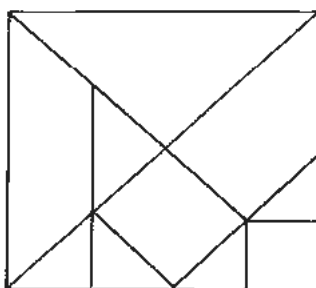


PhD THESIS

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



RNDr. PhDr. Tereza Nekovářová

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Autoreferát rozeslán dne: 14.12.2006

Obhajoba disertace dne: 8. ledna 2007 v 15:00 hodin

**Místo obhajoby: knihovna Ústavu experimentální medicíny AV ČR, 1. patro,
Videňská 1083, Praha 4**

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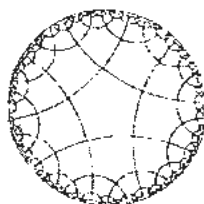
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předseda oborové rady
Neurovědy**

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AIMS OF THE DISSERTATION

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

In my thesis I focus 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 make spatial decisions in the real space based on the information presented on the computer screen and designed as a representation of the real response space; e.g. 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 the computer screen.
- To find out whether rats are able to perceive and discriminate configuration of visual stimuli presented on the computer screen.
- To study whether rats are able to make spatial choices in the real environment based on 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.

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 inner representation of space, to orient in the environment, to perceive positions of prominent objects and of others 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.

For orientation in the space animals used different strategies as dead reckoning, the perception of single beacons or encoding relative positions and directions of multiple landmarks (Jeffery, 2003; Gallistel, 1990).

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

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

One of the strategies to orient in space is to encode the geometric features of the environment: global geometry of space or the configuration of multiple landmarks. This ability is fundamental for our experiments – we trained animals to choose specific position in the real space according to configuration of abstract stimuli. Therefore animals had to first perceive the configuration of stimuli presented on the computer screen and than to transform the relations of virtual stimuli to the real space.

There are number of evidence that under certain conditions animals proved ability to encode geometric features of environment and with appropriate training they are able to abstract geometric rules about space.

The ability to encode global geometry of closed enclosure was demonstrated in various species: in rats (Cheng, 1986; Margules and Gallistel, 1988), in humans (Hermer and Spelke, 1994, 1996; Hermer-Vazquez et al., 1999; Learmonth et al., 2002), in monkeys (Gouteux et al., 2001) in birds (Sovrano and Vallortigara, 2006) and in fish (Sovrano 2002, 2005, 2006). In these experiments the animals were trained to locate a position in a corner of rectangle enclosure. After they learn to locate the position of a goal precisely, they were disoriented. After the disorientation procedure they searched in the correct position and also in the position diagonally equivalent, what suggests that they were able to use geometry of enclosure for reorientation. However, there were interesting differences between the species in the ability to integrate geometric and non-geometric information for orientation.

In the later experiments the ability of mammals and birds to encode relative spatial information was shown. The birds were trained to locate a center of a square enclosure and after they mastered it they searched the center in the enclosures of different shapes or sizes. When the shape or size of enclosure were changed the birds searched in certain circumstances in the center of new arena, however in other circumstances they searched in the distance corresponding to training arena or they compromise between these information. (Tommasi and Vallortigara, 2000; Tommasi et al., 1997, 2003)

Similar ability to locate a center and to transfer this knowledge into the enclosures of different shapes was demonstrated also in rats (Tommasi and Thinus-Blanc, 2004).

The importance of hippocampus for encoding the geometry of the enclosure was shown both in birds and mammals (Tommasi and Vallortigara, 2001; Tommasi and Save, 2005).

In open space, where the shape of environment could not be encoded, the animals could use for orientation the relative distances and directions of multiple landmarks.

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. They used for navigation a configuration of extra-maze cues. Later experiments showed that this ability is highly dependent on hippocampus (Morris et al., 1982; Pearce et al., 1998).

Kamil and Cheng (2001) 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.

Spetch et al. (1992) even demonstrated the ability of pigeons to use multiple landmarks presented on computer screen for locating a goal.

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.

The manipulations with relations among landmarks could demonstrate whether animals are able to deduce general geometric rules. 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 using of a landmark as a beacon and simply searching near the landmark array. This strategy could be used only if the landmarks are situated very close to the goal with increasing distance it becomes ineffective.

The transformation of landmark array (for example expanding) should reveal which of the specified strategies is used.

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 and colleagues (Spetch 1995; Spetch et al. 1996, 1997) 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.

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 when 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 hidden in one of the discrete places, at the center of four identical landmarks. All subjects could locate a goal during the training, but only human adults succeeded in the expansion test.

Collett et al. (1986) trained gerbils in similar task to locate a goal, which position was determined by an array of multiple landmarks. Gerbils locate the goal readily, but after some landmarks were removed or the array was expanded they fail to use configuration strategy and used single landmarks for orientation.

However, in contrast to these experiments demonstrating the lack of ability to abstract geometric rule in expansion tests (Spetch et al. 1995, 1996; Collett et al., 1986; MacDonald et al., 2004) Kamil and Jones (1997, 2000) 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 corvid (Clark's nutcrackers; *Nucifraga columbiana*), a non-seed-caching corvid (jackdaws; *Corvus monedula*), and a non-seed-caching columbid (pigeons; *Columba livia*).

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 phylogenetic 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, MacDonald, 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.

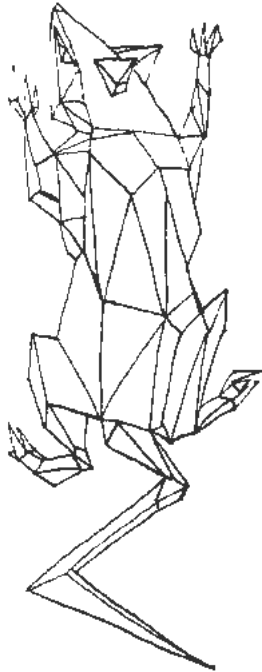
We developed new behavioral tests to study the cognitive ability to perceive configuration of visual stimuli and to perform spatial choices in a real space according to these abstract stimuli not directly connected with the response space.

We tried to determine whether the animals could interpret inner configuration of these visual stimuli or whether they perceive them simply as geometrical patterns and associate the spatial response 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*).

SUMMARY OF THE EXPERIMENTS



EXPERIMENT I

Nekovarova T, Klement D. Rat's operant behavior can be controlled by the configuration of objects in an animated scene displayed on a computer screen. *Physiol Res*, 2006;55(1): 105-13.

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.1, 2).

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 first group, but with no visual stimuli presented on the computer screen.

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 displayed visual stimuli was carried out. (Fig.2)



Fig.1: 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.

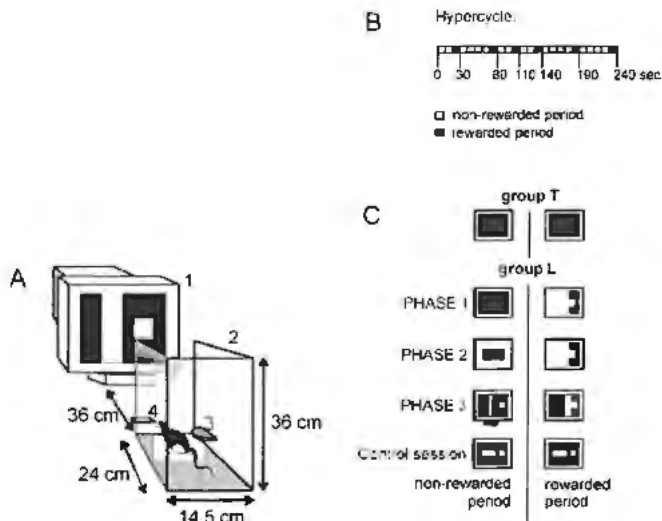


Fig.2: (A) Scheme of the apparatus: 1 – monitor, 2 – rat chamber, 3 – dipper, 4 – lever. (B) Hypercycle: a fixed sequence of rewarded and non-rewarded periods used in all sessions. The hypercycle repeated 10 times during each 40-min session. (C) Patterns displayed on the computer screen during the rewarded and the non-rewarded periods. Group T tested whether rats can identify the rewarded periods within the hypercycle by timing. Rats in group L were successively trained to discriminate light and dark conditions (Phase 1), to discriminate two discrete patterns (Phase 2) and finally to recognize the configuration of objects in the animated scene (Phase 3). During the nonrewarded periods the bar moved from the left side of the screen toward the stationary rectangle. The control session was carried out at the end of Phase 3.

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 timing strategy, thus the group T was significantly worse than group L and its efficiency did not change during the whole Phase 1. (Fig.3)

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.

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).

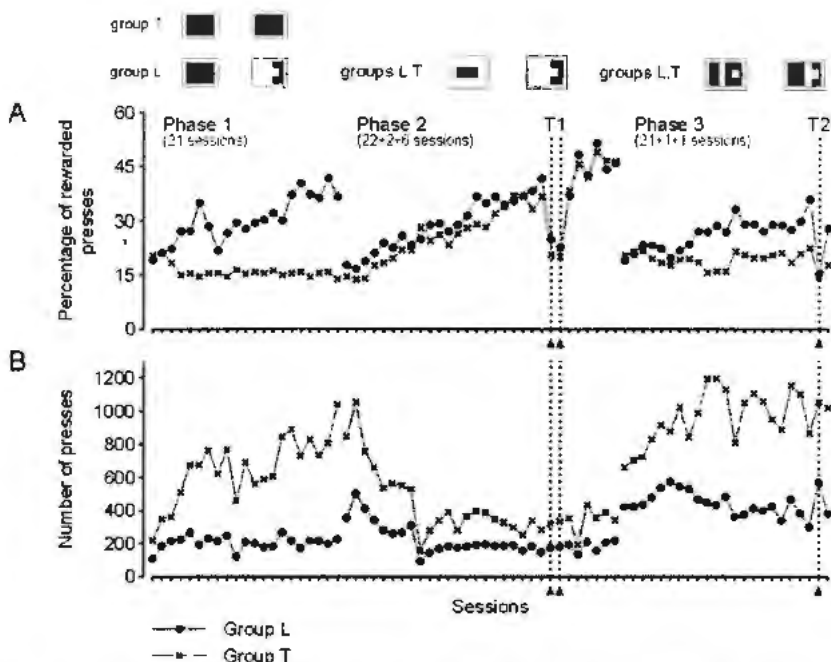


Fig.3: A: The percentage of the rewarded responses (efficiency) (the ratio of correct responses to the number of all responses) per session.

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.

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.

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

EXPERIMENT II

Nekovarova T, Bures J. Spatial decisions in rats based on the geometry of computer-generated patterns. *Neurosci. Letters*, 2006;394(3):211-215.

In the Experiment II (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.

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. (Fig.4, 5)

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.6)

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, but 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. (Fig.6)

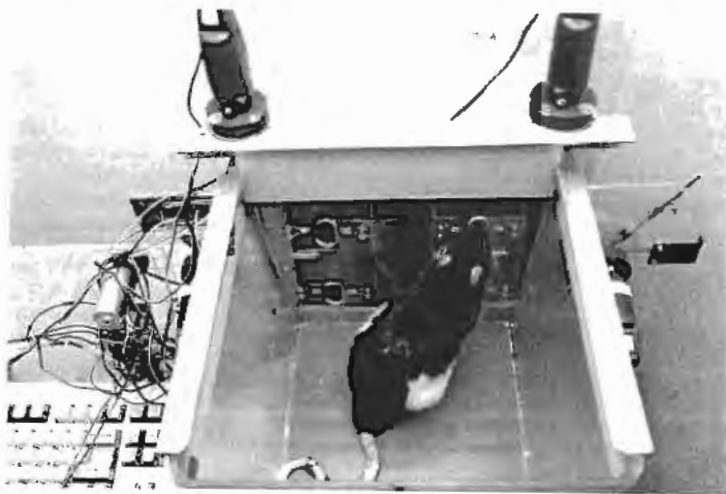
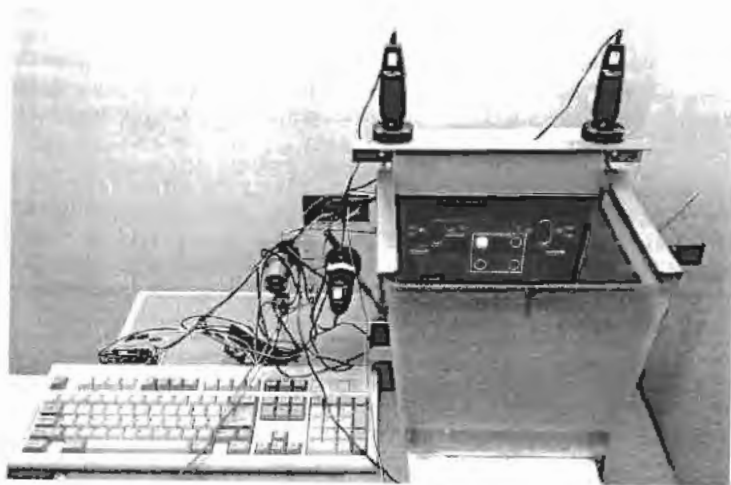


Fig.4: Apparatus used in Experiment II.

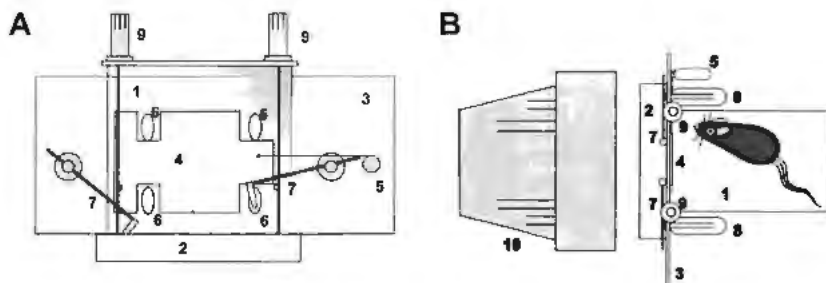


Fig.5: The scheme of the apparatus (A) top view; (B) front view. (1) Box, (2) water reservoir, (3) extended front wall, (4) sliding barrier, (5) electric motor closing the barrier, (6) nosing holes, (7) dippers, (8) electric motors lifting the dippers, (9) electric motors selecting the upper and lower positions to which the dippers will be raised, (10) computer monitor.

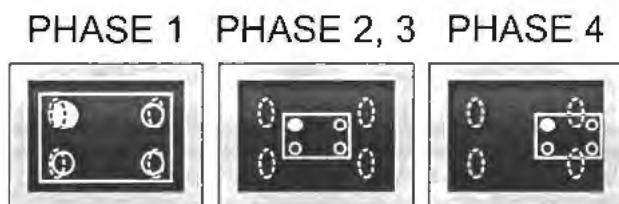


Fig.6: The visual stimuli displayed on the screen in particular phases of Experiment II.

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.

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 without the visual stimuli at the end of this phase (Fig.7).

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 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.

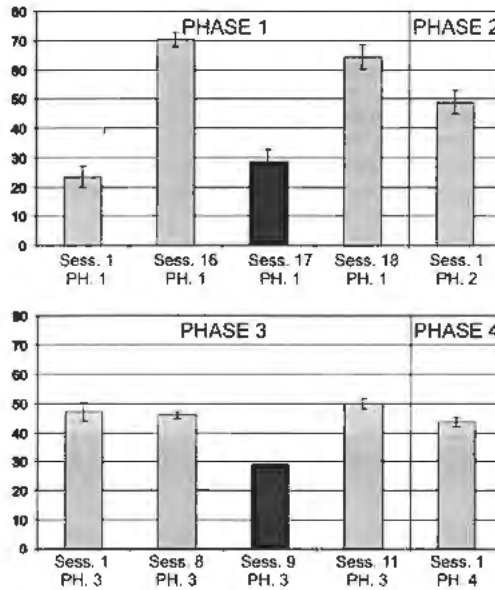


Fig.7: The percentage of rewarded presses \pm S.E.M. Dark columns represent control sessions without visual stimuli. *Upper graph*: column 1 shows session 1 of Phase 1, column 2 session 16 preceding session 17 (column 3). Column 4 shows the last session 18 of Phase 1. Column 5 represents the first session of Phase 2. Columns 1 and 3 differed significantly from columns 2 and 4, but did not differ significantly from each other. Column 5 differed significantly from all other columns. *Lower graph*: Column 1 shows session 1 of Phase 3, column 2 session 8 preceding session 9 (column 3). Column 4 shows the last session 11 of Phase 3. Column 5 represents the first session of Phase 4. Columns 1, 2 and 4 differed significantly from columns 3 and 5, but did not differ significantly from each other. Columns 3 and 5 differed significantly from all other columns.

The sequence previously used in Phase 1 and 2 was generated in the pseudorandom sequence and consisted of eight elements. 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 and thus the each position could be followed by every other position, including itself.

The efficiency in the control session with changed sequence 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. (Fig.7)

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.

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, when no visual stimuli were 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. (Fig.7)

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

Nekovarova T, Nedvidek J, Bures J. Spatial choices of rats based on abstract visual information: Pattern- or configuration-discrimination? Behav Brain Res, 2006;172: 264-271.

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.8)

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.

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.8)

After we changed the visual stimuli in Phase 2, the efficiency of both groups decreased significantly. However, it was important, that the 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).

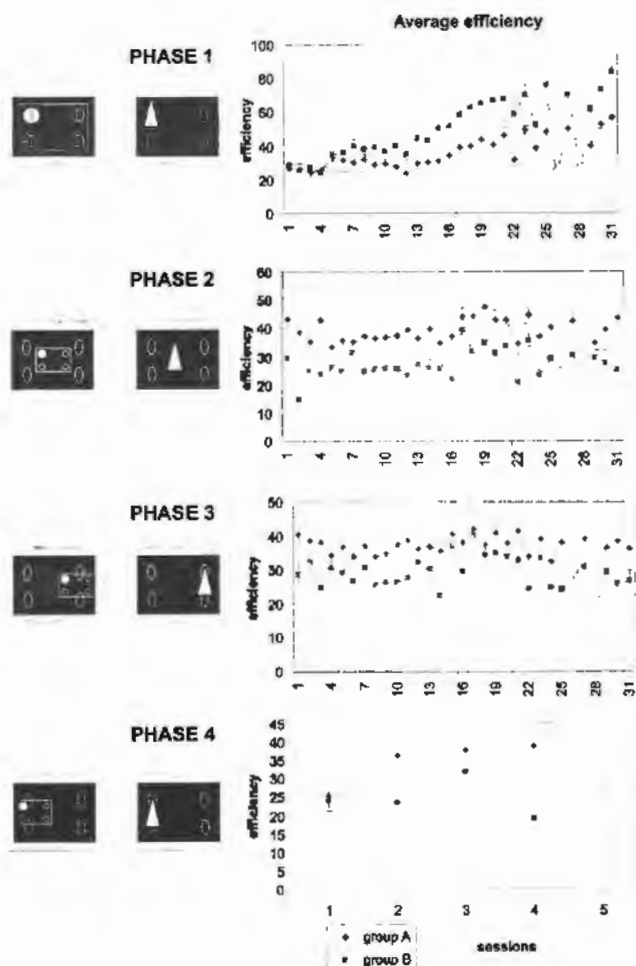


Fig.8: The percentage of the rewarded responses (efficiency; the ratio of correct and all responses) per session. And the visual stimuli displayed in the particular phases for group A (left) and group B (right). The dark points represent the efficiency of group A, bright points of group B. The empty points marked the control sessions, when the monitor was off and no visual stimuli displayed.

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 (naive animals), nor from the control session of Phase 2 (no visual stimuli).

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.

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.

EXPERIMENT IV.

Nekovarova T, Nedvidek J, Bures J. Spatial choices of macaque monkeys based on abstract visual information. Behav Brain Res, 2006b;174: 93-100.

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.9, 10-A)

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 (Fig.10-B, C).

By contrast, the second monkey (subject B - Attila) was trained to associate geometrical patterns (without any implicit spatial component) with the particular positions of the touch-holes (Fig.10-B, C).

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. (Fig.10-C)

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.



Fig.9: Photo of the apparatus. The monitor, the feeder and the box for a monkey.

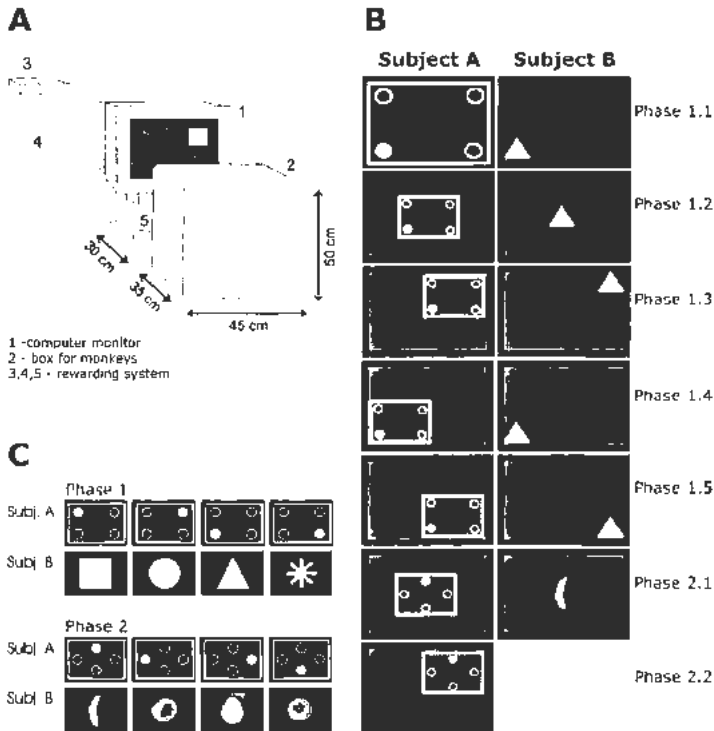


Fig.10: (I) The scheme of the experimental apparatus. The monkeys were placed in the box in front of the computer monitor presenting the visual stimuli. (II) The "screen shots" seen by the monkeys. It shows the position and the size of the visual stimuli used in various phases of the experiment. The left column shows the configuration (spatial) visual stimuli (subject A), the right column the patterns without any information about response space (subject B). For phases 1.1–1.5, the examples show only stimuli marking the upper left lower position. In phase 1.1 the visual stimuli marked directly the rewarded touch-hole, in phase 1.2 the size of configuration stimuli was reduced and both the configurations and the patterns were shifted to the center of the screen. In phases 1.3–1.5 the visual stimuli were displayed in different positions on the screen. In the second phase, new visual stimuli were used. In phase 2.1 the stimuli were displayed at the center of the screen, in phase 2.2 the configuration stimuli were shifted, but the patterns were still displayed in the center. (III) The figure shows the particular stimuli connected with particular positions in phases 1 and 2. The session consisted of a succession of stimulus-presentations. In one presentation only one stimulus from the set of four was displayed to indicate the position of the rewarded touch-hole: either the configuration stimulus (for subject A) or the pattern (for subject B).

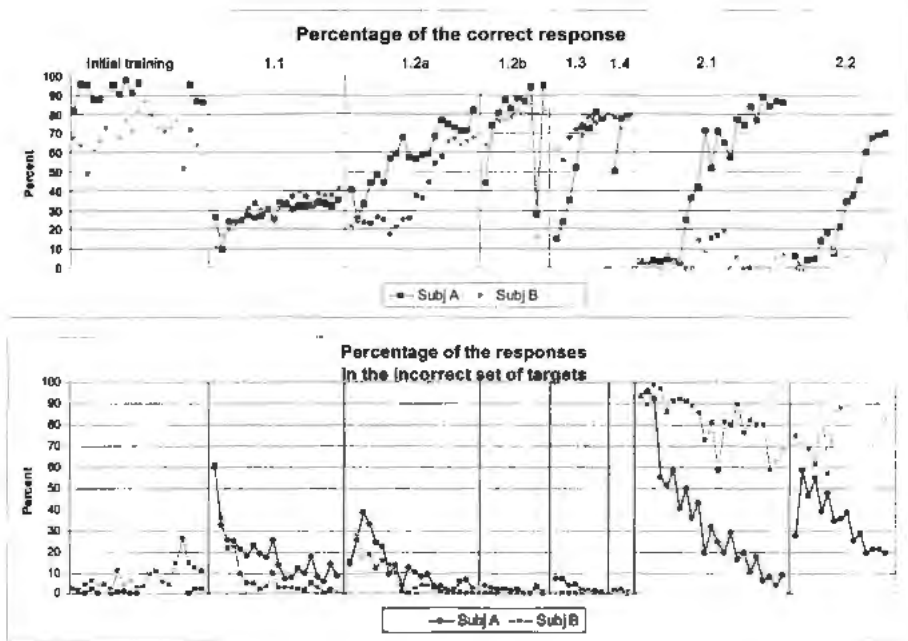


Fig.11: Upper graph: Percentage of the correct responses (ratio of the correct to the number of all responses) per session in particular phases. Lower graph: Percentage of the responses in the incorrect set of targets. In Phase 1 the incorrect (non-rewarded) nosing holes were: 2, 4, 5, 6, 8; In Phase 2 the non-rewarded nosing holes were: 1, 3, 5, 7, 9.

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 signaling 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 in the sessions immediately after the change of the position of the stimuli, but rapidly returned to previous level. (Fig.11)

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.

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.10-C). 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.

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.11)

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. 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 the new positions, 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.

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

Afterwards, we showed that rats are 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 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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