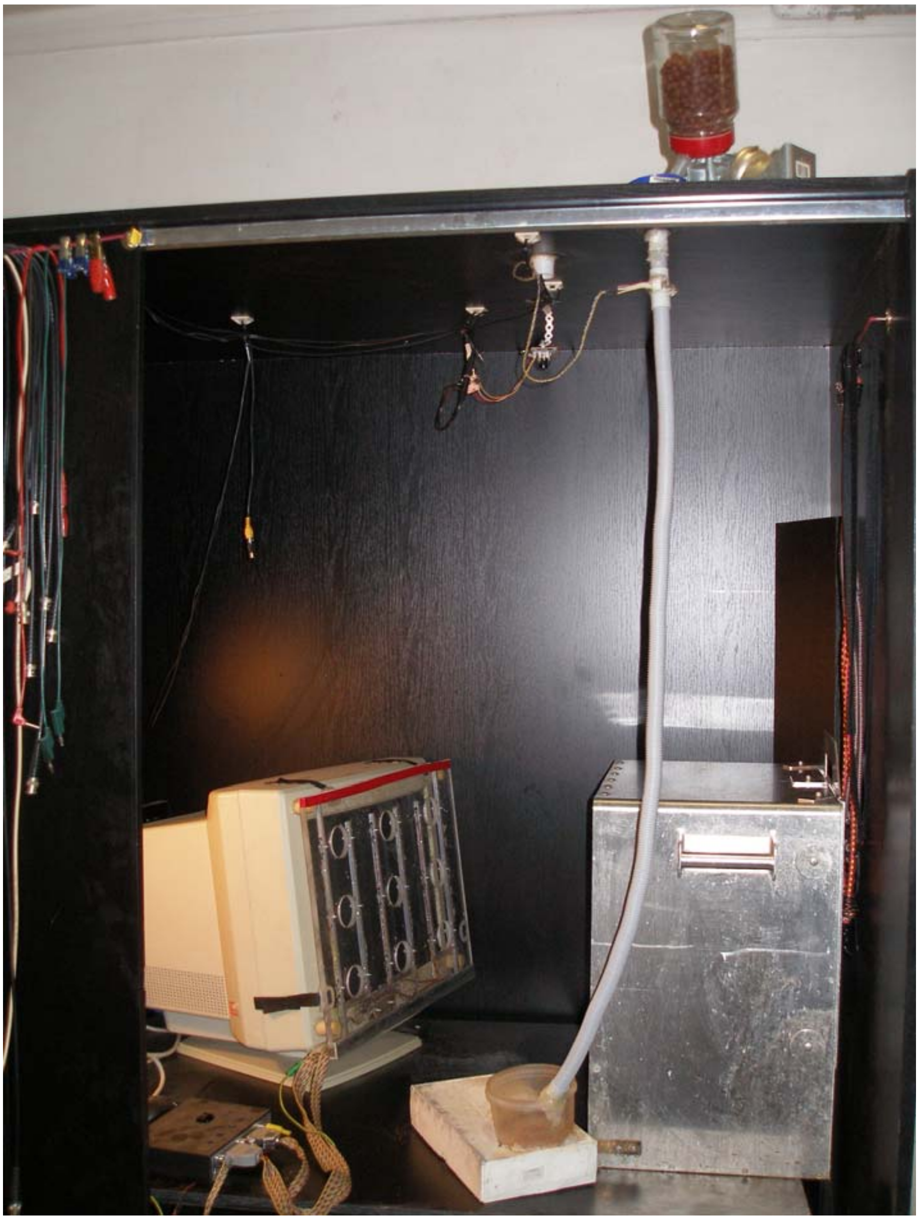
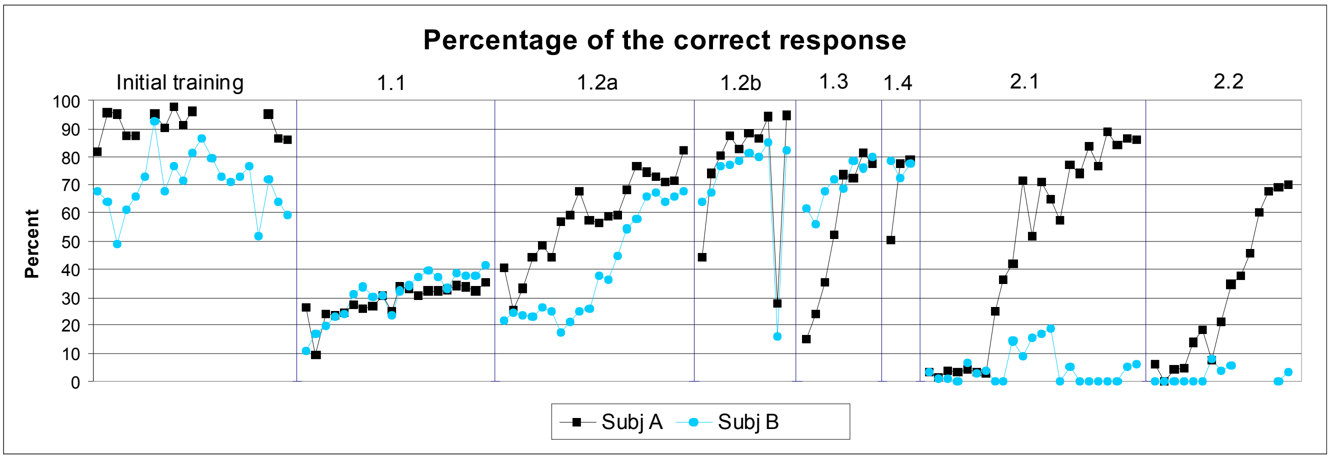


Fig.18: Photo of the apparatus. The monitor, the feeder and the box for a monkey.



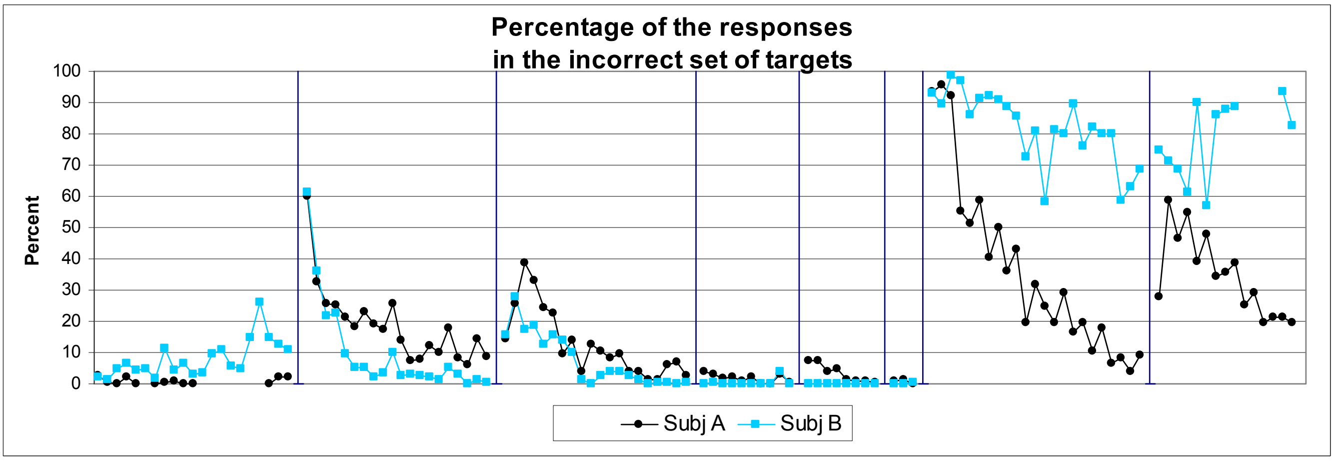


Fig.19: Upper graph: Percentage of the correct responses (ratio of the correct to the number of all responses) per session in particular phases. Lower graph: Percentage of the responses in the incorrect set of targets. In Phase 1 the incorrect (non-rewarded) nosing holes were: 2, 4, 5, 6, 8; in Phase 2 the non-rewarded nosing holes were: 1, 3, 5, 7, 9.

In the first phase of the experiment the stimuli were designed similarly as in Experiment III: they varied in the size and in the position, but their shapes remained the same.

In the second phase the visual stimuli were changed and the different set of the touch-holes was rewarded. The visual stimuli of subject A (configurations) were changed otherwise, but the principle of representation remained the same – only the circles in the rectangle represented the different set of touch-holes.

On contrast, the geometrical patterns of subject B were replaced by entirely new series of stimuli associated with the new set of touch-holes.

The comparison of the two monkeys using different types of stimuli were expected to reveal potential differences between pattern-discrimination and using of configuration information included in the spatial stimuli.

The results showed that both monkeys were able to adopt brightness-discrimination strategy (during the pre-training). At the beginning of the training (Phase 1.1) the configuration stimuli had the same size as the response space and thus the bright circle signalizing the position of reward appeared just behind the appropriate touch-hole. Similarly, the geometrical patterns were displayed just behind the touch-holes which had to be rewarded.

In the next phase (Phase 1.2) the configuration stimuli were reduced approximately to one half of the previous size and remained at the center. The geometrical patterns had the same size but they were shifted to the center of the screen. After the change of the stimuli the efficiency of both monkeys decreased and raised again only slowly and not to the previous level. When we set a punishment of incorrect responses (prolonged time interval after incorrect response), the percentage of rewarded responses of both monkeys increased significantly to the previous level of efficiency.

In the following phases the stimuli had the same size, but the position on the screen where the stimuli were displayed was changed in particular phases. The percentage of the rewarded responses of subject B did not change markedly through these phases. Subject A decreased its efficiency immediately after the change of the position of the stimuli, but rapidly returned to previous level.

This could indicate that there was a difference in perception and processing of the spatial (configuration) and non-spatial stimuli.

However, on contrast to previous Experiment III, when the rats with non-spatial stimuli failed to solve the task, the monkeys under similar conditions showed that they were able to use both types of stimuli to choose the correct position in the space (Fig.19).

To find out whether there was really a difference between configuration stimuli and stimuli without any information about the configuration or space, we carried out the second phase of experiment: In this phase we changed the visual stimuli and we used four different positions of touch-holes where the monkeys could obtain the reward.

The configuration stimuli of subject A changed, but the principle of representation of the response space remained the same: the circles represented the rewarded and non-rewarded touch-holes, but the circles had different positions.

For subject B entirely new visual stimuli were used (Fig. 1-III in Nekovarova et al., 2006b). Immediately after the introduction of the new stimuli the percentage of the rewarded responses of both subjects significantly decreased nearly to zero. However, during the training a distinctive difference appeared between the subjects. During the training with described stimuli (Phase 2.1), the efficiency of subject B stayed close to the zero, whereas the efficiency of subject A started to increase after several sessions. At the end of the training, the efficiency of subject A was close to the previous level and significantly higher than the efficiency of group B, which was still near to zero (Fig.19).

The results showed that there was not only difference in the percentage of the rewarded responses, but also in the distribution of responses in the particular positions: it took to subject B more time to learn to use new the set of stimuli at all. (Fig 3. in Nekovarova et al., 20006b)

Nevertheless, these differences could have been caused not by the difference in visual stimuli, but by the difference between the monkeys. To examine this possibility we trained the subject B (previously trained with non-spatial information) with configuration stimuli in the same way as was used previously for training subject A (control phases, see Fig. 2-II and 3-III in Nekovarova et al., 2006b). This training demonstrated that subject B was able to learn “configuration stimuli” quickly and precisely. The results in the first phase were similar to those of subject A: when the configuration stimulus was shifted to a new position, the percentage of the rewarded responses decreased in the first session, but immediately returned to the previous level in the subsequent sessions: this tendency was not demonstrated in this subject in the previous training with the simple geometrical stimuli. The results were also similar to subject A in the second phase. Subject B learnt to associate new configuration stimuli with the new set of possible rewarded touch-holes quickly on contrast to the previous training with simple “non-spatial” patterns.

The difference in learning between subjects with “configuration” and “non-configuration” stimuli suggested that there was a difference in the processing of (1) the visual stimuli reflecting the configuration of the response space and of (2) the simple geometrical patterns lacking relevant spatial component.

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GENERAL DISCUSSION

We carried out series of the experiments concerning the ability of animals to perceive visual stimuli and their configuration. We developed an apparatus and an experimental design, which makes it possible to study how animals make spatial choices in the real space according to abstract visual stimuli.

We used various types of experimental arrangement to develop appropriate tasks.

Apparatus

First, it was necessary to make the rats watch the computer screen and to emit proper behavioral responses. The computer screen must catch the rats' attention and the sensory input should be appreciable. Operant responding had to be easy and natural to emit.

In Experiment I we used a Skinner box with removed front wall to catch the attention of the rats and to make them watch the computer screen. The screen was 35 cm far from the Skinner box. This distance is supposed to be an optimal distance for rats' optical accuracy (Gaffan and Eacott, 1995). The results of Experiment I suggested that rats perceived the stimuli on the screen, but the arrangement of the experiment allowed them to emit considerable number of redundant incorrect responses.

In the following Experiments with rats (Experiments II and III) we used the modified Skinner box with "nosing holes" – openings in the front wall forming a rectangular array. Each of the nosing holes was equipped with a photoelectric device registering rat's exploration (nose poking) in the particular nosing hole. Contrary to the previous experiment, the computer monitor was placed close to the Skinner box. There was only a narrow gap between the screen and the front wall, through which the dippers with water could be lifted and thus the rats obtained the reward "directly" from the screen. Also this arrangement was established to make the screen and the displayed visual stimuli for the rats more interesting.

The maximal number of operant responses in this arrangement could be the same as the total number of stimulus presentations in the session, what prevented the rats from emitting the large number of redundant responses. Moreover, contrary to the operant responding (lever pressing) in the previous experiment, the responses were spatial – the animal had to choose correct position of the nosing hole in the response space. Simultaneously, they did not perform any locomotion through the environment.

The apparatus used in the experiment in monkeys (Experiment IV) was similar to those used in Experiments II and III. The monkeys sat in the box and performed operant responses by touching the "touch-holes" (openings in the perspex board attached to the screen and equipped with a photoelectric device). It was easier to watch the screen for the monkeys than for the rats, because rats depend more on the olfactory and tactile sensory input than on the visual information. However, it took longer time than we expected to train the monkeys to use the apparatus.

Motivation

We used various ways of motivation to make the animals respond to the presented stimuli with appropriate operant responses. In all described experiments we used positive reinforcement.

In Experiment I we trained the food-deprived rats and we used little pellets as a reward. The rats in such arrangement emit operant responses during the whole session willingly and their motivation did not decrease markedly. It was also possible to keep quite stable motivation of animals between the sessions – their weight was maintained at 90-95% of free-feeding weight.

On the other hand, the animals emitted too high number of responses, even during non-rewarded intervals. This could be caused by a low "energetic cost" of the lever pressing – there was no punishment and thus no pressure not to emit redundant presses. The recent experiments suggest that during the training, when no every response is rewarded (variable ratio schedule), the total number of non-rewarded responses decreased and thus the relative efficiency increase.

In the next experiment (Experiment II) we changed the way of rewarding – the rats were water deprived and the possibility to drink was used as a reward. We used this type of reward to make the incentive for animals stronger. Motivation was indeed more pressing, but there were also disadvantages: the rats were sometimes gratified before the end of the session; it was also difficult to keep the stable level of motivation of the experimental animals between sessions.

To overcome these problems we used another type of reward in Experiment III – after the correct response the rats could drink sugar solutions for a few seconds. This ensured that rats responded during the whole session almost on every stimulus. In contrast to the previous experiment, where the level of responding was sometimes very low, the ratio of the emitted responses to all stimulus-presentations was in Experiment III usually above 90 %

For macaque monkeys in Experiment IV we also used positive reinforcement – the monkeys were rewarded for the correct responses by sweet cereal pellets. However, similarly to Experiment I, it was very easy to emit operant behavior and thus the monkeys often emitted redundant responses. This was shown during Phase 2.1, when the monkeys did not exceed 45 % of efficiency. Nevertheless, after we had introduced punishment for incorrect responses (a prolonged time interval between an incorrect response and displaying of a new stimulus), the efficiency of both monkeys started to increase. With the same visual stimuli as before it reached about 70 %.

Sensory inputs

The presented behavioral tasks imposed requirements mainly on visual sensory system. We designed Experiments I-III with visual representation of spatial relations although the rats could be more dependent on olfactory or tactile modality. We chose this way because it is natural for many animal species to represent spatial relations in visual modality and thus such experimental arrangement allows us to compare different animal species in similar tasks. Nevertheless, there are evidence that rats can also use visual information quite precisely (Keller et al., 2000, Robinson et al., 2000).

Moreover, in some experiments previously carried out in rodents, a computer screen was successfully used to present the visual stimuli (Sun et al. 1992, Sahgal and Steckler 1994, Gaffan and Eacott 1995, Keller et al. 2000, Bussey et al. 2001, Prusky et al. 2004). In these tasks, with the exception of Sun et al. (1992), animals responded to stationary stimuli. In the experiment of Sun et al*.* (1992), the stimulus on the screen gradually changed its size as the gerbils were running toward a screen and estimated time-to–collision according to its size. In the others experiments the animals were trained to discriminate stationary objects, patterns or complex scenes. In some of the experiments the stimuli on a screen served as allothetic cues for spatial desicions (Gaffan and Eacott 1995, Prusky *et al.* 2004), but none of the used stimuli encoded the information about environment itself.

Hölscher et al. (2005) even used an apparatus simulating fully the virtual environment: rats were running on the zenith of a hollow polystyrene sphere 50 cm in diameter. The sphere was anchored in such a way that when the rat walked on its surface, it stayed in the zenith and rotated the ball about a horizontal axis. The locomotion and the heading of the animals were registered. The stimuli were projected on a toroidal screen of 140 cm diameter and 80 cm height surrounding the animal. The screen covers the visual field from –20° below to +60° above the horizon of the rat and 360° of azimuth. The results of this experiments demonstrated that the rats were able to solve spatial tasks even in the virtual environment. The recent study (Schnee et al., 2006) proved that similar neuronal mechanism (hippocampal place cells) was involved not only in spatial tasks in the real but also in the virtual environment.

In Experiment I the rats watched the moving strip approaching the stationary rectangle on the screen. Rats had started to emit a huge number of responses before the moving object touched the rectangle. We asked whether the rats increased the number of responses (1) because they could not discriminate between "rewarded pattern" (touching objects) and "non-rewarded pattern" (moving strip approaching the rectangle) because of sensory constraints, or (2) because they anticipated the approaching reward as the stimulus was changing.

However, the rats increased the number of emitted responses far before the point corresponding to the limits of visual acuity - visual acuity of rats is approximately 1° (Birch and Jacobs 1979, Dean 1981, Keller *et al.* 2000) (shown on Figure 3 in Nekovarova and Klement, 2006).

In Experiment II the rats demonstrated their ability to respond according to the configuration of the visual stimuli on the computer screen. However, with increasing cognitive and sensory complexity of the task their efficiency decreased.

In Experiment III we used two types of stimuli:

(1) For the first group of rats we used similar configuration stimuli as in the previous experiment. However, because of the low level of the average efficiency in the previous task, we made the stimuli more distinguishable: the circles and rectangle were drawn with bold lines and the stimulus was reduced not to one third (Phase 2 of Experiment II) but only to one half (Phase 2 of Experiment III) of the original size. The efficiency of the rats using these novel stimuli was indeed higher than in corresponding phases in Experiment II.

(2) For the second group of rats we used simple geometrical patterns without any information about configuration of the response space. After the first phase of the experiment, when the rats could not discriminate the patterns but only the bright, their efficiency steeply decreased close to the random level and it did not change systematically during the rest of the training. The decrease of efficiency could have been caused by a cognitive or a sensory lack.

However, if we suppose that rats have visual acuity 1° and that they are placed approximately 6 cm away from the screen with visual stimuli, they should have been able to discriminate visual stimuli about 0.1 cm large. The size of the geometric patterns used in this experiment was severe centimeters. Thus we could assume that the lack in using geometric patterns was not caused by sensory incompetence. (Fig.20, 21)

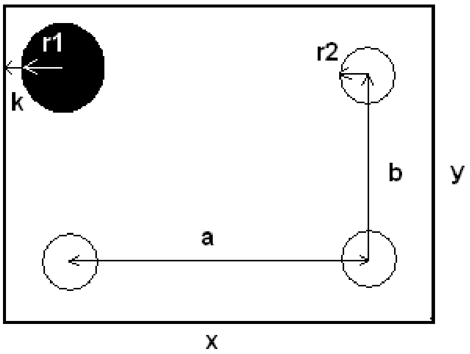

Fig.20: The dimensions (in pixels) of the configuration stimulus displayed on the computer screen in Phase 1 of Experiment III. The dimensions of the stimulus after the reduction in Phases 2 and 3 of Experiment III. The stimulus was approximately one half of the response space and of the stimulus used in Phase 1.
$a = 380$; $b = 8.5 * a / 14 \approx 230.7$; $r1 = (b - 4 * c1) / 4 \approx 50$; $r2 = r1 / 1.5 \approx 25$; $x \approx 510$; $y \approx 310$; (contour of the rectangle) $c1 = 8$; (contour of the circles) $c2 = 5$.
1 pixel is approximately 0.4 mm.

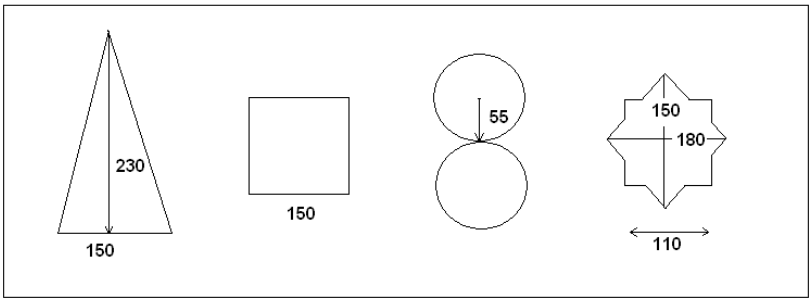

Fig.21: The different geometric patterns displayed to the group B and their sizes in pixels.
1 pixel is approximately 0.4 mm.

We used visual stimuli to represent the space also for macaque monkeys in Experiment IV.

Recently, many studies confirmed the ability of primates to solve spatial tasks presented on a computer screen. The displaying of stimuli on the screen allows simulation of both 2D and 3D mazes. For example Fragaszy et al. (2003) compared navigation and planning of capuchin monkeys and chimpanzees in 2D mazes. All subjects used in the study solved significantly more mazes without errors than expected by chance. Sato et al. (2004) trained two macaque monkeys to navigate in a virtual building (3D maze); the results suggested that monkeys could navigate in a virtual environment. In the study of Washburn and Astur rhesus monkeys demonstrated that their capability to orient in 3D mazes was not only based on operant behavior but that they perceive depth, movement and space in the virtual mazes. Such results proved that computer screen can be successfully used for presentation of visual stimuli, even for quite sophisticated spatial tasks, to monkeys. This also demonstrated that monkeys could navigate not only in the real but also in the virtual environment.

In our experiment we concluded that there was a difference between processing of configuration (spatial) and non-spatial stimuli. We postulated this difference because the monkey with configuration stimuli could adopt in Phase 2 new configuration arrangement of stimuli, whereas monkey with patterns without spatial information could not learn a new set of stimuli at all. The new non-spatial stimuli differed both in a shape and a color. We supposed that the lack of efficiency of subject B in Phase 2 was caused by cognitive and not by sensory lack, because the ability of macaque monkeys to discriminate colors has been previously demonstrated in many experiments (Roger et al., 2004; Sato, 2005).

Generations of rewarded positions

In Experiments II, III and IV we displayed the visual stimuli associated with the different positions on the response space. The positions that should be rewarded were generated in different ways.

At the beginning of Experiment II (Phases 1 and 2) we used fixed sequence of generated position. The sequence consisted of eight positions in pseudorandom sequence ("1-4-2-3-4-1-3-2"). The reward was generated in the same position until the rats did not respond correctly.

We chose this method to cause the rats visit nosing holes in all positions, but after long training the rats learnt to use fixed order of rewarded positions as a cue to solve the task. They probably learnt that after a given position, only two others positions could follow. However, the results of experiments proved that the rats could use as cues both the visual information and fixed sequence. Thus in the next phases we changed the way how to generate the position of rewarded nosing hole. The positions were generated completely randomly. This made it possible to generate all positions symmetrically.

We used the same method – completely random generation of the positions - also during the pretraining in Experiment III. Nevertheless, under these conditions the rats emitted the responses predominantly only in one easily accessible nosing hole and they reached only 25% efficiency (the level of random choices).

For that reason we wanted in the further training in Experiment III to ensure that the rats would visit all positions of the nosing holes and simultaneously to keep from using fixed sequence as a cue.

Therefore we chose following pseudorandom method: at first, the position was generated randomly. After incorrect or no response, the same position was generated. After correct response the position was generated randomly from all four possibilities. This ensured that rats had to visit all positions of nosing holes and at the same time they could not use the fixed sequence of positions as a cue. Only one disadvantage appeared: the positions were not generated symmetrically during the session, because the rats preferred the lower nosing holes and they did not visit upper positions so often, even when the stimuli marked the upper positions more frequently. Such preference could slightly influence the efficiency.

However, we used the same method even in Experiment IV with macaque monkeys. There was no evidence that the monkeys preferred systematically some of the touch-holes.

Cognitive requirements

In the last phase of Experiment I (Phase 3) we trained the rats to recognize the position of the moving object in relation with the stationary object. The rats were rewarded during 10-sec interval, when the moving strip stopped and stayed in contact with the stationary rectangle.

We considered three possibilities how the rats could solve this task. The rats could discriminate: (1) moving object versus stationary objects; (2) touching object versus separated object (pattern discrimination); (3) the configuration of the objects (spatial relations).

Ad (1): The rats probably did not recognize two discrete stimuli (moving x stationary stimulus), because the pattern of responding was different in comparison with previous Phases 1 and 2, when the rats recognized two discrete stimuli. The number of incorrect responses increased during the non-rewarded time interval much more steeply in Phase 3 than in Phase 1 or 2 (Fig. 3 in Nekovarova and Klement, 2006).

Ad (2): The rats did not respond to the separate or the touching objects. If they did so, they would increase the number of responses, when they could not see the gap between the objects, but actually they increased the rate of responding far before this point (Fig. 3 in Nekovarova and Klement, 2006).

Ad (3): The rats increased the number of responding even when they saw the stimuli that were never rewarded before. The pattern of responding (steep increase of responses) indicated that rats anticipated the possibility of reward as the moving strip approached to the stationary rectangle. This suggested that the rats learnt the relation between positions of the moving strip and the stationary rectangle. Because of the anticipation, the rats in Phase 3 missed fewer rewarded periods and obtained more rewards than in Phases 1 and 2, where the rats could not anticipate. The exact time of reward could be calculated from the position of moving strip and its speed. However the results (Fig. 3 and 4 in Nekovarova and Klement, 2006) implied that the rats anticipated not the time to reward but the position only.

Similar anticipatory behavior, when the rats used a position in a space to anticipate the reward, was found in earlier experiment with rotating arena. Klement and Bures (2000) trained the rats to recognize a certain position in a space. The rats were passively transported in a box attached to the rotating arena. They could press a lever for reward, but the lever-pressing was rewarded only within a short part of trajectory. In the next experiment (Pašťalkova et al., 2003) rats watched the objects rotating on a circular trajectory around a common center. The rats were rewarded for lever-pressing only when the objects rotated in a specific part of their trajectory. In both mentioned experiments the rats performed anticipatory behavior – they increased the number of emitted responses before they alone or the observed objects entered the reward area.

The results of Experiment I proved that the rats could interpret the spatial relations between the objects presented on the computer screen. The question remains whether the rats interpret the stimuli in Phase 3 as a spatial task with continually moving objects or as a series of configuration snapshots.

In this experiment we demonstrated that the rats could recognize the configuration of the visual stimuli presented on the computer screen. In the following experiments we studied whether they would be able to connect such abstract information with spatial choice in the real environment.

In Experiment II we presented to the rats the visual stimuli designed as a representation of the response space. The results of the experiments proved that the rats could use such visual stimuli to increase their efficiency above the level of the random choice. They could use these stimuli even if the stimuli were displayed on the side of the screen and thus the rats could not use them simple as a pointer.

However, we could not decide whether the rats could use the information about configuration of the response space included in the stimuli or whether they learnt to perceive stimuli as discrete patterns, each associated with a particular nosing hole. To resolve this, we carried out Experiment III.

In Experiment III we trained (1) one group of rats (group A) with visual stimuli similar to those used in the previous experiment (stimuli designed as a representation of the response space) and (2) the second control group (group B) was trained to associate simple geometrical patterns (without implicit spatial information) with particular positions of the nosing holes.

In Phase 1 the stimuli were presented directly behind the appropriate nosing holes, thus the rats could solve the task as a brightness discrimination task. In the following phases the stimuli were displayed at the center or at the side of the screen in such a way that the rats could not use brightness as a cue.

The comparison of groups A and B should reveal whether the rats could interpret configuration information or whether they perceived the stimuli only as discrete patterns. The results showed that when the rats could not use brightness discrimination the group using configuration stimuli responded significantly better than group using simple patterns.

In Phase 1 the rats from both groups learnt to use visual stimuli as a cue. Nevertheless, when the brightness could not be used for solving the task, group B failed to associate simple patterns with the positions in the real space and they did not master it during the rest of training.

On contrast, rats from group A had significantly higher efficiency even immediately after the change of stimuli in the first session of Phase 2. It could indicate that the stimuli of group A brought some information about configuration that could be used even when the stimuli did not mark directly the correct position. The rats from group A could transfer the information about positions from Phase 1 to Phase 2, contrary to group B, which failed.

The failure of group B was in the contrast with the results of experiments, where the rats performed well in object-place memory (Eacott and Norman, 2004; Gilbert and Kesner, 2004) and where they proved their ability to make associations between motor responses (body-movements) and real objects (Kesner and Gilbert, 2006). In these experiments the real objects were used (not the abstract representations) what could also make the task easier.

The lack of efficiency of group B could arise because the rats from this group depended only on brightness discrimination during Phase 1 and could not adopt any new strategy. They did not associate the positions with the object in Phase 1 and in the following phases they were not able to do it because the objects were not shown in the appropriate positions.

Thus this type of training demonstrated the advantage of the configuration stimuli.

Nevertheless, when we repeated similar experiment in macaque monkeys (Experiment IV, Nekovarova et. al, 2006b), the same training did not reveal the difference between using configuration (spatial) and non-spatial stimuli, and so we had to carry out additional tests to find out whether the monkeys perceive differently spatial and non-spatial information.

The first phase of Experiment IV corresponded to the training of the rats in Experiment III. But on contrast, both monkeys (the first using the configuration stimuli and the second using geometrical patterns without spatial information) learnt to use these stimuli to make correct spatial choices in the real environment.

In the second phase we introduced new stimuli. However, the principle of representation of the response space in the configuration stimuli (subject A) was the same, while the patterns (subject B) were changed entirely.

If the monkey perceived the configuration stimuli as discrete patterns without any spatial component, both monkeys would learn new stimuli similarly. But the results did not support this presumption – subject A using configuration stimuli could adopt new stimuli, contrary to subject B exposed to simple patterns without spatial component, which failed to learn new set of stimuli at all.

This result suggested that configuration stimuli, contrary to simple arbitrary patterns, provide some additional spatial information, enabling the monkeys to relearn in the new situation. Subject B could not associate the patterns with positions when the patterns were not displayed at first at appropriate positions.

It could resemble the previous experiment with rats – the rats from group B in Phase 1 could not pay attention to particular stimuli and focused only on brightness. Thus in Phase 2, when all geometrical patterns were displayed at the center of the screen, they could not make the appropriate association.

Finally, we can discuss whether the presented tasks employed spatial cognition and which component of spatial cognition.

It is not navigation in senso stricto, because the animals did not perform locomotion through the environment.

The animals choose correct position in the response space, according to the visual stimuli. In presented experiments we demonstrated that the animals perceive in some way configuration of these visual stimuli. Thus we can talk about spatial cognition manifested by processing the configuration of stimuli.

CONCLUSION

The animals often demonstrated their ability to perceive configuration of landmarks and geometrical features of the environment.

We tested their ability to perceive configuration of abstract stimuli and to make spatial choices in the real environment according to this information.

We developed behavioral tests using a modified Skinner box to test spatial cognition of animals with minimization of motoric component of the response.

First, we demonstrated the ability of the rats to discriminate configuration of objects presented on the computer screen (Experiment I – Nekovarova and Klement, 2006).

Afterwards, we showed that the rats were able to perform spatial choices in the real space (operant responses) according to configuration stimuli designed as a representation of this response space and presented on the computer screen (Experiment II – Nekovarova and Bures, 2006).

Consequently, we proved that the rats perceive such spatial stimuli (with information about configuration of the real space) differently from the simple stimuli without any spatial information (Experiment III – Nekovarova et al., 2006a).

Finally, we carried out a similar experiment in macaque monkeys (Experiment IV – Nekovarova et al., 2006b) to compare cognitive functions of different animal species. The results of this experiment suggested that, unlike rats, monkeys were able to associate the positions in the real space both with spatial and non-spatial information displayed on the computer screen. However, additional tests demonstrated a difference between processing of these two types of stimuli.

Contrary to the most of the studies concerning the ability of animals to represent geometric features of environment ("geometric cognition"), we focused on the ability of animals to perceive the configuration of stimuli in one “spatial frame” and to transfer this ability to another “spatial frame”. The animals had to demonstrate the ability to abstract geometric relations of presented stimuli.

The presented tasks enable to separate cognitive functions involved in encoding of the geometric relations, in object recognition and in object-place memory. In subsequent experiments it might be possible to use such tests to study a role of the hippocampus in abstract spatial tasks.

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