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Research report

Spatial orientation strategies in Morris-type virtual water task for humans

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Abstract

The present study characterized frequent motion patterns (search strategies) that occurred during spatial navigation in a virtual maze. The research focused on identifying and characterizing some search strategies, the temporal progression of strategy-use, and their role in spatial performance. Participants were 112 undergraduate students (42 males and 70 females). We identified three search strategies that predicted spatial performance. *Enfilading* refers to an approach-withdrawal pattern of active exploration near a target location. *Thigmotaxis* refers to a search strategy that involves continuous contact with the circular wall of the maze. *Visual scan* involves active visual exploration while the subject remains in a fixed spatial location and turns round. In addition to identifying these motion patterns, some significant points of the spatial learning process were also detailed where strategies appeared to shift systematically. The applied search strategies in these transitional points have determined overall spatial performance.
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Morris-type water maze (MWM) [26] is a frequently applied laboratory tool in the study of spatial cognition in animals. Growing evidence demonstrated that several factors influence the learning process of the spatial position of a hidden escape platform in a circular arena guided by allocentric references and these also reveal differences in how spatial maps are constructed. The most investigated factors are sex, age and location of lesions [9]. MWM permits investigators to examine the results of lesion and pharmacological intervention and to thereby understand the neurological basis of the spatial map construction in animals. Obviously it would be of some benefit if this tool was available for humans.

In humans, constructing a spatial representation of real or virtual space appears to require the acquisition of at least three kinds of knowledge: landmark, route, and map-like knowledge. Only after getting in touch with distinct cues and learning the paths between them can one construct a cognitive map. This general cross-sectional model also corresponds to the ontogenetic development of children's spatial abilities [35]. Neurological evidences of place learning and map constructing also support this three-stage model [28].

Hence, salient cues for orientation have an important contribution to the process; these navigational cues mark the interface between the person and the environment. Usually, visually emergent features (i.e., corners, signs) serve as landmarks. In the early stage of spatial construction the landmarks appear to be processed in isolation and the relations among the other cues or to the surroundings do not appear to be encoded.

Route learning involves the pair-wise association of cues along a known path, but without an appreciation of the overall direct relations between the starting and target positions. Route representations can exist in parallel and independently from each other even when they occur in one geographic area. During walks on a learnt path (a route) the direction of travels change from time to time, but the focus is on pro-

cedural knowledge (i.e., turn right on the corner) instead of on the relative positions of the cues (a cognitive map). Hartley et al. [12] argued that such route following involves an action-based representation, with response learning at its core. The activation of a distinct neural substrate (the head of the right caudate nucleus) accompanies this type of spatial performance. On the other hand, way finding on novel routes requires place learning in a cognitive map; the corresponding neural structure is the right posterior hippocampus [12,42].

Configuration or survey (map) knowledge is an integrative and global knowledge of the space where the topological relations of salient cues and learnt routes are represented in a Euclidean coordinate system. Such map-like representations are at least partially composed of route knowledge previously acquired from either procedural (i.e., exploration) or declarative (i.e., observational learning) learning [1,38]. Although some argue that procedural and declarative learning create unique configurational representations, this difference can be diminished if the subject is instructed to pay attention to the settings of the applied task [23]. Nevertheless, the source of this difference is still not clear. Perhaps the most puzzling demonstration of this difference is spatial learning in virtual reality, where no self-motion is present.

A survey representation provides an overview of spatial layout and has an allocentric frame of reference. In this frame, distal objects, and the relations among them, are represented in a dynamic mental map. Data about "what" and "where" are recorded in interconnected networks of cues and landmarks in certain brain areas [22]. Although the observer is a part of this representation, the centre of the map is mentally weighted and computed based on the salience of the spatial features [27]. Movement of the observer does not have an effect on the configuration. Continuous updating in the vectorial summation of the object-relations occurs as a consequence of changes in the perceived reality (i.e., motion, structural modification, etc.).

Hartley and Burgess [11] describe similar processing modes, suggesting that the two reference systems differ in both spatial and temporal characteristics and that the related neural substrates are also different. They suggest that hippocampal processes are concerned with large distances and long timescales, whereas parietal processes are more concerned with short timescales and the space immediately surrounding the body [11, p. 2]. The importance of updating positions and headings is also emphasised in connection with the egocentric frame of reference, while in the case of the allocentric frame, the computational functions of the locations on the anchored cognitive map are emphasized [6,7,16].

Thinus-Blanc et al. [37] assume the existence of two levels in spatial processing: a lower visual and a higher abstract one. By this view, visual images of some parts of the environment are stored in a panoramic snapshot-view; and the role of early spatial orientation is to gain multiple numbers of perspectives of the space. The second level is made up of more abstract representations conceived as schemata, which guide and organize information-gathering processes and extract spatial invariants.

All of these authors agree that the agent, cues, and target are equally represented on the final allocentric map centred in the hippocampus [27].

1. Different levels of spatial strategies

The concept of spatial strategy varies in the research literature. The term "strategy" causes this confusion, as it refers to sets of strategies applied to specific behavioural situations. The most classic way in which psychology investigates the structure of behaviour is to observe performance across many situations and attempt to determine the possible commonalities of performance. Analysing the trajectories (search strategies) of rats during the completion of spatial tasks, for example, and describing the most common of these strategies is a simple and effective way to uncover invariance in exploration. Most of the studies using this method focus on exploratory activity centred on a specific object or area of the search space [10]. From another perspective, every goal-directed spatial action might be interpreted as spatial strategy [28,27]. If an animal uses landmarks in its navigation for exploring or avoiding a certain place, this behaviour is evidentially a fruitful and adaptive response to the environment. Other researchers emphasise the macro features of spatial behaviour such as modes of information acquisition or individual differences in cognitive sub-processes [30].

Gaunet and Thinus-Blanc [36] described two types of exploratory patterns: a Cyclic pattern and a Back and Forth pattern. The "Cyclic pattern" consists of visiting all the objects successively, beginning and finishing at the same one. The "Back and Forth pattern" involves making repeated contacts between two objects. According to these authors, their data support the idea that specific organizing strategies underlie spontaneous exploratory behaviours, the use of which produce more or less accurate spatial representations.

Hill et al. [13] identified another set of search strategies. The first strategy involves the boundaries of the surrounding space. When this strategy is used, exploration is minimal, as the explorer stays close to the wall to maintain relative safety in a novel and frightening environment. The second strategy is a network-type exploration. The third strategy, an object-to-object strategy, involves random wandering until the first cue or landmark is found. After the exploration of this landmark, any possible relation to other closely located cues is sought. If successful, the same procedure is executed with the next object. If the organism does not find another cue or landmark nearby, it again begins to wonder. A mixture of the first and third strategy also occurs; when the organism uses the boundary of the space as a reference point; nearby objects will be explored. A fifth strategy, which the authors identified as a special case, occurs when the organism uses a salient landmark as base reference and carries out all exploratory activity in relation to this point.

Thinus-Blanc et al. [37] have suggested a close relation between exploration, as a sensorimotor activity, and spatial knowledge through functional reciprocal links. In the first phase of spatial learning the information is organized along a body-centred reference, while in the latter phase the representations are distributed in allocentric topographical cognitive maps.

2. Goal-directed strategies

In their seminal book, O'Keefe and Nadel [28] identified a set of spatial behaviours they call spatial strategies. These strategies involved exploration of a novel environment, detection of changes of a familiar environment, navigation to a goal from different starting locations and detour behaviour. The main feature of a strategy is that subjects utilize it during their goal-directed spatial response to the environment. These strategies are usually directed toward objects or boundaries or an obstacle. Note that on this level of interpretation the action representations and their neural correspondents play a central role, but the route is not detailed as the strategies are being carried out.

It is assumed that the representation of an environment is originally constructed during exploration; this process is viewed as a cognitive activity that keeps the maps in register with the environment. When an animal or a human enters an environment, the mapping system first searches for a match between the represented set of cues and boundaries and the incoming sensory data. Competitive fine-tuning and error-correction of computational settings begin immediately after the first encounter with the novel space [27].

3. Virtual Morris water task in spatial research

By creating virtual rooms or cities and asking people to find certain locations in them, precise investigation of human spatial navigation and place learning under highly controlled conditions seems possible [15,14].

The geometric and local features of the landmarks used inside a virtual reality (VR) have a huge impact on the performance. Navigational learning is affected by different types of navigational cues. These cues need to have memorable forms if subjects' navigational efficiency is to be improved [33]. The use of distal or proximal landmarks also contributes to the construction of the cognitive map in a Morris-type virtual maze task [14].

Other factors might influence spatial cognition as investigated in virtual spaces, such as the prior degree to which general computer experience transfers specifically to VR [41] or the effects of age on virtual place navigation and allocentric cognitive mapping [18,25,39].

Considering all these results, there is still a good correspondence between the level of virtually acquired knowledge and the real world performance; hence VR can be used with high reliability to examine spatial and other behavioural interactions in simulated settings [5,31].

The present study focuses on three hypotheses of spatial strategies in a virtual MWM: (a) the observable search strategies (patterns in the path of navigation) can be used as reliable and valid measurements for making predictions about spatial performance; (b) there are shifts in dominant strategy-use as spatial learning progresses; (c) the level of success in the spatial task depends on the application of different spatial strategies.

4. Method

4.1. Participants

Participants were 112 undergraduate students (42 males and 70 females) from various faculties of the University of Pecs, Hungary. The mean age was 21.4 years (S.D. = 1.6) with a range of 18–27 years. Each was paid volunteer, recruited through advertisements. The participants were informed in advance about the aims and procedures of the experiment. None had previous psychiatric illnesses nor any physical disabilities that would interfere with completing the computer-based spatial task. Anticipating a possible distortion coming from individual differences of computer game playing practice [41], the participants were pre-selected during recruitment on the basis of a questionnaire, which asked about computer using habits. Only those students whose computer game playing did not exceed a half an hour per week were eligible for the study.

4.2. Apparatus

For measuring spatial performances and registering motion patterns in virtual environment, a desktop-based computer program Computer-generated Arena (CGA) [14] was used (for further details about the program, see http://w3.arizona.edu/~arg/data.htm).

In this virtual maze, participants are tested on a standard PC displaying a coloured view of a circular arena, that is located within a square room. Each wall in the room has a distinctive pattern of windows or arches, thereby providing a means by which participants could orient themselves within the virtual space. The actual viewpoint of the participants was a first-person perspective, so they were looking at the scene as though standing on the floor of the arena.

4.3. Procedure

Participants were seated next to a standard desktop-based PC equipped with a 17 in. SVGA screen, stereo speakers and a joystick. In the CGA program, there were two types of rooms. The first was a practice room, with no objects or platform in it. The only purpose of this room was to get familiar with the virtual environment and to practice virtual locomotion with no time constraint or actual task. After finishing in the practice room, the subjects pressed the space bar to be teleported to the test room. Inside the test room there are distal objects on the walls and a blue rectangular platform on the floor, which is visible in the first two trials (Trial 1 and Trial 2), and invisible from Trial 3 to Trial 10. The participants' task was to find and navigate onto this target platform under the shortest time possible, and to remember its place. There were eight test trials and the
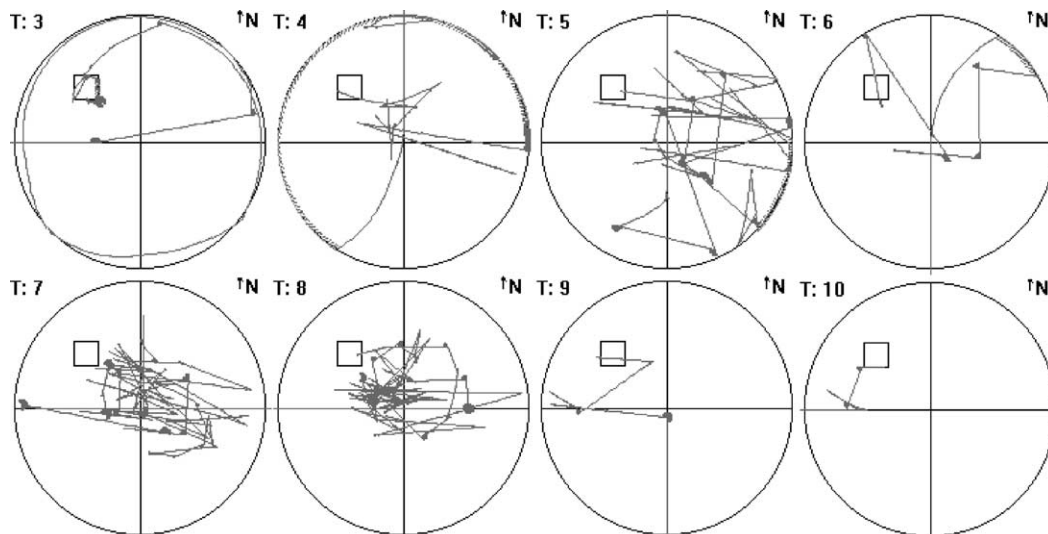
Fig. 1. Navigation paths of one subject in the eight test trials within the virtual Morris-type water maze. The maze has a circular shape and it is divided into four imaginary quadrants. The invisible square platform is also displayed in each case with a fictive North axis that is marked with an "N" sign and an arrow. The subject's route is followed by a continuous line form different starting positions to the platform.

positions of the distal objects and the platform were constant during all the trials. Each trial lasted for 3 min. If the participants failed to find the platform within 3 min, the CGA program automatically teleported them to the next practice room. After the last trial, the program terminated and the trial set was over.

The CGA collected quantitative data of the subjects' navigations. Path length and latency are the two most characterizing variables of spatial performance. The program also recorded the path maps in a bitmap format for strategy analysis (Fig. 1).

The circular arena is showed in a plan-view and it is divided into imaginary quadrants. The location of the platform is also indicated on these maps so as the trial number (i.e. T:6) and the fictive direction of North (↑N). Navigation path is drawn with a continuous line.

4.3.1. Movements in CGA

Any motion in this virtual space is a set of binary variables. Vector coordinates of the subject were recorded in a regular time fashion, therefore virtual motion means that either there is a change in these coordinates or not between two consecutive periods of time. In other words, the participant either walked at full speed or stand still. Speed then is a function of a ratio of path length over time. Hence, speed is an index of navigation activity as a consequence of constant velocity, rather than the actual speed produced by a movement.

4.3.2. Categorizing search strategies

Search strategies are composed of repeated motion patterns that form distinct parts of a participant's movements (search path or navigation path). These repeated patterns are qualitative data that are distinctively present on the search paths (see Fig. 1). Search strategies are usually composed of search patterns, thus a precise description for all of observed patterns are essential for the identification. By analysing the principal components of the navigation maps, four distinct spatial search strategies could be distinguished: thigmotaxis, circling, visual scan and enfilading.

4.3.3. Thigmotaxis search strategy

Thigmotaxis represents a circular part of the path that is passed along close to the arena wall (Fig. 2). This is a summed value of every such motion pattern in the actual trial. In many cases thigmotaxis re-occurred on the same portion of the arena wall, so the final summed value may exceed 360° (the total circle of the arena wall).

This strategy keeps the person in a constant contact with a stable element (i.e. wall) of the environment and gives the person a frame of reference by virtue of its own independent existence. A 'virtual touch' is a necessarily component of thigmotaxis because it permits the person to define his/her own position in a bordered virtual space.

4.3.4. Circling search strategy

We defined "circling" as an arc shaped search path, which occurred somewhere inside the arena but not close to the wall and with the same curvature as the arena wall (Fig. 3). Every curve was measured that fitted this rule.

The dimension of circling is in virtual meters and a summed value of this motion pattern is counted in each trial. During circling, the person could monitor the distal cues on the wall that corresponded to their own allocentric changes in virtual space. This monitoring requires only visual feedback and therefore no 'virtual touch' is needed. Astur et al. [4] named an identical search strategy "circle".
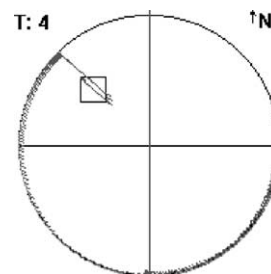

Fig. 2. The figure shows an example of a thigmotaxis search strategy in Trial 4. Subject walks close to the circular wall and stand away from it only when the platform is close enough to approach it.
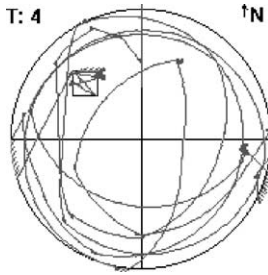
Fig. 3. The figure shows examples of some circling search strategy in Trial 4. Every arch shaped pattern that has the same curvature as the wall was added to the overall value of circling.
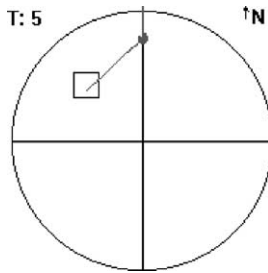

Fig. 4. The figure shows an example of a single visual scanning strategy in Trial 5. The strategy appears like a small spot on the path map as the subject turns around in a fixed position and the CGA program records the new directions for the same location coordinates.

4.3.5. Visual scan search strategy

A visual scan occurred when a subject remains in a fixed position and turns (Fig. 4). Only those turns were counted as a visual scan, that were greater than 20°. With this restriction, small corrections in trajectory were not counted as a visual scan.

Visual scan represents an active exploration of the distal cues, the relations among them, and more importantly, shifts from one cue to another. The 20°-criteria ensured that the person had switched visual focus between cues on the wall. This is the minimal angle of a turn needed from any part of the arena for a visual shift.

4.3.6. Enfilading search strategy

Enfilading is composed of relatively small position corrections and non-strategic motions. During this search strategy, it seems that the subject performs a rapid search, small direction changes and some straight lines of walk on a limited area of the virtual space.
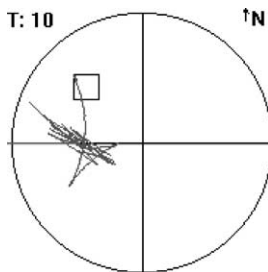

Fig. 5. The figure shows an example of a typical enfilading search strategy in Trial 10. The subject performed a rapid search with some small direction changes in his walk on a limited area that was relatively close to the platform.

Astur et al. [4] named a similar strategy as "zigzag". It is the virtual equivalent of "Back and Forth" exploratory strategy, named by Gaunet and Thinus-Blanc [10]. Note that enfilading may occur with, or without the cognitive control required by the other three search patterns. Hence, it is not clear whether enfilading is a conscious strategy or non-strategic motion. Either a cognitively loaded, goal-directed search or an almost totally motion-directed, automatic process, enfilading is focused in a limited area and, as a search pattern, it is easily identified on the navigation maps (Fig. 5).

Enfilading is measured in virtual meters and counted with a subtraction of the non-zero length strategies (thigmotaxis, circling) from total path length.

5. Results

5.1. Variables

During the process of data evaluation the following variables were used: CPFT (platform finding latency in seconds needed for the subject to locate and move onto the target platform); CPFL (platform finding length measured in virtual meters[1] from the starting position to the target platform); CGTHIGM (thigmotaxis search strategy measured in virtual meters); CGCIRC (circling search strategy measured in virtual meters); CGENFI (enfilading search strategy measured in virtual meters); CGVS (visual scanning search strategy counted individually per trial).

Thigmotaxis (CGTHIGM) and circling (CGCIRC) search strategies were first measured in degrees and than transformed into virtual meters. We calculated virtual meters using the following formula:

$$\mathrm{CGWALL} = \frac{\pi}{180} \times \mathrm{wall}^\circ \times r_{\mathrm{CGA}}$$

where wall° is the degree in radius of the measured distance and r_{CGA} is the radius of the CGA in virtual meters, which was 50 virtual meters in this experiment.

Similarly, circling was transformed into virtual meters using the formula:

$$\mathrm{CGCIRC} = \frac{\pi}{180} \times \mathrm{circling}^\circ \times r_{\mathrm{CGA}}$$

We examined the distribution of each dependent variable using the Kolmogorov–Smirnov test. Levene's test of homogeneity of variances were significant in case of all the variables—CPFT: $F(7,888) = 10.26$, $P < 0.001$; CPFL: $F(7,888) = 7.31$, $P < 0.001$; CGTHIGM: $F(7,888) = 5.72$, $P < 0.001$; CGCIRC: $F(7,888) = 4.45$, $P < 0.001$; CGENFI: $F(7,888) = 6.49$, $P < 0.001$; CGVC: $F(7,888) = 8.95$, $P < 0.001$.

Temporal linearity in each variable was also tested with ANOVA Linear Contrast and found to be significant in all instances CPFT: $F(7) = 9.04$, $P < 0.001$; CPFL:

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[1] A virtual meter is the dimension of the CG Arena software and proportionally equivalent to the real world distance of 1 m.

$F(7) = 5.65$, $P < 0.001$; CGTHIGM: $F(7) = 2.94$, $P < 0.05$; CGCIRC: $F(7) = 2.40$, $P < 0.05$; CGENFI: $F(7) = 4.89$, $P < 0.001$; CGVS: $F(7) = 13.86$, $P < 0.001$. This means that the changes in performances and search strategies across trials can be considered linear and therefore linear regression models can be applied to these data.

For analyses of place learning and search strategies, data coming from the first two trials (Trial 1 and Trial 2) were ignored as these were only practice trials.

5.2. Validity test for the spatial orientation strategies

A stepwise linear regression was used to examine the assumption that the search strategies are reliable and valid constructs for predicting spatial orientation performances in virtual space.

Latency of platform finding (CPFT) was used as a dependent variable in the regression model and the four strategies (CGTHIGM, CGCIRC, CGENFI and CGVS) were used as predictors. The stepwise method filtered out the nonsignificant predictors and left only those which were strong enough for the model to reach the level of significance.

Out of the four predictors, three remained in the model (CGTHIGM, CGENFI, CGVS) and one (CGCIRC) dropped out. With this correction the R^2 value became 0.865 for our model. Plate 1 illustrates the strong linear correlation and probability index of the model.

This result shows high predictability between a well-established measure of place learning (platform finding latency) and the set of search strategies we have identified (excluded circling). The result of this analysis confirmed our first hypothesis, that the some spatial search strategies are reliable and valid indicators of spatial orientation in virtual space.
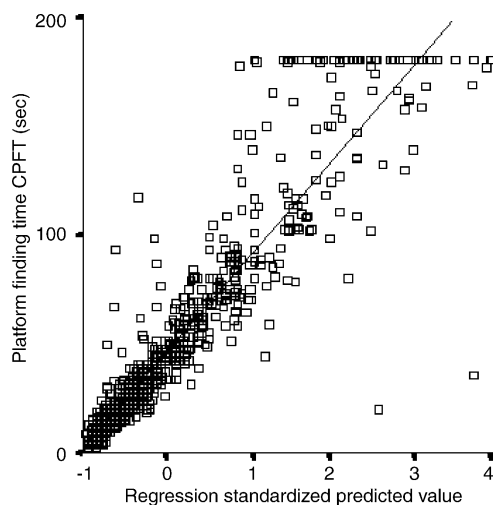

Plate 1. Linear regression plotting shows the strength of predictability of spatial performance (CPFT) with spatial strategies (enfilading, thigmotaxis, visual scanning). The value of predictability is $R^2 = 0.865$.

Table 1
Results of a Duncan post-hoc analysis, with the eight test trials (Trial 3 to Trial 10) clustered into four subsets based on the mean platform finding time (CPFT)

	Subset 1	Subset 2	Subset 3	Subset 4
Trial 3				69.53
Trial 4			56.25	
Trial 5			53.78	
Trial 6			47.28	
Trial 7		37.47		
Trial 8		37.21		
Trial 9	31.52			
Trial 10	35.96			

5.3. Dynamics of search strategies

As mental representation of the search space improves in time, the application of the search strategies will change systematically according to our second hypothesis. This argument was tested by examining dynamical changes in CPFT, CGTHIGM, CGENFI and CGVS over trials in a multivariate ANOVA test.

The between-subject effects confirmed this prediction, as platform finding latencies (CPFT) decreased significantly over trials ($F(7) = 14.613$, $P < 0.001$), such as the measures of CGTHIGM ($F(7) = 3.172$, $P < 0.05$); CGENFI ($F(7) = 9.598$, $P < 0.001$); and CGVS ($F(7) = 11.890$, $P < 0.001$).

To explore these results in-depth, we performed Duncan's post-hoc tests on each of the identified search strategies. This procedure permitted us to group homogeneous subsets of data by temporal means. Subsets derived from platform finding time (CPFT) based on strategies showed that there were shifts in strategy-use during the eight test trials. These qualitative changes in search strategies happened immediately after the first test trial (Trial 3), than a second shift appeared around Trial 6, and a final shift could be observed after Trial 8. Post-hoc analysis identified four distinct subsets of trials (see Table 1).

5.4. Difference between good and poor spatial performances

On the basis of the subjects' spatial performance (CPFT) two groups were created.[2] Those subjects whose mean platform finding time (CPFT) was less than the median of the total group (Mdn = 41.45 s) minus one standard deviation (24.94) belonged to the "good spatial performers" group ($n = 14$; mean CPFT = 15.19; S.D. = 3.38). Subjects having a mean CPFT greater than the median of the total group plus one standard deviation belonged to the "poor spatial performers" group ($n = 18$; mean CPFT = 89.38; S.D. = 17.45).

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[2] In some cases a relatively low platform finding latency (CPFT) can be obtained by an almost random-like search with respectively long platform finding length (CPFL). This behaviour should not be considered as good performance, therefore subjects using extremely high (over +2 S.D.) platform finding length (CPFL) were put into poor performers group.
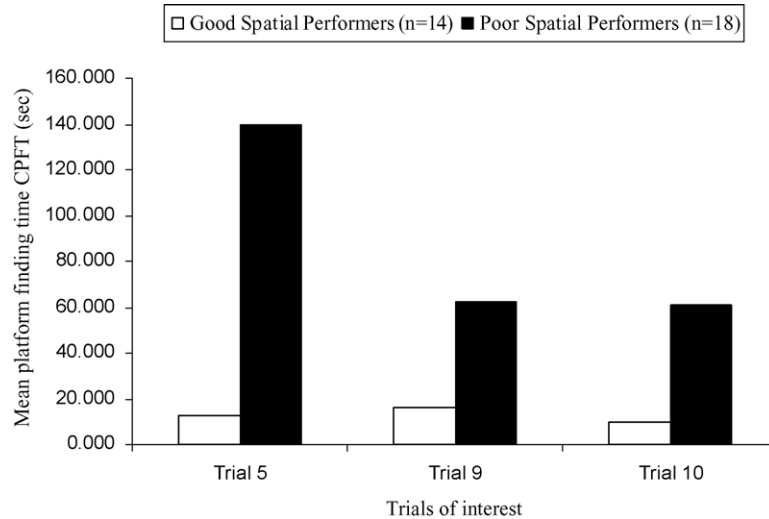
Fig. 6. Differences between the two spatial performance groups around some major turning points (Trial 5, and Trials 9 and 10). These differences can be predicted by thigmotaxis and visual scanning strategies with a predictability value $R^2 = 0.686$.

Table 2
Results of a stepwise linear regression model, with thigmotaxis (CGTHIGM) in Trial 5 and Trial 10 and visual scanning (CGVS) in Trial 5 as predictors for spatial performance differences

R value	R^2
0.830	0.689

Dependent: spatial performance grouping variable. Predictors: CGTHIGM5, CGTHIGM10, CGVS5.

To analyse the differences in search strategy used by the good and poor spatial performers groups, we used a second stepwise linear regression (Table 2). The dependent variable was again platform finding time (CPFT) and the predictors were the three search strategies we identified previously (CGTHIGM, CGENFI, CGVS).

The results indicated that differences in spatial performances between the two groups could be predicted on the application of two spatial strategies: visual scanning (CGVS) and thigmotaxis (CGTHIGM). In other words, the subjects in the good and poor performance groups used different strategies (Fig. 6). In addition, this result is even stronger around the previously described turning points.

6. Discussion

In the present study, we characterized and examined the functional utility of specific search strategies during spatial orientation in a Morris-type virtual maze.

The presented results indicate that the quality of spatial performance is highly depended on the search patterns used by the agent. Out of the four previously observed spatial patterns three were related to the quality of spatial performance significantly. The strategies we labelled as thigmotaxis, enfilading and visual scanning were strong predictors of overall performance changes and have predicted the level of success in the spatial task. Based on the present results, the hypothesis that the visually observed search strategies are functionally interconnected to the quality of spatial performance is justified. This finding is consistent with the assumption that spatial performance could be analysed in terms of the search strategies observed on the path maps [4,36].

Thigmotaxis creates an egocentric linkage to the boundary of the CGA space that, following the neophobia literature [8] may give a feeling of safety via the notion of being in contact with something tangible. In contrast, visual scanning is a strategy for active exploration of distal cues and the relations of one cue to another. Applying visual scanning in the early phase of spatial learning process should help the subject to determine the attributes of the surrounding space. Thigmotaxis defines the borders of space and visual scanning reframes it. We humans appear to use these strategies during our everyday exploratory activity in novel situations [27].

Enfilading was present on all trials of spatial learning. Although the variation of enfilading predicts spatial performance, it can, at the moment, only be considered as an indicator of the level of exploratory activity and virtual self-motion. Enfilading may be interpreted as an ambiguous behaviour that either can represent a cognitively loaded activity or a non-strategic search. Further experimenting is needed to clarify the basis of this motion pattern.

The circling strategy was not found relevant in any aspects of spatial performance nor temporal shifts in strategy-use in the present examination. One possible explanation for circling for not reaching the statistical significance in the present study might be that this strategy predicts spatial performance only through a secondary or intervening process, but not directly or by itself.

As a second hypothesis, we predicted that the use of search strategies is dynamically changing in time as the subjects

learn to locate the invisible platform. This leads to observable shifts in the usage of the search strategies at specific transitional points. It was also proved that there are indeed significant changes in the temporal distribution of performance data immediately after the first test trial (Trial 3), then around the middle of the learning phase (Trial 5, Trial 6) and at the end of the trial set (Trial 9). As a result of these transitional points, four subsets of trials were identified.

One subset covers only Trial 3, which is different from the other trials both in terms of strategy-use and the relatively long latencies required to locate the invisible platform. This trial represents the first real encounter with the place-learning task. Hence, the temporal distribution of the search strategies used in Trial 3 appears to be due to the novelty of the situation, the necessity to locate the invisible target for the first time, and the difficulty of the task.

Trials 4, 5 and 6 composed the second set of transitional trials. The spatio-relational changes in this phase were represented by unstructured spatial movements that may be accounted as a consequence of early map structuring processes. In the early stages of spatial learning these elements are fragmented. The landmarks have been identified but these landmarks are not yet fitted into a coherent map.

Short latency trials (Trials 7, 8, 9 and 10) were grouped in the third and fourth subsets of transitional trials. By Trial 7, the subjects appeared to acquire the basic relational structure of the space (a cognitive map) and constructed a topological notion of the objects. In these trials, it appears the subjects have represented the space in an allocentric frame of reference and performed mental computations concerning their own location and the location of the invisible target. The relations among the landmarks appeared to have become incorporated into their cognitive maps and therefore goal-driven navigation or alternative route findings were carried out more confidently.

It is worthwhile noting that the transition between the second and third subsets (around Trials 5 and 6) is associated with the high predictability of spatial performance by two strategies: visual scanning and thigmotaxis. This increased importance in the use of visual scanning and thigmotaxis indicates that a qualitative change in spatial representation occurs when there is an informational "need" for more active exploration of the environment (visual scanning) and at the same time, a "need" for fixed reference with the boundary of the space (thigmotaxis). The in-time appearance of these strategies on transitional trials and the proportional distribution of the strategies in these key stages of spatial learning are responsible for individual differences in performance.

Our third aim was to understand the differences between good and poor spatial performers. There is an obvious conceptual problem concerning the distinction between the two groups of individuals. It is often not clear in the literature, what makes the bases of these group divisions. In this study, we created two groups by having the median of the platform finding times and added one deviation for the poor performers and subtracted one deviation for the good performers group. We have also corrected the groups for the extremely long platform finding lengths that were not considered as good performances. With this grouping method the extremities of spatial performances for both directions could be well identified.

The difference between the two performance groups was due to application of different strategies but only around the second and fourth trial subsets (Fig. 6). The functional differences of the strategies account for this finding—the primary aim of thigmotaxis is the formation of spatial context and to grab the boundary settings of the environment, while for an effective exploration there is a need for active visual monitoring, which can be found in the visual scanning strategy. If visual scanning is less intensive, than the probability of a successful trial is much lower, and may increase the subjective feeling of uncertainty. So, poor performance is a consequence of a recurring need of safety referencing from the most stationary element of the surrounding space that is the circular boundary of the arena maze. This behaviour rises the platform finding time hence the performance will be low. On the other hand, good performers can better refine their concepts of spatial relations with the more active visual scanning strategy without the need for returning to the context references all the time.

Human spatial studies have been focusing on the construction of representations [10,21,35], the role of related neural structures [6,3,22,28] and individual differences [30,2,19,20], while an examination of search strategies had been studied less extensively. The present study found and characterized three fundamental strategies (thigmotaxis, visual scanning, enfilading) that humans use in a virtual environment and described their spatio-temporal distributions and effects on the process of place learning. Based on the present results we suggest that the way in which humans use these search strategies are deeply related to different phases of spatial learning and are related to the process of the spatial map construction. Examining the neural bases of these strategies, and the changes in the way they appear on functional event-related brain mapping images would enhance our further understanding of how the spatial maps are constructed.

Some may question the use of virtual reality to examine exploratory strategies and thereby spatial cognition in humans. Does exploration of a computer-generated space adequately represent the behavioural and cognitive processes enacted during exploration of normal space? An adequate answer to that question is not simple. One branch of scientists dealing with virtual space argue that total immersion is possible [15,41,34]. This approach proposes that a transfer of abilities from computer-generated space to a real one is possible and efficient. Successfully applied virtual reality techniques of desensitization [32,40] and simulation devices [29] support this assumption. There are, however, some who are sceptical about this approach. These scientists emphasize the importance of modalities (e.g. vestibular, self-induced locomotion,

effects of gravity) that are omitted in computer-generated tasks [17,24]. Although many studies have revealed shaded details of the transfer processes, from which the actual rate of learning can be determined [41], our present state of our knowledge does not cover all aspects of the relationship between computer-generated space and reality.

Another limitation may result from design of the task itself. Morris [26] demonstrated that relations among extra-maze landmarks are sufficient for place learning for rats. Similarly, it was demonstrated that humans also rely on abstract distal visual cues when learning places in a virtual maze [14]. The results of other studies, however, suggest that abstract cue-points decrease the efficiency of spatial performances [33]. If this latter point is correct, then more realistic arena settings and proximal cues may increase the sense of immersion and may modify the usage and the distribution of search strategies.

Finally, although it is a well-established fact based on the experimental results that there is a relation between search strategies and the quality of spatial performance, it is not easy to determine which one is the cause and which is the effect. Is it behaviour that determines strategies or inversely, strategies that form the measurable performance? Further detailed experiments are needed to answer this question.

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