Spatial Orientation and Spatial Memory Within a 'Locomotor Maze' for Humans

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Abstract. Spatial behavior was investigated using a locomotor maze for humans which incorporates basic features of widely used animal paradigms. Experiments are based on the 'cognitive map' theory originally put forward by O`Keefe & Nadel [22] and allowed the assessment of place learning, and spatial working and spatial reference memory errors. In our procedure, subjects and patients have to learn and remember five out of twenty locations within a 4 x 5 m area with completely controlled intra- and extramaze cue conditions. Usually, participants learned to reach the criterion. A probe trial from an opposite starting position with transposed intramaze cues followed. Results showed that it is possible to assess cue-dependent orientation, to dissociate spatial working memory and spatial reference memory and to identify 'place-behavior' using specific parameters derived from inertial navigation theory [16]. This will be demonstrated in selected cases with circumscribed cerebral lesions and in unimpaired subjects.

1 Introduction

One of the most prominent theories of spatial behavior is that of O'Keefe & Nadel [22]. Based on the findings and assumptions of Tolman [36, 37] they distinguished three basic types of spatial learning: learning of places, of routes and of responses [20, 21]. Place learning is characterized by the formation of an observer-independent representation of the external world, i.e. a so-called 'cognitive map'. This representation is assumed to be initially established by simultaneously encoding distal stimuli and their mutual interconnections. In contrast, 'route learning' depends on the acquisition of single 'landmarks' spatially related to the goals, whereas 'response learning' solely depends on the processing of proprioceptive, kinesthetic and vestibular cues.

Despite the extensive literature about spatial behavior and its determinants in animals [e.g. 11], the experimental work in humans is only fragmentary. Apart from newer developments using virtual reality [e.g. 17], Howard and Templeton [9] summarized the older human real space maze-literature and concluded that orientation from a contraligned position depends on the subject's ability to verbalize and imagine spatial concepts. Thorndyke and Hayes-Roth [35] found subjects to be superior in orientation tasks from new perspectives if they had had the opportunity to actively move around in space instead of learning the same environment from a map. Presson and Hazelrigg [29] also demonstrated that 'alignment errors' were observed if subjects had to learn a path from a map from one perspective and then to judge directions from a different one. But if active exploration or direct visual scanning of the path had been possible, no alignment effects were detectable. Presson, deLange, and Hazelrigg [30] showed that alignment effects were minimal when subjects were able to obtain multiple orientations during learning. Presson, deLange and Hazelrigg [31] varied the sizes their arrays and the maps of these arrays and found orientation-specific behavior in small arrays and with small maps and orientation-free behavior in larger arrays and with large maps. They concluded that orientation-specific spatial behavior is primarily egocentric and very precise under aligned conditions. However, in the case of larger environments they assume that the subjects regard themselves as being in an object-based frame of reference which can flexibly be used under contraligned conditions.

Though an orientation-free, observer-independent reference system provides an individual with an allocentric frame of reference and thus allows spatial behavior of high flexibility even when response requirements or environmental conditions are changed, the exact nature of the stimulus conditions hindering or facilitating this flexibility of spatial behavior has still to be investigated. Such an examination requires an experimental setup which allows

- assessment of spatial abilities within locomotor space,
- complete control of intra- and extramaze cues
- strict definition of behavioral response requirements
- automatic recording of inter-response intervals (IRI)
- detection of problem solving behavior (excluding algorithmic strategies)
- dissociation of place-, landmark-, and response-strategies and
- identification of spatial reference and spatial working memory errors.

In animals, learning behavior is usually assessed by means of the Morris Water Maze [18] in which a rat has to swim towards a hidden platform. Place learning behavior is induced by means of rich environmental cues located in distal space. On the contrary, cue learning is induced using an elevated platform or presenting a single landmark which is well visible above the platform's location. Numerous experiments have shown that successful navigation within these two environmental conditions depends on distinct neuronal circuits, i.e. the hippocampal formation in the case of place learning and the basal ganglia, especially the striatum, in the case of the acquisition of S-R based strategies [e.g. 19]. While allocentric and egocentric based search behavior can easily be assessed in the Water Maze [e.g. 2, 3], the different types of spatial memory errors are mostly investigated using the Radial Maze [26]. In this task, rodents are placed in the center of an eight, twelve, or sixteen arm maze and allowed to

explore the endpoints of the arms, which are baited with food. Sometimes, only a subset of the arms is baited. Using this setup, three types of spatial memory errors can be obtained. Firstly, within the same trial an animal can revisit an already visited arm. In such a case it has not developed a 'win-shift' rule and thus a 'working memory' error is recorded [28]. Secondly, if the animal visits an arm which has never been baited, it was unable to build up a rule which stays valid across trials and has thus violated a 'win-stay' rule. In such a case a 'reference memory' error is recorded. Thirdly, if the animal revisits an arm which has never been baited within the same trial, a combined 'reference-working memory' error can be identified. This distinction from the other two types of errors was shown to be necessary by Colombo, Davis, and Volpe [1] and Okaichi and Oshima [23], who demonstrated different psychological mechanisms underlying reference and reference-working memory processes in the case of brain damage.

Only a few attempts have been undertaken to develop experimental setups for humans which are equivalent with respect to the task characteristics used in the non-human maze literature. Foreman was one of the first who tried to overcome the specific difficulties one is confronted with if purely 'spatial' behavior is to be obtained in children. In an experimental chamber like a radial arm maze two- and four-year-olds had to find hidden chocolates from eight identically labeled positions in an unfamiliar room [5]. Results showed that working memory errors were far more frequent in younger children, and that above chance performance was controlled by distal cue configurations. This result has been extended in further work with four- and six-year-olds showing that performance was associated with choice autonomy and active locomotor behavior [6]. In experiments with children from eighteen months to five years who were subjected to a maze with subsets of baited arms, reference memory was assumed to develop earlier than working memory [7]. Moreover, differences between groups of six-year-olds who were either actively or passively moving around and who either had or had not freedom of choice were best reflected by the reference memory component of the spatial task [8].

While Foreman and coworkers emphasized the distinction of reference and working memory errors across age groups in infants, Overman, Pate, Moore & Peuster [27] explicitly tried to assess place learning in children and adults by means of an eight arm radial maze similar to that of Foreman et al. [6, 7, 8], and a Morris Water Maze adaptation. Working memory seemed to be fully developed in children above the age of five, but unfortunately, algorithmic strategies were found in about 50% of the older children and ceiling effects were observed in adults. The 'water' Maze was constructed in such a way that a large cardboard 'pool' was filled with plastic packing chips. Children were requested to find a hidden 'treasure chest' located at the bottom of the pool. In the absence of any sex differences it was shown that place representations could be established from age five onwards and that the presence of proximal cues improved performance.

Since, up to now, no experimental procedure has been available for humans which fits the requirements listed above, a maze-like open field analogon (i.e., a 'locomotor maze') was constructed which incorporates the basic features both of the Radial Maze and the Morris Water Maze. This apparatus was constructed for adults [12] and adapted

for children [10]. The experiments were designed so that the full range of abilities can be tested without ceiling or bottom effects. Preliminary results in healthy adults have shown that acquisition in a place condition is superior to the landmark condition which in turn is superior to condition of egocentric encoding. Analysis of a subsequent probe trial revealed that subjects of the egocentric groups were only inferior to landmark- and place-individuals if the task required the updating of the subject's orientation or if verbal or spatial material was interpolated. If task characteristics remained stable, the three orienting conditions did not affect recall of the spatial representation. Egocentric learning errors were mostly of the working memory type, whereas place learning yielded errors which were almost exclusively of the reference memory type [13]. As in the Overman et al. [27] study, no sex differences were found. These results were replicated and extended with brain impaired patients [14].

In the following, the basic principles of the locomotor maze and testing of healthy subjects and brain impaired patients will be outlined. Especially in selected cases, it will be shown, how cue dependent behavior can be assessed in contrast to orientation free behavior, how spatial working memory errors and spatial reference memory errors can be obtained and how 'place orientation' can be assessed using specific parameters derived from inertial navigation theory of McNaughton, Chen & Markus [16].

2 METHOD

2.1 Apparatus

Subjects were exposed to a dimly lit chamber with a 'circular platform' 3.60 m in diameter. The platform was covered with a black carpet and surrounded with black cloth leaving only 'gates' of about 1.5 m within each corner (**Fig.** 1). These gates served as starting points for the acquisition and probe trials (see below). Extramaze cues were controlled completely by means of eight distinct fluorescent symbols of about 30 x 30 cm in size each. Two of these symbols were attached deep in the corner of the four gates, respectively. The gates were enclosed by the same black cloth enclosing the platform. The chamber was completely painted black and was prepared in such a way that the subjects were prevented from orienting themselves according to acoustic stimuli from outside the experimental room.

The circular platform consisted of a wooden floor of about 20 cm height Twenty magnetic capacity detectors were fixed to this floor in a semi-irregularly fashion (Fig. 1). These detectors registered the presence or absence of a human limb and are thus a mean of assessing the track of spatial behavior within an experimental chamber. This arrangement was supposed to resemble the 'hidden platform' paradigm by Morris [18]. The detectors were connected individually to a microcomputer in a neighboring room. The location of each detector was marked on the carpet by identical light points

provided by very thin glass fiber cables inserted into the wooden floor next to the capacity detectors. Such a light point could only be seen when the subject positioned himself/herself about 30 cm away from a capacity detector. Since the brightness of the diodes could be adapted according to the subject's height, no array of light points could be scanned and only two to three light points could be seen simultaneously. Thus, the subjects were prevented from employing simple geometric encoding strategies. Subjects had to move towards these light points and to step on them. Five out of twenty were designated 'correct'. This was signaled by a 40-Hertz tone whose source could not be located. A second step on one of these five 'correct' detectors did not yield another 40-Hertz tone. Thus, within one experimental trial, only the first stepping on a correct detector was characterized as a 'correct response'. The other fifteen detectors were labeled 'incorrect locations'. Stepping onto an incorrect location did not yield a 40-Hertz tone. IRIs as well as incorrect and correct responses were recorded automatically.

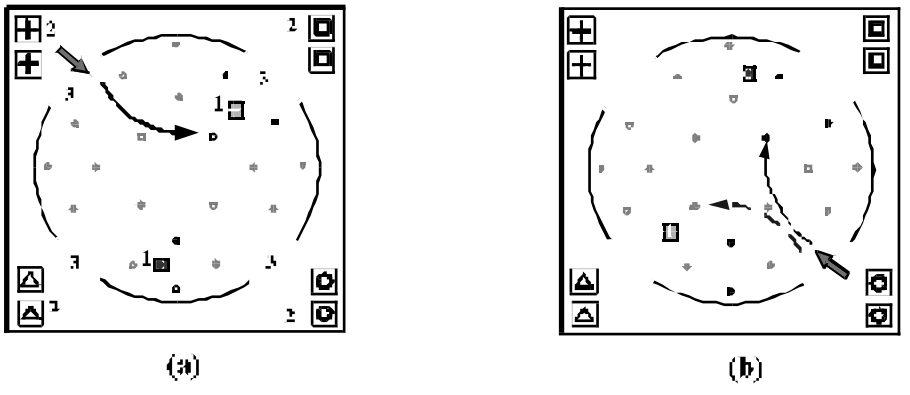


Fig. 1. Standard layout of the 'Locomotor Maze' (a) Acquisition phase; (b) probe trial. Probe trial manipulation is characterized by rotation of the starting point and rotation of the proximal cues by 180°, respectively. a: 1 = proximal cues; 2 = distal cues; 3 = gates; b: bold arrow = correct path (place orientation); dotted arrow = incorrect path (cue-/ egocentric orientation); a & b: black dot = correct location; grey dot = incorrect location (not visible for Ss)

2.2 General Procedure

Prior to exposure to the experimental chamber subjects heard and read elaborate instructions to convince them about the nature of the task. After informed consent had been obtained, subjects were then guided to the experimental chamber and given the following instructions (i) to explore the chamber, to visit each location, to step onto each detector, to remember the correct locations and (ii) to try to visit correct locations only once within each trial.

Each subject was then guided by the experimenter to his/her initial starting position and was again given the instructions for the exploration phase of the experiment ("please visit all of the twenty light points, step on them and try to remember the 'correct locations'. After having visited all twenty locations the subject was guided back to his/her starting point.
Before the first learning trial began, the subject again listened to the learning instruction ("now, please try to visit only the 'correct locations' - i.e., "those with the tone" - and "try to visit these 'correct locations' only once"). The subject then began to visit the correct locations while trying to avoid reference memory errors, working memory errors and reference-working memory errors. During each trial the experimenter herself moved to different positions within the experimental chamber. In order to spare the subjects the additional memory load of memorizing the number of successfully found correct locations, the experimenter counted aloud the number of correctly identified locations from different positions in the chamber. When the five 'correct locations' had been visited, this was signaled by a double tone and the subject was guided back to his/her starting point by means of a meander walk. Then the next acquisition trial began. The acquisition phase was always performed from the same starting point but the subjects were free to move around and to make their own choices. Subjects had to learn the location of the correct detectors until they completed two subsequent trials without errors.

3 Experiments

3.1 Assessing cue dependent orientation

Background. Within the framework of spatial navigation theory the distinction between an observer independent, 'orientation-free' and an observer-centered, 'orientation-specific' type of navigation is of major importance [31]. Farah, Brunn, Wong, Wallace and Carpenter [4] designated this dichotomy as 'environment centered' and 'viewer centered'. These dichotomies correspond to O'Keefe & Nadels [22] 'locale' and 'taxon' systems. Within the locale system memories are formed in a spatial-temporal context whereas the taxon system operates by means of the rules of category inclusion [21]. The locale system is driven by novelty and determined by distal cue configurations thus enabling the observer to encode relations between stimuli instead of single landmarks. On the contrary the operation of the taxon system depends on a distinct above-threshold stimulus. Repeated presentation of such a stimulus enhances response probabilities whereas the locale system will cease to operate if the same stimulus is presented repeatedly. This can be investigated experimentally by presenting a set of stimuli attached in the distal space while transposing stimuli attached in the proximal space. If the subject is bound to a viewer-centered taxon system he or she will use these proximal cues for navigation even if this is no longer adaptive. If, on the contrary, the locale system is activated and an orientation-free,

environment-centered perspectivecan be obtained, spatial behavior has to rely on the set of distal cues. For this investigation no dissociation of error types will be undertaken.

Procedure, Recordings and Participants. After the subjects had reached the learning criterion of two successive error-free trials, a break of about two minutes was filled by informal conversation. This was done to prevent the subject from developing rehearsal strategies. Then a subsequent probe trial was scheduled. For this purpose the subject was guided by the experimenter to the new starting position by a meander-walk. The new starting position was rotated 180° with respect to the initial starting point. Moreover the proximal cues were also rotated by 180°. This manipulation leads to a viewer's perspective which is equivalent to that obtained during acquisition (Fig. 1b). Thus, this probe trial can only be mastered if the distal cue configuration is taken into account. If the subject relies on a cue or a response strategy (Fig. 1b, dotted lines) he or she will not be able to complete the task successfully. If, on the contrary, the set of distal stimuli are taken into account - i.e. 'place'-learning is obtained - the subject will orient towards the correct locations, irrespective of proximal cue distribution.

For each trial in the acquisition phase the total number of errors was calculated. In order to detect response stereotypes the path of the last acquisition trial is analyzed by means of a graph and compared to that of the probe trial. This is demonstrated in two experimental subjects with no known history of CNS-disorders. Subject S1, was male 20 years of age and subject S2 was female, 24 years of age.

Results. Fig. 2 shows that the performance of the two subjects with respect to the sum of errors across trials is largely comparable if the course of errors across trials is inspected. Though the S1 subject needed six trials to fulfill the learning criterion of two consecutive error-free trials whereas the S2 subject showed error-free performance immediately after the exploration phase, the total number of errors displayed within acquisition trials was quite low even in subject S1. Moreover, the exploration trials were performed comparably with nine and ten errors, respectively. Even the probe trial yielded comparable results for both subjects with seven errors in S1 and five errors in S2.

A distinct pattern of results emerges when the paths taken by the subjects are analyzed (Fig. 3).

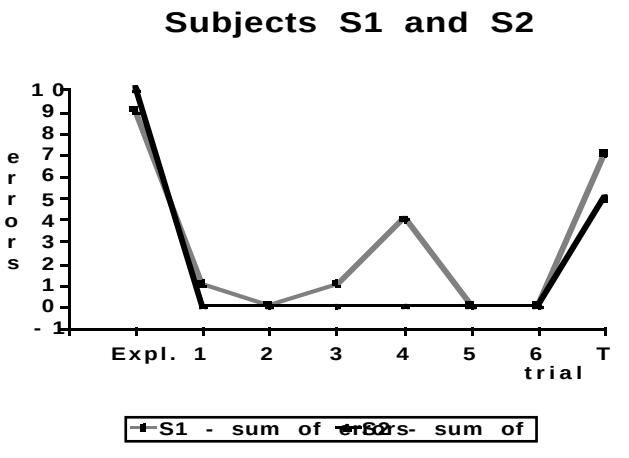
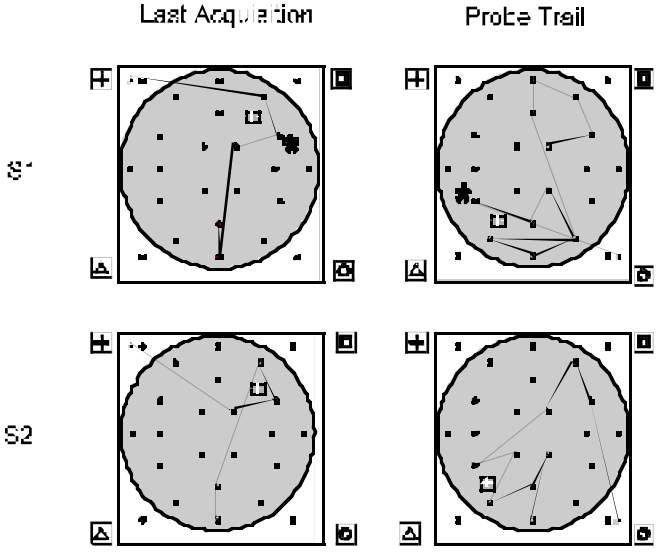


Fig. 2. Sum of errors across acquisition trials and in the final probe-trial of two experimental subjects



number of errors during probe trial

	RM	WM	RMWM
S1	6	0	1
S2	4	0	1

Fig. 3. Performance in the last acquisition trial and the probe trial of subjects S1 and S2, respectively. For simplicity only one proximal cue is shown; * denotes an example for two locations which are equivalent with respect to the S1 viewer's perspective (because the proximal cue and the subject's starting position were rotated). (RM = reference memory errors; WM = working memory errors; RMWM = reference-/ working memory errors)

Though subject S1 was comparably good at acquiring the locations within the spatial layout, his first probe trial move was directed towards a location which was equivalent to step 2 within his last acquisition phase (see * in Fig. 3, upper row). His search behavior in the probe trial was then bound to the 'southern' part of the environmental space which was identical to the 'northern' part of the environment during acquisition. The search seems to be guided by the proximal cue located in the 'northern' part during acquisition and in the 'southern' part during probe trial testing. On the contrary, probe trial manipulation did not much affect subject S2 because she initially moved towards the 'northern' part of the experimental chamber.

Discussion. Obviously the two experimental subjects oriented in different ways. The S2 subject showed an errorless performance immediately after the exploration phase. According to O'Keefe and Nadel [22] this 'one trial learning' is indicative for the locale system. But overall, performance across acquisition trials did not differ remarkably between subjects (Fig. 2). On the contrary, probe trial behavior showed that while the S1 subject seemed to be bound to a cue strategy, the S2 subject was initially able to maintain an orientation-free behavior. Thus, it has to be assumed that she oriented with respect to the distal cues. Using the locale and not the cue (or taxon) system she was enabled to update her position in the very difficult probe trial condition. Since the viewer's perspective of the experimental chamber looked alike irrespective of whether the subject's position was in the 'North-West' or in the 'South-East', the task could only be solved if the subjects relied on distal cue information.

3.2 Dissociating spatial reference and working memory errors

Background. As outlined in the introduction the dissociation of spatial reference memory errors and spatial working memory errors has been shown to be of major importance in animal research investigating the effects of different cerebral lesions. With respect to this matter the basal ganglia, a subcortical structure of the telencephalon, are of specific importance. Lesions within these ganglia have been shown to lead to deficiencies in sequencing motor acts and switching behavior from one mode of response to another. In general, behavioral and cognitive responses deteriorate if the algorithms necessary to solve these tasks have to be generated in the absence of external cues or if these algorithms have to be adapted rapidly to changing task characteristics and varying response demands. The concept of reference memory errors is an example of such an algorithm. Since the position of the correct and incorrect locations remains stable across trials it incorporates the development of a 'win-stay' rule [28]. On the contrary, working memory depends on the updating of one's ongoing behavior and thus remains valid only for the current trial. If patients with lesions of the basal ganglia are exposed to a locomotor maze which enables the investigator to dissociate reference memory errors and working memory errors, these patients should display persistent reference memory errors.

Procedure, Recordings, and Participants. Within the working memory paradigm, subjects had to learn and remember the five correct locations out of twenty locations and not to return to any of these correct locations during the same trial. Revisiting a previously visited correct location was called a 'working memory' error and was considered functionally equivalent to visiting a previously visited baited arm in the radial arm maze paradigm of Olton et al. [26]. Stepping on a detector of an incorrect location was called a 'reference memory' error and was considered functionally equivalent to visiting an arm without food in a radial maze. Pressing an incorrect location in one trial more than once was considered a 'reference-working' memory error. These three types of spatial memory errors were recorded for each acquisition trial. Two patients with Parkinson's disease, a degenerative disorder with known lesions within the basal ganglia, and two age and sex-matched controls were taken from an ongoing study [15]. Both patients had verified diagnoses but differed with respect to age and duration of disease (Table 1).

Results. Fig. 4 shows that the PD1 patient not only displayed the largest number of errors (see Table 1) but that the distribution of error types markedly differs between participants.

Table 1. Characteristics of Parkinson patients (PD) and controls (PC)

	PD1	PC1	PD2	PC2
age	66	66	35	35
sex	male	male	female	female
diagnosis of disease	7 yrs.	-	2 weeks	-
number of trials	6	7	9	5
criterion	no	yes	yes	yes
sum of errors	157	10	40	16
mean of errors	10.7	1.3	3.2	3.0
error type				
reference memory	64	9	29	12
mean reference	10.7	1.3	3.2	3.0
working memory	27	0	8	3
mean working	4.5	0	0.9.	0.8
reference-working memory	66	1	3	1
mean reference-working	11	0.1	1.0	0.3

Thus, the PD1 patients showed a constant rate of about eleven reference memory errors without any sign of improvement. On the contrary, the rate of working memory errors decreased across trials 1-4 to close to zero and then increased to a score near twenty in trial 5. Such a dissociation of error types was absent in the two control subjects who displayed hardly any working memory errors and constantly improved with respect to reference memory errors. Moreover, the recently diagnosed, younger PD2 patient showed a pattern of results similar to that of the healthy subjects. Especially, the slope of reference memory errors decreased to quite a similar degree to

that of her age-matched control. Though the two unimpaired subjects differed by 30 years in age the distribution of their error types was roughly similar.

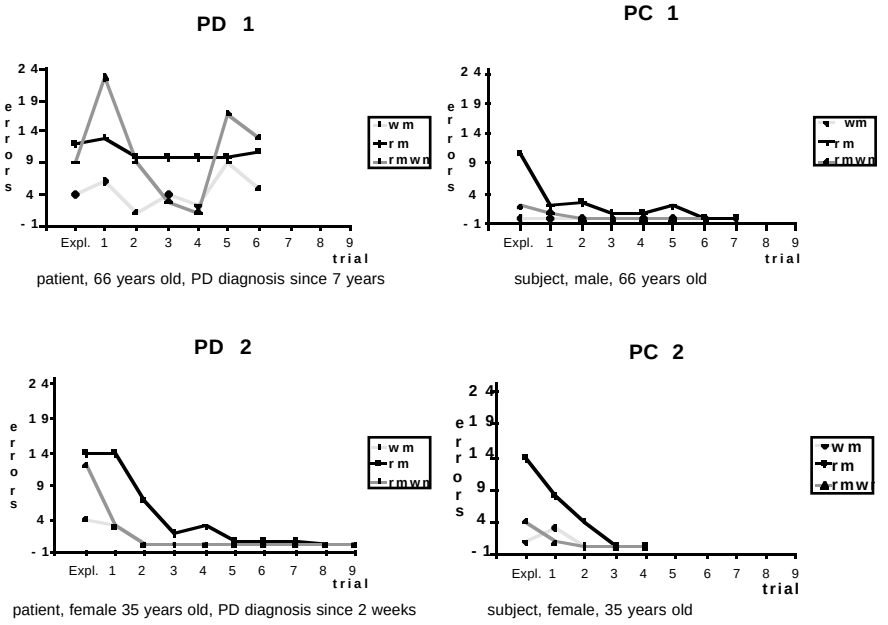


Fig. 4. Types of spatial memory errors across acquisition trials in two Parkinsonian patients (PD) and their controls (PC) (wm: working memory error; rm: reference memory error; rmwm: reference-/ working memory error)

Discussion. This presentation underlines the use of dissociating error types because persisting reference memory errors are exactly what can be predicted from a basal ganglia related disease. Moreover, this typical result of a PD patient corresponds to animal research with experimental lesions within the striatum, an important part of the basal ganglia. These lesions usually lead to severe deficits in procedural learning. Thus, the reference memory component may be an indicator for specific alterations in spatial behavior in advanced Parkinson's disease which are not reflected by the total sum of errors.

3.3 Identifying place orientation

Background. 'Place' strategies [25] have been shown to depend on distal cue configurations. If the spatial task is manipulated in such a way that distal and proximal cues are dissociated, it can be shown that spatial orientation behavior in younger children [10] and in brain impaired patients [14] is controlled by proximal

cues. Thus, it can be concluded that place orientation has not occurred. In order to investigate the nature of place orientation in more detail, the actual behavior of the participants in the experiment has to be quantified. For this task, at least two aspects seem to be important: the participant's rotational behavior and the distances he or she is moving. Traveling through our experimental chamber necessarily induces a rotation around the vertical body axis. This angle is of theoretical and practical importance. Since 'head direction cells' have been identified in the dorsal presubiculum, a structure functionally related to the hippocampus, it is known that at least in rodents these cells fire with respect to their 'preferred direction' in extrapersonal space and irrespective of the actual place an organism is moving to [32, 33, 34]. Based on these and other findings, McNaughton et al. [16] proposed an inertial navigation model which incorporates a so-called 'H'-part recording angular size (i.e. by means of the 'head direction cells') and an 'H''-part which computerizes angular velocity and which is located within the vestibular and sensorimotor systems. Some cells of both H-system-parts are presumed to converge to a so-called H-H'-system. The whole system is supported to be started by means of the hippocampal 'local view'-'place cells' [24]. Thus it can be expected that lesions within the hippocampal formation should lead to severe disturbances in acquiring information between local views and directions [16].

Procedure, Recordings, and Participants. For our purposes we used the 'H'-component from McNaughton's model and included distance information [3]. We calculated the mean of all rotational moves a participant performed within one trial. This angular 'A'-component was compared with a second angular measure derived from the distance a participant moved after having turned his/her body axis. For this calculation each angle was divided by the distance moved. The mean of all divisions within one trial served as the second measure, denoted henceforth as relative angular or 'Ar'-component. If a participant shows a large 'A'-component and a comparably smaller 'Ar'-component, he or she has traveled long distances with respect to the angular turns. If, in addition, the error rates are low, it can be concluded that he or she was able to move well throughout space, obtaining a large number of perspectives and approaching the goals only. If, on the contrary, a participant shows an 'Ar'-component which is larger than the 'A'-component, it means that he or she has traveled rather short distances with respect to angular turns. This pattern of results would be typical for inefficient, stereotyped behavior.

The following examples serve to demonstrate the relationship between the 'A'- and 'Ar'-components of the navigational system and error rates in patients with circumscribed cerebral lesions and unimpaired subjects. For this purpose four patients with cerebral tumors and four age and sex-matched controls were taken from another ongoing study [14]. The patient characteristics are shown in table 2. Results are presented by showing the paths taken by each participant within the exploration trial, the composed paths of acquisition trials 1 to 3, the last acquisition trial and the probe trial, which was performed twenty minutes later from a starting point rotated by 90°. In this investigation, only distal stimuli were used. The position of these stimuli remained constant throughout the experiments.

Table 2. Characteristics of patients with cerebral tumors (CT)

CT1	large right frontal meningeoma, affecting the corpus callosum
CT2	circumscribed small right hippocampal astrocytoma
CT3	large left frontal, anterior temporal meningeoma
CT4	medium-sized, right temporal, parahippocampal glioblastoma

Results. Fig. 5 shows the paths of the participants and the courses of the 'A'- and the 'Ar'-measures, respectively. The CT1 patient was obviously not able to solve the task and after the sixth acquisition trial the experiment had to be aborted. As can be seen from Fig. 5, this patient was not only unable to acquire a strategy, but she also displayed the expected 'A-Ar' discrepancy. This is indicated by the relatively large 'Ar'-component compared to the 'A'-part of the 'A-Ar'-system. Contrary to this 'A < Ar'-behavior her control (TC1) not only reached the learning criterion after eight trials but also showed a corresponding 'A > Ar'-behavior, as indicated by the last graph in the upper row of Fig. 5. A completely different picture is displayed by the CT2 patient and his TC2 counterpart. Both participants displayed 'one trial learning' and showed the optimal 'A > Ar' pattern but the CT2 patient performed very poorly in the delayed probe trial condition (Fig. 5).

A largely stereotyped behavior is revealed both by the paths and the 'A-Ar'-system of the CT3 patient (Fig. 5). Despite a relatively small overall number of errors he showed a circular exploration behavior which was largely reproduced within his last acquisition trial. Furthermore and in correspondence with the theoretical assumptions, this patient displayed an 'A < Ar'-behavior whereas his control subject showed the 'A > Ar'-behavior. Since the CT3 patient did not reach the learning criterion and was obviously unable to display an efficient spatial strategy to solve the task, he showed extremely poor performance within the subsequent probe trial.

The CT4 patient showed paths which are largely similar to those of his TC4 counterpart. But although he made nearly twice the number of errors within acquisition trials 1 to 3 and though he tried unsuccessfully for more than twice the number of trials to reach the criterion the behavioral pattern as shown by the paths does not seem to be very different from that of his control (Fig. 5). Again, and more importantly, the CT4 patient displayed an 'A < Ar'-behavior throughout the experiment, while his counterpart was successful in developing an 'A > Ar'-behavior from acquisition trial 3 on. This may, at least partly, account for CT4's poor performance in the delayed probe trial.

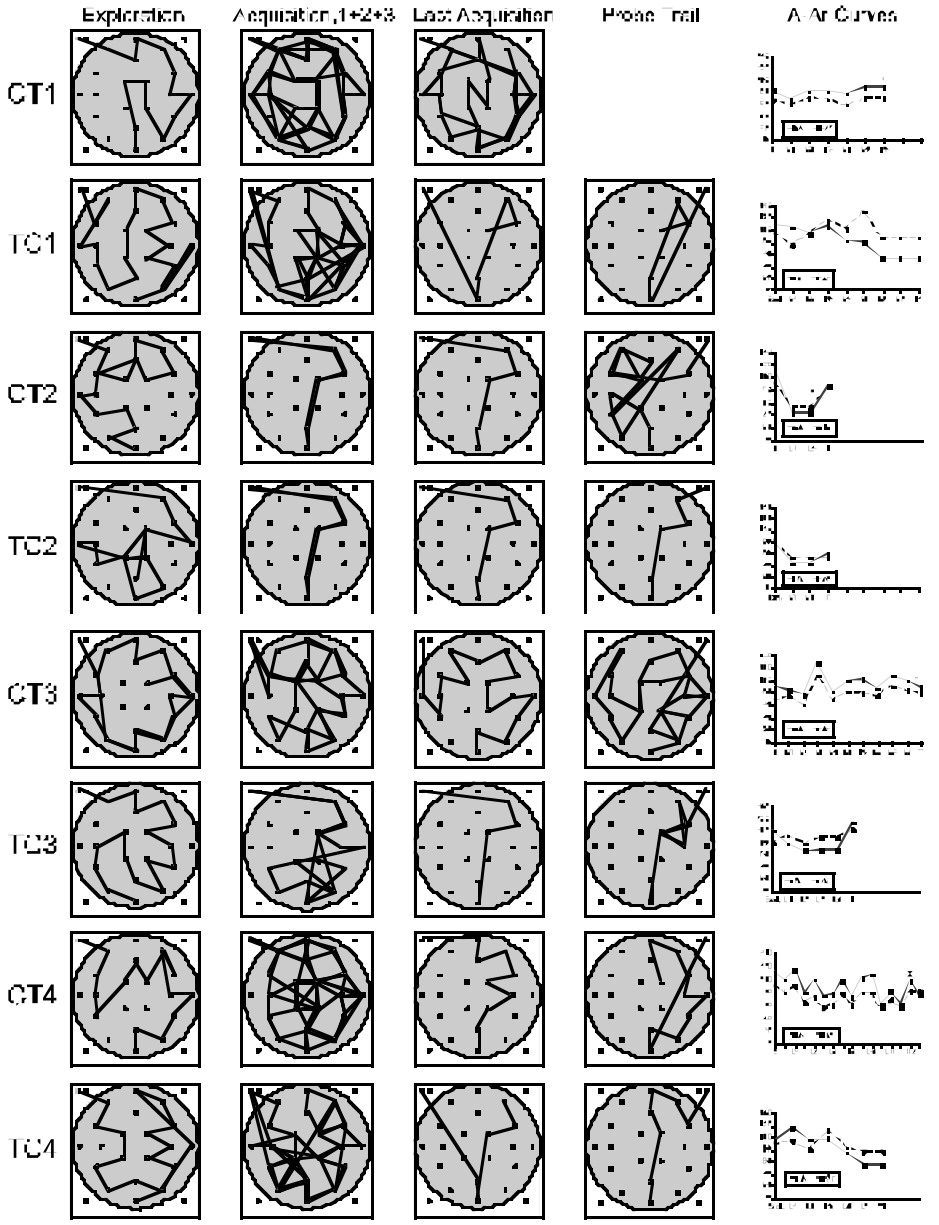


Fig. 5. Paths of patients with circumscribed brain lesions (CT) and their controls (TC). Last column: 'A-Ar'-system (further explanation see text). Ar - component: bold lines; A - component: dotted lines

Table 3. Results from tumor patients (CT) and their controls (TC)

	sum expl.	no. trials	mean err.	mean 1-3	crit.	probe
CT1	9	6	20.0	19.0	no	-
TC1	16	8	5.6	12.0	yes	0
CT2	12	2	0.0	0.0	yes	16
TC2	11	2	0.0	0.0	yes	0
CT3	22	9	16.1	9.0	no	22
TC3	12	4	2.3	3.0	yes	7
CT4	11	14	10.0	20.0	no	4
TC4	13	6	6.7	3.3	yes	2

Note: sum expl. = sum of errors during the exploration phase; no. trials = number of trials necessary to reach the learning criterion; mean err. = mean sum of errors during acquisition; mean 1-3 = mean sum of errors during acquisition trials 1-3; crit. = learning criterion; probe = probe trial.

Discussion. The results of this investigation show that it is possible to identify different types of spatial problem solving strategies and to relate the breakdown of these strategies to different cerebral lesions. For example, the CT1 patient with a large right frontal tumor including the corpus callosum was obviously unable to develop orientation-free behavior, as indicated both by her paths in the experimental chamber and by her 'A-Ar'-pattern. On the contrary, the 'A > Ar'-behavior of her control may indicate the activation of a viewer-independent, 'place'-orientation. From the results of the CT2 patient, however, it can be concluded that the deterioration in probe trial performance did not result from poor strategy development as in the previous CT1 patient. This is in accordance with the cerebral lesion of the CT2 patient which was restricted to the hippocampus. Thus, it can be concluded that in this patient the major deficit may be attributed to a consolidation deficit of a spatial layout which was successfully acquired.

A different type of spatial problem solving deficiency is revealed by the CT3 recording. This patient showed a highly stereotyped behavior which is often seen in experimental animals. Though the hippocampus was spared in the CT3 patient with a left frontal/anterior temporal tumor, his circling behavior at the outer border of the maze strikingly resembles that of rodents with hippocampal lesions. Again, the deficiencies were reflected both by the paths obtained and the 'A < Ar'-pattern. The CT4 patient with a right temporal tumor including the parahippocampal region showed a strategy deficit which seems to be less severe than in the previous patients. Since he had a temporal lobe tumor and his paths resembled that of the TC4 participant, the patient’s probe trial performance may at least partly be due to a temporal lobe-specific memory deficit.

4 General Discussion

The aim of the present investigation was to study spatial behavior within a maze-like environment for humans. The following criteria had to be fulfilled: (1) Spatial orientation and spatial memory should include gross motor behavior, (2) assessment of spatial behavior should be performed under completely controlled cue conditions, (3) investigation of spatial behavior should be conceptually equivalent to animal studies, (4) the spatial task should allow the investigation of spatial reference and spatial working memory, and (5) basic assumptions of one of the most prominent theories of spatial behavior should be testable. For this purpose, a locomotor maze was developed incorporating basic features of the Morris Water Maze [18] and the Radial Maze of Olton et al.[26].

In the present report we documented the principles of the experimental setup, data recording, methods of data analysis and its interpretation. In order to underscore the benefit of this approach selected patients and unimpaired subjects were examined. Group studies are now required to examine interindividual differences and their determinants. What we have shown is that it is possible to comply with the requirements mentioned above and in the introduction. Moreover, it is of theoretical and practical interest that we have outlined a procedure for the assessment of cue dependent behavior in contrast to place orientation, for the dissociation of spatial working memory and spatial reference memory errors, and to identify place behavior, which we have defined as a behavior characterized by large distance with respect to angular turn (i.e. 'A > Ar'). Obviously, this type of response pattern is highly associated with low error rates, whereas the opposite behavior characterized by short distance with respect to angular turns is associated with high error rates.

This last level of analysis has to be extended with respect to the velocity component. Up to now we have only included the angular transposition of a participant's body and hence only the so-called 'H'-part of the HH'-system of McNaughton et al. [16]. Though we integrated the distances of the moves between locations which are not part of McNaughtons's system, velocity information (i.e. distances and angles by time, respectively) has to be taken into account too. This angular velocity corresponds to the H'-part of the HH'-system.

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