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RESEARCH ARTICLE

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Cerebellar contribution to spatial event processing: characterization of procedural learning

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Abstract Recently, we demonstrated the prevalent role of cerebellar networks in the acquisition of the procedural components of spatial information by testing hemicerebellectomized (HCbed) rats in a classical spatial task, the Morris water maze (MWM). As procedures used in the water maze are a mixture of different components (that is, general procedures, exploration procedures, direct reaching procedures), for optimally solving a spatial task all procedural components must be opportunely managed. Thus, severely impaired procedural learning of cerebellar origin can be better comprehended by fractionating the procedural facets. To this aim, a two-step water-maze paradigm was employed. Normal rats were first trained to search for a hidden platform moved to a different position in each trial, utilizing a water maze setting in which visual cues were abolished by heavy black curtains surrounding the tank. In this paradigm, normal animals solved the task by using general and exploration procedures, but they could not use direct reaching skills. A subgroup of these pretrained animals was then HCbed and, after recovery from cerebellar lesion, was tested in a water maze with normal environmental cues available, a paradigm in which normal animals develop abilities for reaching the target with very direct trajectories. Pretrained HCbed animals, however, did not display the typical spatial deficits of naive HCbed rats, persisted in exhibiting the scanning strategy learned during pretraining, and never displayed direct reaching skills. In conclusion, cerebellar networks appear to be involved in the acquisition of all procedural facets necessary for shifting behavior within the maze until direct reaching of the platform. The lack of flexibility in changing exploration strategies displayed by pretrained HCbed rats is interpreted by taking into account the well-known cerebellar frontal interplay sculpting a specific cerebellar role in the acquisition of spatial procedural steps.

Key words Spatial function · Water maze · Procedural learning · Cerebellum · Rat

Abbreviations *HCb* Hemicerebellectomy ·
HCbed Hemicerebellectomized

Introduction

It has become apparent that, analogous to other forms of memory, there are many distinct subsystems in the spatial domain, each with a separate neural representation (Nadel 1992; Squire 1992). Evidence for these multiple forms of spatial memory derives from experimental and clinical findings, supporting the conceptual distinction between declarative spatial memory, which involves the recollection and recall of exact relations of environmental cues, and procedural spatial memory, which is represented by the habits necessary to guide the subject within a new environment (Schenk and Morris 1985). Although many experimental and clinical studies have provided a wealth of evidence on the role of hippocampal and neocortical structures in mediating declarative spatial abilities (Morris et al. 1982; Kolb et al. 1983; O'Keefe 1983; DiMattia and Kesner 1988; Nadel 1991; Davis et al. 1992; Eichenbaum 1992; McDonald and White 1994; Cain et al. 1996), fewer detailed findings on the neurobiological basis of procedural spatial components are available in the literature. Recently, experimental findings have clarified the procedural role played by cerebellar circuits in spatial-information processing (Petrosini et al. 1996, 1998). This evidence is mainly based on the analysis of the behavior exhibited by hemicerebellectomized (HCbed) rats in a classical spatial task, that is, the Morris water maze. In this test, rats with cerebellar

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damage, although not affected by motoric deficits in swimming performance, display a characteristic impairment in executing complex and effective exploration behaviors. Rather than searching for the escape platform, HCbed animals simply swim off to the periphery of the pool, displaying inappropriate circling. This behavior is rather ineffective for acquiring spatial information and allows spatial relations to be only slowly learned and only when proximal and distal cues are simultaneously present, as occurs when the platform is kept raised above the water level. Despite this inability in displaying effective searching strategies, cerebellar animals are not impaired in utilizing a spatial map once it has been somehow (preoperatively or by enhanced cue training) acquired (Petrosini et al. 1996). This supports the assumption that the cerebellum is primarily involved in acquiring the procedural aspects of the spatial task. The prevalent role of the cerebellar networks in procedural learning has also been demonstrated in clinical studies in which patients with cerebellar lesions displayed severe impairment in the procedural learning of a motor sequence (Pascual-Leone et al. 1993; Molinari et al. 1997b).

However, the procedural aspects linked to how a spatial problem is solved embrace different components (Whishaw 1985a, 1985b, 1991; Whishaw and Mittleman 1986). They include general procedures, such as inhibiting non-adaptive behaviors (scrabbling at pool walls or circling in the pool periphery), as well as spatial procedures based on processing of allothetic (visual, auditory, and olfactory) information as well as self-movement idiothetic cues (Mittelstaedt and Mittelstaedt 1973; Whishaw et al. 1997). The integration of all these kinds of cues allows appropriate exploration strategies to be developed, including first searching for the escape platform by swimming across the pool, uniformly scanning its surface, non-persistence of visiting already explored pool sectors, and successively developing skills to reach the platform through the most direct trajectory. Experimental findings already reported (Petrosini et al. 1996) did not allow the cerebellar role in managing these different aspects of spatial procedures to be characterized. The present study aimed at analyzing the cerebellar role in procedural learning by fractionating the procedural facets. This was achieved by pretraining normal animals to search for a hidden platform moved to a different position in each trial, utilizing a water-maze setting in which visual intra- as well as extra-maze cues were abolished by heavy black curtains surrounding the tank. This task makes almost the same procedural demands on the animal as the version without curtains, except that it does not allow progressively more direct and adaptively tuned trajectories for reaching the platform to be developed. After this training, a subset of these animals was HCbed and then tested in the water maze with visual environmental cues available.

Materials and methods

Subjects

Useful data were collected from 30 adult male Wistar rats (250–300 g), housed two animals to a cage with free access to food and water throughout the experiment and with a standardized dark/light schedule (10/14 h.). They were divided into three experimental groups: pretrained normal rats used as controls (*n*=11), pretrained HCbed animals (*n*=7), and non-pretrained HCbed rats (*n*=12).

Surgery

The rats were anesthetized with sodium pentobarbital (Nembutal, 40 mg/kg, i.p.). A craniotomy was performed over the right hemicerebellum. The dura was excised and the right cerebellar hemisphere and hemivermis were ablated by suction, with care being taken not to lesion extracerebellar structures. The cavity was filled with sterile gelfoam, and the wound edges sutured. After recovery from anesthesia, the animals were housed two per cage and testing was performed 2 weeks after the HCb, when no changes in cerebellar symptomatology were observed. The following aspects were taken into account: head and body tilts, positions of either hind limbs in relation to trunk, presence of ataxia, tremor, rearing behavior, falls to lesion side, wide-based locomotion, collapsing on the belly, pivoting, vestibular drop reactions, and abilities to traverse a narrow path and to be suspended on a wire. Details and time course of the main cerebellar symptoms have been described elsewhere (Molinari et al. 1990; Petrosini et al. 1990, 1996). It is noteworthy that these previous reports already demonstrated that HCbed animals are very competent at swimming and that motor and postural disturbances do not significantly correlate with spatial abilities in water-maze task.

Water maze

The rats were placed in a circular plastic pool (diameter 120 cm) with white inside walls, located in a normally equipped laboratory room uniformly lit by four neon lamps (40 W each) suspended from the ceiling (3 m). No care was taken to enhance (or, vice versa, to impoverish) extra-maze cues, which were held in constant spatial relations throughout the experiments. The pool was filled with water (24°C), 50 cm deep, made opaque by the addition of 2 l of milk. A white, steel escape platform (10 cm in diameter) was placed in the middle of one cardinal quadrant (NW, NE, SW, SE), 30 cm from the side walls; it was either submerged 2 cm below or elevated 2 cm above the water level. Each rat was gently released into the water, always from the same cardinal wall point (S) facing the center of the pool. The animal was allowed to swim around to find the platform. Blocks of four trials were presented to each rat, two blocks of trials per day. On reaching the platform, each rat was allowed to remain on it for 30 s before being again placed in the water for the next trial. If a rat failed to locate the platform within 120 s, it was guided there by the experimenter and allowed to stay there for 30 s.

Pretraining

Pretraining was performed in the water maze described above, surrounded by heavy black curtains to occlude intra- and extra-maze visual cues (Morris 1989). In all trials, the platform was kept hidden under the water level and moved pseudo-randomly between trials (the only correction to total randomness was that the platform never remained in the same position in two successive trials). After reaching the platform, the animal was put in its waiting cage while the platform was moved, without the rat being able to observe the experimenter manipulating with the platform. This pretraining took place the week before surgery and consisted in 40

Table 1 Searching behavior rating scale

Scores	Behavioral pattern
1	Direct finding of platform without searching
2	Searching in one incorrect quadrant only once before finding
3	Searching in two incorrect quadrants only once before finding
4	Searching in one or two incorrect quadrants more than once before finding
5	Searching in three or four quadrants only once before finding
6	Searching in three or four quadrants more than once before finding
7	Extended searching in all four quadrants more than once longer than 70 s before finding
8	Extended peripheral circling longer than 70 s before finding
9	Extended searching around the pool, no finding
10	Peripheral circling, no finding

trials subdivided into sessions of four trials, two sessions per day for five consecutive days, with an inter-trial interval of 5–10 min.

During testing, successful escapes, latencies in platform finding, and exploration characteristics according to the behavioral rating scale described in Table 1 were recorded. The animals' behavior was observed through a peephole in the black curtains. Swimming trajectories of single specimens were hand drawn and subsequently scored by a researcher unaware of specimens' treatment.

Testing procedure

Pretrained control group

Intact animals (*n*=11) received the pretraining described above in the first week of testing. After two weeks, they were tested again in the water maze without curtains, described below.

Pretrained HCbed group

Intact animals (*n*=7) received the pretraining described above in the first week of testing. They were then hemicerebellectomized and, after two weeks, were tested again in the water maze without curtains, described below.

Non-pretrained HCbed group

Naive rats (*n*=12) were hemicerebellectomized. After two weeks, they were tested in the water maze without curtains, described below.

Water maze without curtains

In this paradigm, the pool was not surrounded by the black curtains to allow sight of the environment and to provide extramaze visual cues. In the first four sessions (trials 1–16), the platform was hidden in the NW quadrant (place navigation I). In the successive two sessions (trials 17–24), the platform was raised above water level in the NE position (cue navigation). In the final four sessions (trials 25–40) the platform was again submerged in the NE position (place navigation II). It is worth noting that this paradigm was exactly the same previously used to assess normal and HCbed rats' spatial behavior (Petrosini et al. 1996).

Statistical analysis

Metric unit results of control and HCbed animals were first tested for homoscedasticity of variance and then compared using one-way or two-way "p×q" analyses of variance (ANOVAs) with repeated measures on one or both factors, eventually followed by multiple comparisons using Tukey's tests.

Histological controls

After completion of behavioral testing, the animals were deeply anesthetized with Nembutal and perfused with saline followed by

Fig. 1 Coronal section through cerebellum and brain stem in a hemicerebellectomized rat. Note the complete absence of the hemisphere and deep nuclei of the right hemicerebellum, with complete sparing of surrounding structures. Nissl staining

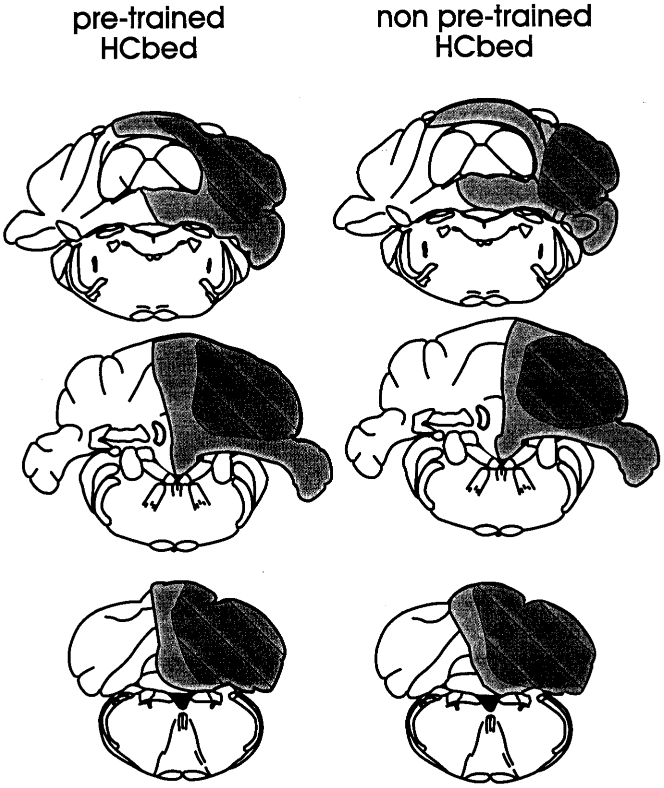


Fig. 2 Reconstruction of minimal (*heavily stippled area*) and maximal (*lightly stippled area*) lesion damage in HCbed animals of pretrained and non-pretrained groups. Schematic coronal sections of brain stem and cerebellum, arranged anterior (*top*) to posterior (*bottom*)

10% buffered formalin. The extent of the cerebellar lesion was determined from Nissl-stained, 40-µm frozen sections. Animals were included in the present study if they had received a complete right HCb with a total ablation of deep nuclei (Fig. 1). In all cases reported here, the left side of the cerebellum and all extracerebellar structures were completely spared, except for the dorsal cap of the right Deiters' nucleus, which in some cases was slightly affected. The variability in the extent of the floccular and vermal lesions was considered to be non-influencing, since in all cases these structures were functionally disconnected due to the ablation of the cerebellar peduncles and deep nuclei of the right side. Representative minimal and maximal cerebellar damage is presented in Fig. 2.

Results

Pretraining

In the absence of visual cues, in the very first trials, normal animals (n=18) swam at the tank periphery and had difficulty in finding the platform, as demonstrated by their low number of successful escapes, their relatively high latencies, and the high scores obtained for the exploration strategy (Fig. 3). However, they rapidly learned to detach themselves from the pool walls and to search for the escape platform, displaying progressively reduced escape latencies and progressively more effective exploration strategies. From the third session on, the rats learned to activate rather effective exploration strategies based on a meticulous scanning of the entire pool without peripheral circling and on reducing the number of repeated visits to the same pool sectors (Fig. 4). Through this effective foraging at the end of pretraining, almost all animals succeeded in finding the platform (Fig. 3A), exhibiting latencies of about 20 s (Fig. 3B) and exploration scores of about 3–4 (Fig. 3C). One-way ANOVAs demonstrated significant session effect on successful escapes ($F_{9,153}$=4.141; P=0.0009) as well as significant trial effects on latencies ($F_{39,663}$=5.481; P<0.0001) and scores ($F_{39,663}$=4.959; P<0.0001), indicating a clear learning of task requirements.

At the end of the pretraining, a subset of these animals was HCbed (n=7). To verify whether statistical differences existed between performances of the "to be control" and "to be HCbed" rats, two-way ANOVAs (group × session or group × trial, according to the analysis) with repeated measures on the second factor were performed. These statistical comparisons failed to reveal any significant group effect on escapes ($F_{1,16}$=0.210; n.s.), latencies ($F_{1,16}$=0.271; n.s.), and exploration scores ($F_{1,16}$=4.051; n.s.), while they demonstrated significant session effect on successful escapes ($F_{9,144}$=3.557; P=0.0005) and significant trial effects on latencies ($F_{39,624}$=4.776; P<0.0001) and scores ($F_{39,624}$=2.797; P<0.0001). Interaction was not significant for escapes ($F_{9,144}$=0.036; n.s.) and latencies ($F_{39,624}$=0.032; n.s.), while it reached statistical significance for scores ($F_{39,624}$=1.439; P=0.0432).

Performances in the water maze-without-curtains paradigm

The performances of pretrained HCbed animals were significantly different from those exhibited by HCbed animals without pretraining (Fig. 5). They never displayed the peripheral circling present in the non-pretrained HCbed group and exhibited, conversely, an extended going around the tank useful for searching and finding the platform (Fig. 4). This effective exploration strategy allowed them to make a high number of successful escapes (Fig. 5A) and to obtain rather low finding latencies and exploration scores (Fig. 5B, C).

When the two groups of HCbed animals with and without pretraining were compared by means of two-way ANOVAs (group × session or group × trial, according to the analysis) with repeated measures on the second factor, significant differences between groups were evidenced for successful escapes ($F_{1,17}$=13.945; P=0.0017), finding latencies ($F_{1,17}$=20.686; P=0.0003), and exploration scores ($F_{1,17}$=11.855; P=0.0031).

The performances of the pretrained HCbed animals were then compared with those displayed by pretrained control animals (n=11) (Fig. 6). Two-way ANOVAs (group × session or group × trial, according to the analysis) with repeated measures on the second factor demonstrated interesting between-group differences. Regarding successful escapes, no statistical difference was found between groups ($F_{1,16}$=0.467; n.s.), while session effect

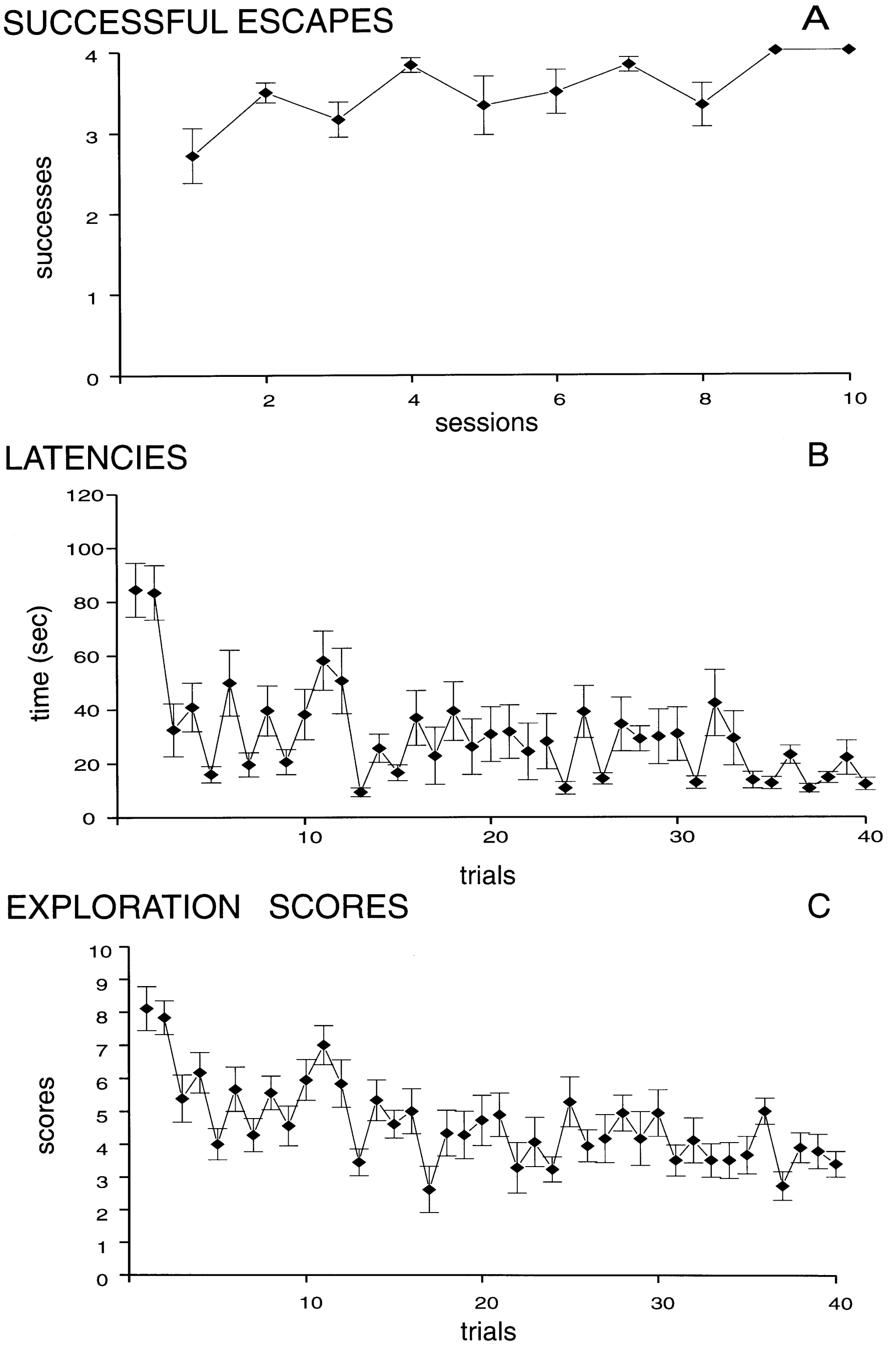
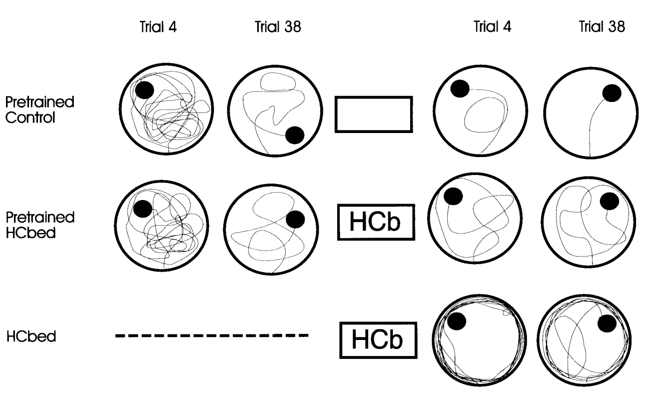


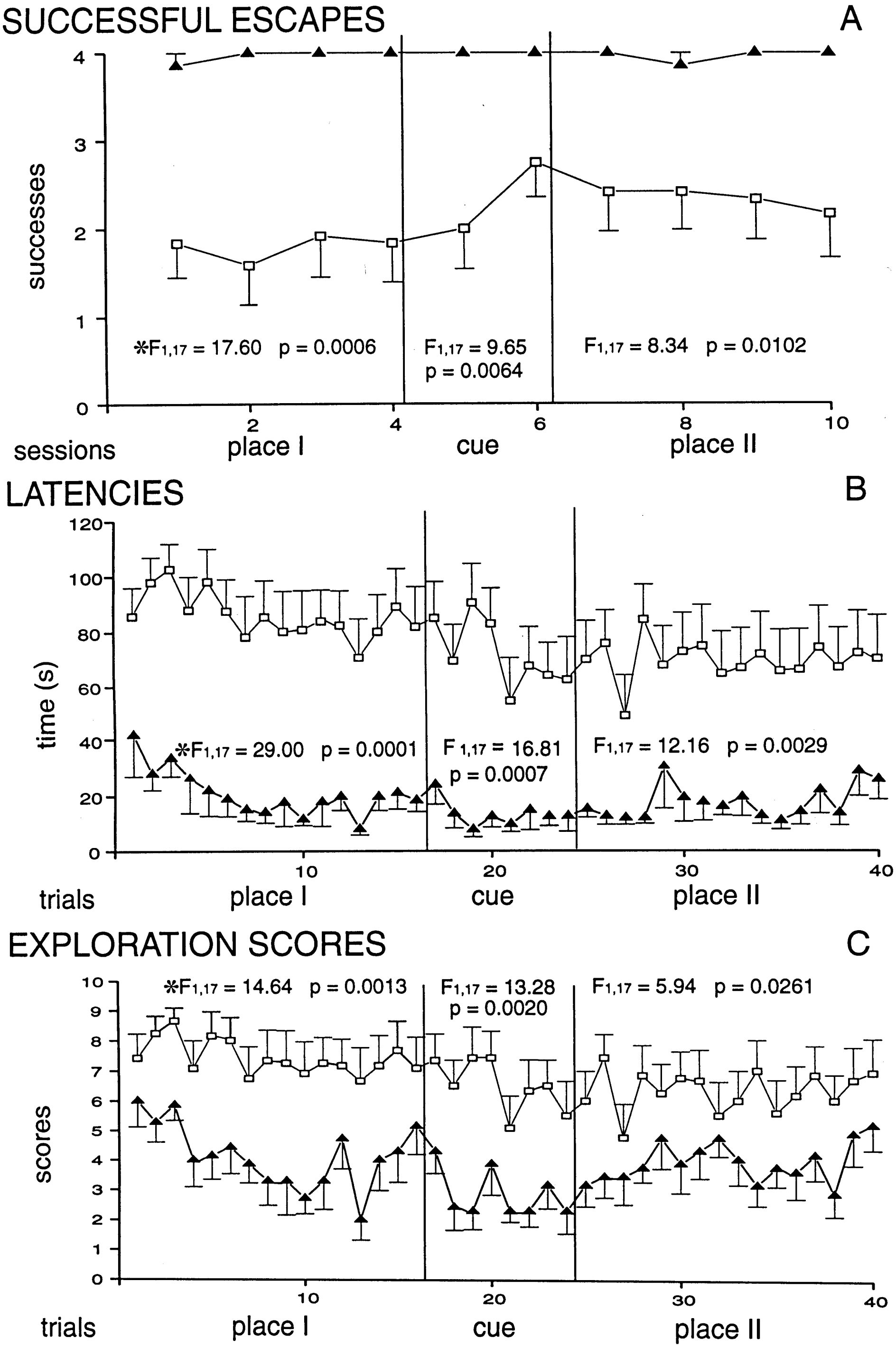
Fig. 3A–C Mean successful escapes (**A**), finding latencies (**B**), and exploration scores (**C**) of intact animals (n=18) during pretraining. *Vertical bars* indicate standard errors

Fig. 4 Swimming trajectories of single specimens belonging to the three experimental groups in both water maze with- and without-curtains paradigms. While control animal scanned the entire pool in the paradigm with curtains and rapidly showed little searching and direct finding of the platform when visual cues were available (water maze without curtains), pretrained HCbed animal continued to display the scanning trajectories learned in the first paradigm, even in the presence of visual cues, and non-pretrained HCbed animal also displayed peripheral circling in the final phases of testing



($F_{9,144}$=5.48; P<0.0001) and interaction ($F_{9,144}$=1.953; P=0.0493) were significant, demonstrating significant learning during the entire testing. Regarding finding latencies, group ($F_{1,16}$=4.808; P=0.0437) and trial ($F_{39,624}$=4.854; P<0.0001) effects were significant, while

Fig. 5A–C Mean successful escapes (**A**), finding latencies (**B**), and exploration scores (**C**) of pretrained HCbed (*triangles*, n=7) and non-pretrained HCbed (*squares*, n=12) rats in the water maze-without-curtains paradigm. * Two-way ANOVAs (group × session or group × trial, according to the analysis) with repeated measures on the second factor of place-I, cue, or place-II data. *Vertical bars* indicate standard errors



interaction ($F_{39,624}$=1.391; n.s.) did not reach statistical significance. Finally, regarding exploration scores, highly significant group ($F_{1,16}$=26.585; P=0.0001) and trial ($F_{39,624}$=4.755; P<0.0001) effects were found. Also, interaction was significant ($F_{39,624}$=1.748; P=0.0040). Since these overall comparisons included different testing conditions (change of platform position, facilitating influence of cued navigation, etc.), two-way ANOVAs (group × session or group × trial, according to the analysis) with repeated measures on the second factor relative to the single phases of testing (place I, cue, place II) were also performed. The results of these statistical analyses are reported in Table 2.

Descriptively, in the water maze without curtains, in which visual cues were available, control animals rapidly abandoned the scanning strategy learned during the pretraining and developed very direct trajectories towards the platform. On the contrary, pretrained HCbed rats persisted in using the scanning strategy preoperatively learned, even when extramaze visual cues were provided

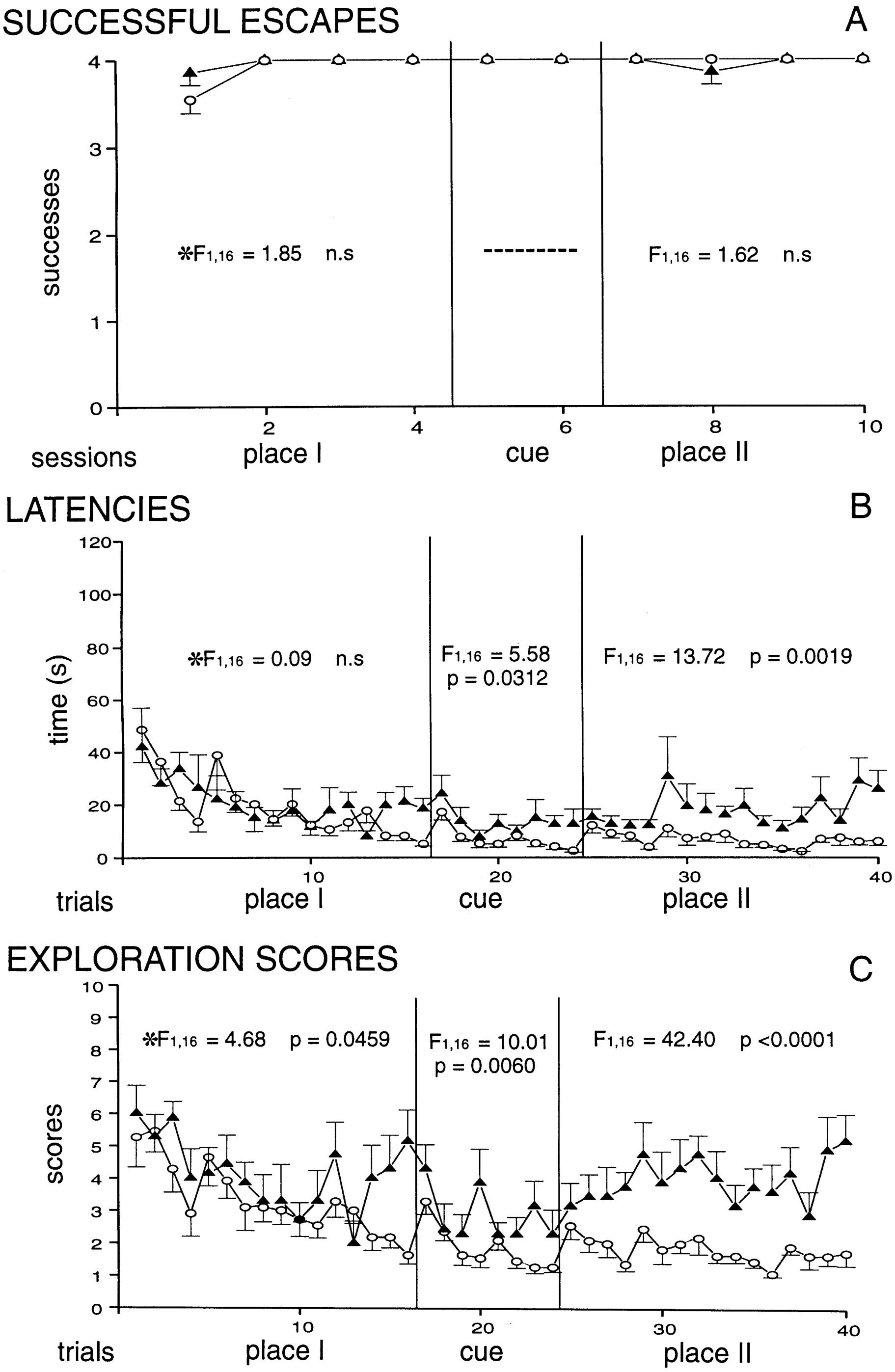


Fig. 6A–C Mean successful escapes (**A**), finding latencies (**B**), and exploration scores (**C**) of pretrained HCbed (*triangles*, n=7) and pretrained control (*circles*, n=11) rats in the water maze-without-curtains paradigm. * Two-way ANOVAs (group × session or group × trial, according to the analysis) with repeated measures on the second factor of place-I, cue, or place-II data. Note that, regarding latencies and exploration scores, progressively increasing levels of significance in group effect were present, indicating a progressive parting of the curves as controls took advantage of visual-cue availability and pretrained HCbed rats remained locked to the scanning strategy. *Vertical bars* indicate standard errors

(Fig. 4). Of course, this behavior was effective in finding the platform, as demonstrated by the high number of successful escapes (Fig. 6A), but it was penalizing regarding finding latencies and modality of exploration (Fig. 6B and C).

The stability of the performances of pretrained HCbed rats after HCb was further demonstrated by comparing their performances during the last 16 trials in the water maze without curtains with the performances they had displayed during the last 16 trials of the pretraining before the lesion. Two-way ANOVAs (condition × trial) with repeated measures on both factors failed to reveal any significant condition effect on latencies ($F_{1,6}$=0.704; n.s.) and exploration scores ($F_{1,6}$=0.003; n.s.).

Discussion

During pretraining in a water maze setting, in which visual cues were abolished by heavy black curtains surrounding the tank, normal animals behaved adaptively and learned to search for the hidden platform moved to

Table 2 Statistical comparison among the three experimental groups by “p×q” ANOVAs. *pH* Pretrained HCbed, *H* non-pretrained HCbed, *C* pretrained controls

	Escapes		Latencies		Exploration scores	
	$F_{(FD)}$	*P*	$F_{(FD)}$	*P*	$F_{(FD)}$	*P*
Place I						
Group	$F_{(2,27)}=21.60$	<0.0001	$F_{(2,27)}=35.98$	<0.0001	$F_{(2,27)}=23.34$	<0.0001
Session/trial	$F_{(3,81)}=1.01$	n.s	$F_{(15,405)}=2.92$	<0.0002	$F_{(15,405)}=3.75$	<0.0001
Interaction	$F_{(6,81)}=0.89$	n.s	$F_{(30,405)}=0.74$	n.s	$F_{(30,405)}=0.93$	n.s
Tukey’s						
pH vs. H		<0.0003		<0.0001		<0.0004
C vs. H		<0.0001		<0.0001		<0.0001
C vs. H		n.s.		n.s.		n.s.
Cue						
Group	$F_{(2,27)}=12.48$	<0.0001	$F_{(2,27)}=24.78$	<0.0001	$F_{(2,27)}=23.42$	<0.0001
Session/trial	$F_{(1,27)}=3.36$	n.s	$F_{(7,189)}=1.92$	n.s.	$F_{(7,189)}=3.50$	<0.0015
Interaction	$F_{(2,27)}=3.83$	<0.0341	$F_{(14,189)}=1.10$	n.s	$F_{(14.189)}=1.12$	n.s
Tukey’s						
pH vs. H		<0.0048		<0.0004		<0.0013
C vs. H		<0.0006		<0.0001		<0.0001
C vs. pH		n.s.		n.s.		n.s.
Place II						
Group	$F_{(2,27)}=11.08$	<0.0003	$F_{(2,27)}=20.25$	<0.0001	$F_{(2,27)}=20.84$	<0.0001
Session/trial	$F_{(3,81)}=0.14$	n.s	$F_{(15,405)}=0.70$	n.s.	$F_{(15,405)}=1.01$	n.s.
Interaction	$F_{(6,81)}=0.31$	n.s	$F_{(30,405)}=0.60$	n.s	$F_{(30,405)}=0.87$	n.s
Tukey’s						
pH vs. H		<0.0087		<0.0017		<0.0144
C vs. H		<0.0010		<0.0001		<0.0001
C vs. pH		n.s.		n.s.		<0.0396

a different position in each trial. In this paradigm, the rats could neither obtain any local knowledge of the environment nor utilize snap-shots of the target view because of the black curtains; they could not acquire praxic strategies for reaching the platform because of its randomly changed position, and they could not acquire taxic strategies because of the hidden platform. And yet normal animals found the platform and, as the training proceeded, reached it with progressively shorter latencies, demonstrating that they had learned something about the task. What had they learned? They had learned not to scrabble at the pool walls and to detach themselves from pool walls, that is, they had learned many general procedures not based on spatial knowledge of the environment. Besides these general procedural components, the animals learned to put an exploration strategy into action, that is, a procedure with a clear spatial nature. Namely, the animals learned to meticulously scan the entire tank, behavior that inevitably resulted in a fortuitous platform encountering. However, this extended searching did not evolve in direct platform reaching, simply because of the experimental setting features. It is important to note that the scanning procedure is certainly effective in reaching a platform randomly moved in a dark environment, but it is not localizing, that is, it is not training where the platform is. If spatial mapping of the environment as well as visual-cue guidance cannot be learned, an animal can still locate itself and move purposefully by using information acquired in the process of self movement. This latter mechanism is based on integrating sensory information generated by vestibular system, muscle and joint receptors, and from the efferent copies of the commands that generate movements, that is the path integration system, as recently defined (Etienne et al. 1996; Whishaw et al. 1997; Whishaw and Maaswinkel 1998). Thus, it is reasonable to state that, in our paradigm, rats learned to find the platform by developing an extended search strategy based on this latter mechanism.

After this training, a subgroup of these rats was HCbed and tested in the water maze without curtains. Pretrained HCbed rats did not display the peripheral circling observed in naive HCbed animals and continued to explore the entire pool with the efficient scanning strategy they had previously learned. The general and scanning procedures acquired when the cerebellar mediation was available were then maintained even in presence of a cerebellar lesion, allowing much better performances than non-pretrained HCbed rats that never developed these procedures. All together, these data demonstrate that the procedural components for getting to the platform linked to path integration system can be acquired only if the cerebellar circuits are preserved, but, once preoperatively acquired, they can be used to effectively search the platform even in presence of a cerebellar lesion. In fact, the lack of differences in the performances of the pretrained HCbed group before and after the cerebellar lesion strongly supports that, in both conditions, the same strategy is used.

When the performances of the pretrained HCbed animals were compared with those of pretrained control rats, peculiar differences were evidenced. While no statistical difference was found regarding successful escapes, latencies and exploration scores were statistically different. In fact, also in the final trials of the water maze without curtains paradigm, pretrained HCbed rats displayed high exploration scores and rather long finding latencies in comparison to controls. Evidently, the navigational scanning strategy pretrained HCbed rats kept on displaying, although effective in finding the platform, was less efficient than the direct finding approach displayed by control animals. It could be argued that the relatively poor performances of pretrained HCbed rats, compared with the pretrained control group, were due to a lessened ability to navigate more or less directly to the hidden platform by using a spatial map representation, or praxic skills. This hypothesis can be dismissed by taking our preceding findings into account, which demonstrated that HCbed rats perform as controls, also displaying effective direct finding, once they have been allowed to acquire the necessary competencies before the lesion (Petrosini et al. 1996).

The use of such a "rigid" exploration strategy has important implications for assessing the nature of the spatial impairment following a cerebellar lesion. During pretraining, the rats could and did learn the general task procedures and different exploration strategies, up to efficient tank scanning. In the successive water maze-without-curtains paradigm, when intra- and extra-maze visual cues were available, intact animals rapidly abandoned the scanning strategy, caught up with the visual cues, and developed a direct reaching of the platform. Conversely, pretrained HCbed rats exclusively activated the procedures they had previously learned. Direct reaching of the platform was never exhibited by pretrained HCbed animals, since they could only acquire it in the water maze without curtains paradigm, but did not due the cerebellar lesion.

Direct reaching of the platform in the water maze-without-curtains paradigm can be performed through different mechanisms. A fixed starting position coupled with a fixed platform position allows direct finding, even based on only praxic abilities. The availability of visual cues allows a direct finding, even based on only taxic or place abilities. As in presence of a cerebellar lesion, direct finding was never observed; it was demonstrated that neither praxic, taxic, nor place-reaching abilities can be built up in the absence of the cerebellar processing. It is to be noted that it was previously demonstrated that the acquisition of other spatial strategies, such as extended searching or restricted searching, is also prevented by a cerebellar lesion (Petrosini et al. 1996). When the cerebellar lesion intervenes during the acquisition of a chain of (spatial) procedures, a freezing of the procedural competencies arises, resulting in a maintenance of the procedures developed before cerebellar lesion and in a block of any further acquisition. These findings clearly put into focus the central role of the cerebellum in procedural learning, in line with recent findings in humans (Molinari et al. 1997b).

Recently, good performances in declarative components of spatial tasks have been reported in totally cerebellectomized rats (Dannahoui et al. 1992) and mice (Hilber et al. 1998). Although Dannahoui's research dealt with the role of cerebellum in location memory, by specifically analyzing the procedural aspects of their results, significant similarities can be found with the present findings. When the cerebellum is ablated before the task, Dahhaoui et al. (1992) report that rats succeed in finding the reward, even if by applying strategies different from those put into action by intact animals. Cerebellectomized rats preferentially explore the external zone of the arena, displaying different path lengths and numbers of cups explored than the controls, thus indicating that the reported good declarative performance in the spatial task was achieved through a quite impaired strategy. When the task was learned before the cerebellar lesion, according to the authors, "the animals have memorised the task to be done", but "..have forgotten the precise location of the reward", demonstrating a maintenance of the preoperatively acquired spatial procedures, in agreement with the present findings.

In the work by Hilber et al. (1998), devoted mainly to the analysis of spatial capabilities in *Lucher* mutant mice, the authors briefly report that cerebellectomized control mice are able to learn to escape as efficiently as intact animals and that a platform location learned before cerebellectomy is completely forgotten after the lesion. Regarding escape learning, besides obvious species differences, other reasons can be advanced to explain the differences between Hilber et al.'s (1998) and our results. Hilber's specimen selection excluded all bad learners, focusing all analyses on successful performances. This approach is quite different from the one applied in our line of research (Petrosini et al. 1996, 1998; Molinari et al. 1997a), in which the only specimen selection is based on the anatomical control of cerebellar lesions. Furthermore, the protocol employed (only a hidden platform in a fixed position) and the parameters analyzed (only latencies without any analysis of the exploration behavior) by Hilber's group are quite different from ours, thus making the comparison with our data very problematic. Regarding the effect of a cerebellar lesion on spatial recall, the two studies address complementary aspects. While Hilber et al. address location memory and report that cerebellar lesions abolish its retention, the present data address spatial procedures and indicate that cerebellar lesions do not affect their recall. All this evidence, taken as a whole, gives further support to the hypothesis that the cerebellum might play distinct roles in declarative or procedural aspects of spatial data processing.

Different explanations can be advanced to interpret the peculiarly fixed exploration behavior in the presence of a cerebellar damage. On one hand, it may be that the lack of flexibility in changing behavior, even when possible, might be due to an impairment in planning intentional strategies, that is, in the ability to access and effectively use different strategies to regulate and change behavior according to the context. This interpretation is in line with the view that cerebellar damage might elicit "frontal-like" cognitive deficits and is supported by clinical reports describing severe problems in initiation/perseveration and in cognitive planning in cerebellar patients (El-Awar et al. 1991; Grafman et al. 1992; Appollonio et al. 1993). On the other hand, the specificity of the cerebellar damage might reside in the impairment of acquisition of new strategies. According to this interpretation, the rigid behavior displayed by pretrained HCbed rats does not depend on difficulties in shifting behavior, but on the inability to acquire and develop a new strategy, even when possible.

This latter interpretation is tempting, since it allows for speculation that the cerebellum and prefrontal cortex interact in planning actions and responses, the former by permitting acquisition of efficient strategies, the latter by providing flexibility among different solutions already acquired and stored. Speculating on the specific contribution of the cerebellum to cognition, Thach (1996, 1998) recently wrote that the "cerebellum may link a behavioural context to a motor response". Following this line, the role of the cerebellum in the spatial function might be that of acquiring the most efficient strategy in a given context and sending it to prefrontal areas. These regions might then choose, from different alternatives, the most apt possibility for the context. Of course, prefrontal and premotor areas could still plan without "feeding" from the cerebellum, but they would be compelled to choose among solutions already present, since no new strategy can be acquired in the absence of the cerebellum.

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