

# Wayfinding in the blind: larger hippocampal volume and supranormal spatial navigation

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## Abstract

In the absence of visual input, the question arises as to how complex spatial abilities develop and how the brain adapts to the absence of this modality. We explored navigational skills in both early and late blind individuals and structural differences in the hippocampus, a brain region well known to be involved in spatial processing. Thirty-eight participants were divided into three groups: early blind individuals ( $n = 12$ ; loss of vision before 5 years of age; mean age 33.8 years), late blind individuals ( $n = 7$ ; loss of vision after 14 years of age; mean age 39.9 years) and 19 sighted, blindfolded matched controls. Subjects undertook route learning and pointing tasks in a maze and a spatial layout task. Anatomical data was collected by MRI. Remarkably, we not only show that blind individuals possess superior navigational skills than controls on the route learning task, but we also show for the first time a significant volume increase of the hippocampus in blind individuals [ $F(1,36) = 6.314$ ;  $P \leq 0.01$ ; blind: mean = 4237.00 mm<sup>3</sup>, SE = 107.53; sighted: mean = 3905.74 mm<sup>3</sup>, SE = 76.27], irrespective of whether their blindness was congenital or acquired. Overall, our results shed new light not only on the construction of spatial concepts and the non-necessity of vision for its proper development, but also on the hippocampal plasticity observed in adult blind individuals who have to

## Introduction

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Wayfinding requires the proper encoding, processing and retrieval of spatial information. Successful spatial navigation also requires the activation of a network of brain regions that are essential for the processing of space (Ghaem *et al.*, 1997; Maguire *et al.*, 1998). The hippocampus, in particular, plays an important role for navigation in large-scale environments (Burgess *et al.*, 2002). The contribution of this structure to the processing of spatial information has been demonstrated in several human (Vargha-Khadem *et al.*, 1997; Barrash *et al.*, 2000) and animal studies (Morris *et al.*, 1982; Moser *et al.*, 1993; Colombo *et al.*, 1998). It has also been shown that hippocampal volume varies as a function of experience: the more spatial memory is important or essential for the survival of a species, the larger is the structure (Barnea and Nottebohm 1994; Clayton and Krebs, 1994; Lee *et al.*, 1998).

Interestingly, a study carried out by Maguire *et al.* (2000) revealed structural differences in the hippocampi of London taxi drivers compared with control participants. Taxi drivers were selected because they undergo 2 years of training before obtaining their taxi license, thus making them experts in spatial navigation. Taxi drivers showed a bilateral increase in grey matter density in the posterior sections of each hippocampus as well as a bilateral decrease in grey matter density in its anterior sections compared to control participants. Moreover, a positive correlation was found between the number of years spent driving taxis and the grey matter density of the right posterior hippocampus.

Like taxi drivers, blind individuals require extensive storage of information regarding their environment because they cannot rely on vision to understand the spatial organization of their environment

spatial layout of the far space environment (Strelow, 1985). Consequently, they rely more on idiothetic cues, such as vestibular and proprioceptive information and the monitoring of the movement made by oneself (Millar, 1994; Thinus-Blanc and Gaunet, 1997). Since it has been shown that the hippocampus is essential for the processing and use of idiothetic information in animals (Whishaw *et al.*, 2001) one might expect to see differences in hippocampal volume in visually deprived individuals.

The aim of the current study was two-fold. First, we submitted our subjects to a series of spatial navigation tasks to ascertain whether or not the blind develop these skills, and possibly, as shown in other tasks using this subject population, whether they actually show enhanced skills with respect to wayfinding and orientation in space. Second, we looked at possible structural correlates of performance by measuring hippocampal sizes (both whole and identified sub-regions) in these individuals. It was predicted that blind individuals would not only better perform in our spatial tasks, but would also show differences in hippocampal size compared with the sighted. Moreover, we investigated both early blind subjects and individuals who lost their vision later in life, in whom plastic changes are known to be more limited.

## Materials and Methods

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### Participants

Thirty-eight participants with no history of neurological, cognitive or sensory-motor deficits, other than blindness in the case of the blind participants, participated in the experiment and were divided into three groups. The first group ( $n = 12$ ) consisted of early-blind individuals (loss of vision before 5 years of age), aged between 19 and 55 years (mean age 33.8 years), nine of whom were men (three

either total blindness or at most light perception. There was one control group composed of blindfolded sighted participants paired for age, gender, education and laterality score, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), with each of the two groups of blind participants. The sighted control group ( $n = 19$ ) were aged between 19 and 56 years (mean age 36.0 years), 13 of whom were men (six women). The research protocol was approved by the ethics committees of the Center for Interdisciplinary Research in Rehabilitation, which coordinates in the Province of Quebec research with blind participants and is sponsored by the Institut Nazareth & Louis Braille, by the Research Center of the Institut Universitaire de Gériatrie de Montréal, where the testing was carried out, by the Centre Hospitalier de l'Université de Montréal (CHUM), where the MRI scans were collected, and by the Université de Montréal, where the project originated. All participants provided written informed consent prior to testing.

## Behavioural tasks

Participants performed the tasks before undergoing the MRI scans. It is important to keep in mind that the sighted individuals were blindfolded before entering the testing room and throughout the entire experiment in order to exclude any visual information of the spatial context. As shown in rats, animals rely heavily on idiothetic information to travel in space when vision is not available (Wishaw *et al.*, 1997). Sighted participants were blindfolded ~15 min prior to the beginning of the behavioural tasks. Afterwards, while remaining blindfolded, all participants were then familiarized with the maze setting by exploring, with the aid of the experimenter, a small portion of the maze. As a result, all subjects were blindfolded for about half an hour prior to testing.

In order to eliminate a possible discrepancy between the groups in attention abilities, the digit span subtest from the Weschler Adult

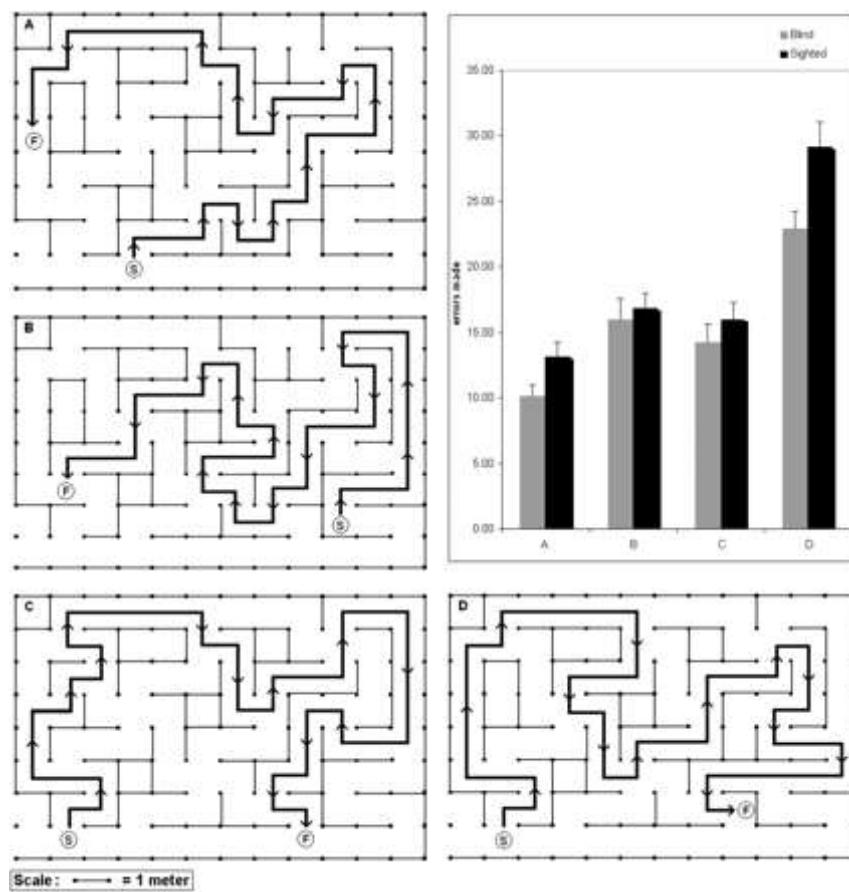
## Maze tasks

Two different tasks were administrated in a human-sized experimental labyrinth setting formed by a series of panels ( $1\text{ m} \times 2\text{ m}$ ) occupying a space of  $9\text{ m} \times 15\text{ m}$ . The protocol used for the spatial tasks in the labyrinth was developed in earlier studies (Passini *et al.*, 1990; Chouinard *et al.*, 2003).

### Learning a route task

The first navigational task consisted of learning a series of routes in a human-size maze which rely on linear acquisition of information. Subjects memorized a route once, and then had to follow the same path a number of times while trying to make as few errors as possible. The participants were first guided once by the experimenter in the labyrinth along a predetermined path and were invited to explore the space along the way in order to learn and memorize the specific path taken. The experimenter walked in front of the participant and guided him/her by repeatedly saying ‘this way’ while the participants were touching the walls surrounding them. When the guided tour of the route was completed, the participants were brought back to the starting point where they were invited to follow the same path by themselves while the experimenter, walking behind, pointed out and corrected their errors. This was done by touching the participants and placing them in the correct orientation without giving any information on the spatial context (for example, ‘turn left here’). This procedure was repeated five times. There were four different paths increasing in complexity. The complexity of the path was related to the number of decision points (6, 8, 10 or 12, see Fig. 1). The different degrees of complexity were obtained by moving walls in order to change the setting of the maze. The errors committed by the participants were noted on a sheet by the experimenter. An error was noted each time a participant entered an incorrect alley by crossing with their two feet an imaginary line going from the decision point

**Fig. 1**



The learning a route task. (A) The 6 decision points path. (B) The eight decision points path. (C) The 10 decision points path. (D) The 12 decision points path. The subjects were first guided along the path, as indicated by the arrows, from the starting point **S** to the finish point **F**. They were then asked to follow the same path by themselves five times. The numbers of errors made by the sighted (in black) and blind (in grey) subjects for each route (A, B, C and D) are illustrated in the graph.

## Pointing task

The participants were brought to three different points in the labyrinth. At each new point, they had to point as precisely as possible towards the starting point or towards the last pointing position (Fig. 3). They had to do so by placing their foot on a specific mark on the floor and extending their arm along the axis of the body in the estimated direction. The angle was measured by holding a stick

## **Spatial layout task**

The participants were conducted to a small room ( $4\text{ m} \times 5\text{ m}$ ) adjacent to the labyrinth. In order to discover the principles of the spatial organization of a small spatial layout placed within the room using the same panels as for the labyrinth, they were asked to freely explore this spatial layout by walking through it. There were two different configurations with different degrees of complexity, each of which was presented in a counterbalanced manner across all subjects in each group (Fig. 4). The walls were placed according to an axial symmetrical layout and a central symmetrical layout. All the subjects explored each layout once at their leisure. Right after the exploration of the first layout presented to them, the participants explored five small-scale models with their hands and then chose the correct model representing the explored layout (one represented the correct configuration and the four others contained one or two errors). This procedure was repeated for the second layout. A correct identification was noted when a participant chose the correct small-scale model from all the models presented. The difference between each erroneous small-scale model and the correct one was limited to only one cue (one error) for the complex configuration and to two cues (two errors) for the simple one.

## **Anatomical data**

### **Image acquisition and pre-processing**

For each participant, high-resolution volumetric MRI was performed on a Siemens 1.5 Tesla Magnetom Vision MRI scanner (Siemens, Erlangen, Germany) at the Notre-Dame Hospital (CHUM). Each participant was investigated with a high-resolution ( $1 \times 1 \times 1\text{ mm}$ ,  $T_1$ -weighted 3D) sagittally oriented MRI echo sequence with TR: 1100; TE: 4.38; flip angle of 15;  $256 \times 256$  matrix and FOV: 250.

and then registered into standard stereotaxic space based on the MNI 152 template (Collins *et al.*, 1994) to account for individual differences in head size. These pre-processing steps reduce inter-scan variability due to scan artifacts and correct for global brain size differences.

The segmentation and volumetric analyses were performed using DISPLAY, a software developed at the McConnell Brain Imaging Centre of the Montreal Neurological Institute. This program allows simultaneous viewing and navigating in brain volumes in coronal, sagittal and horizontal orientations in 1 mm slice intervals (Fig. 5).

## Image analysis

The anatomical boundaries used for segmentation have been described in detail elsewhere (Pruessner *et al.*, 2000). In short, the procedures described below for delineation of the hippocampus were employed.

The most posterior part of the hippocampus was defined as the first appearance of ovoid mass of grey matter inferiomedial to the trigone of the lateral ventricle (TLV). The lateral border at this point was the TLV, whereas medially, the border was identified by the presence of white matter. Further anteriorly, an arbitrary border was defined for the superior and medial border of the hippocampus, in order to differentiate hippocampus grey matter from the grey matter of the Andreas Retzius gyrus, the fasciolar gyrus and the crus of the fornix.

For the hippocampus body, the most visible inferolateral layer of grey matter was excluded, assuming that it actually represents entorhinal cortex. Next, the white matter band at the superomedial level of the hippocampus body, the fimbria, was included. If grey matter was found superior to the fimbria, the first row of grey matter was also included. The dentate gyrus, located between the four California regions in the hippocampal formation, together with the California regions themselves and part of the subiculum, were included. The

between these two structures. The lateral border at this point was identified by the inferior horn of the lateral ventricle.

The hippocampus head was defined by the emergence of the uncal recess in the superomedial region of the hippocampus. The most important structures for identification of lateral, anterior and superior borders of the head were the uncal recess of the inferior horn of the lateral ventricle and the alveus. Besides the coronal view, the sagittal and horizontal views were employed for identification of the anterior border of the hippocampus.

This protocol with proven reliability and validity has been implemented in numerous studies (Pruessner *et al.*, 2000, 2001; Buss *et al.*, 2007) and benefits from superior visualization of the target structures in 3D (coronal, sagittal and horizontal). The intra-rater intra-class reliability coefficients ranged between 0.81 and 0.84 for one rater (P.V.) measuring the hippocampi in four participants two subsequent times, with at least 1 month elapsing between consecutive measurements. The intra-rater intra-class reliability coefficients ranged between 0.86 and 1.00 for one rater (M.F.) dividing the hippocampi in three parts for the same four participants. The inter-rater intra-class reliability coefficients range between 0.73 and 0.82 for two raters (P.V. and C.L.) measuring hippocampal volumes independently in eight randomly selected MRI scans. The inter-rater intra-class reliability coefficients range between 0.99 and 1.00 for two raters (M.F. and C.L.) dividing the hippocampus in three parts for the same eight participants. All the raters were blind with respect to the group and performance of the subjects.

## Results

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### Behavioural data

There was no difference between the blind and the sighted on the

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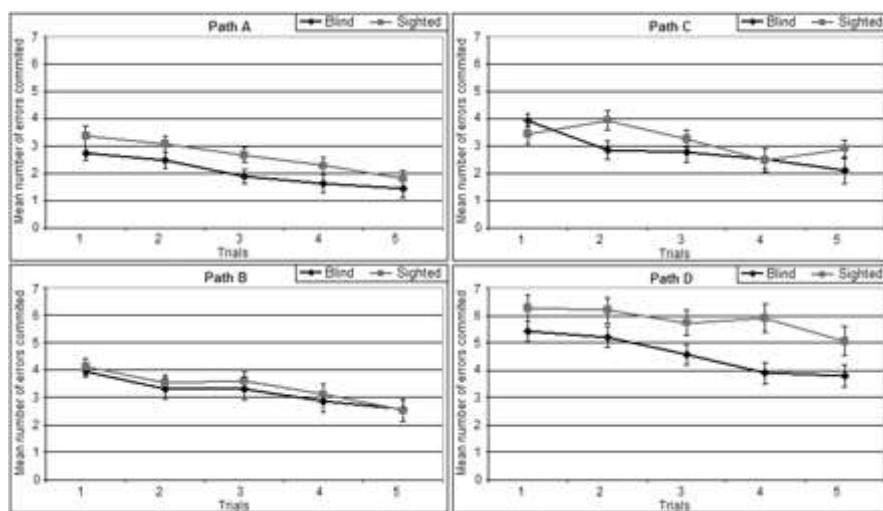
the blind participants pooled together and their paired sighted controls ( $P > 0.05$ ). Hence, the differences obtained on the other task cannot be attributable to a discrepancy in working memory or attentional abilities.

In the ‘learning a route’ task, the participants were required to follow a specific path in the human size maze, to which they had been previously exposed, while keeping errors to a minimum. There were four different routes to learn, each presented for five trials. Each new route increased in its level of difficulty by augmenting the number of decision points by 2 (6 decision points for the first route; 12 for the fourth). The number of errors for each trial was computed and the five trials were pooled in order to obtain the total number of errors for each route. An analysis of the performance on this task was first examined with respect to whether the blindness occurred early or later in life. For these participants, a two (early blind versus late blind) by four (complexity of the routes) repeated measures ANOVA revealed no significant effects between the two groups of blind participants [ $F(1,17) = 0.183; P > 0.05$ ]. There was a route effect [ $F(3,51) = 25.536; P \leq 0.001$ ], the number of errors generally increasing with the number of decision points. There were no significant interactions between the groups (early and late blind) and the complexity of the routes [ $F(3,51) = 1.850; P > 0.05$ ].

Hence, the blind participants were pooled together for comparison with the sighted controls. A two (blind versus sighted) by four (complexity of the routes) repeated measures ANOVA was carried out. As was the case for the analysis involving only the blind participants, there was a route effect [ $F(3,108) = 64.85; P \leq 0.001$ ], the number of errors generally increasing with the number of decision points. The analysis revealed a significant effect between the blind and the sighted [ $F(1,36) = 4.352; P \leq 0.05$ ], with the blind making in total less errors (mean = 63.26 errors, SE = 3.94) than the sighted (mean = 75.16 errors, SE = 4.12) (Fig. 1). A trend was found for the interaction between complexity of the routes and visual experience (blind versus

for the sighted individuals than for the blind [ $P \leq 0.01$  (blind: mean = 22.89 errors, SE = 1.34; sighted: mean = 29.16 errors, SE = 1.95)]. There was also a difference for the easiest route (6 decision points), whereby the sighted made more errors than the blind individuals [ $P = 0.04$  (blind: mean = 10.16 errors, SE = 0.86; sighted: mean = 13.16 errors, SE = 1.11)]. There were no significant differences between the sighted and the blind for the other two routes (8 and 10 decision points). In addition, Fig. 2 clearly illustrates that differences between groups were not attributable to different learning rates. Additional repeated measures ANOVA were also performed for each route with the trials serving as the repeated factor. The lack of significant interactions between the trial variable and the group variable [with the exception of route 3;  $F(4,144) = 2.605, P = 0.045$ ] also supports the notion that both groups did not differ in terms of learning rate.

**Fig. 2**

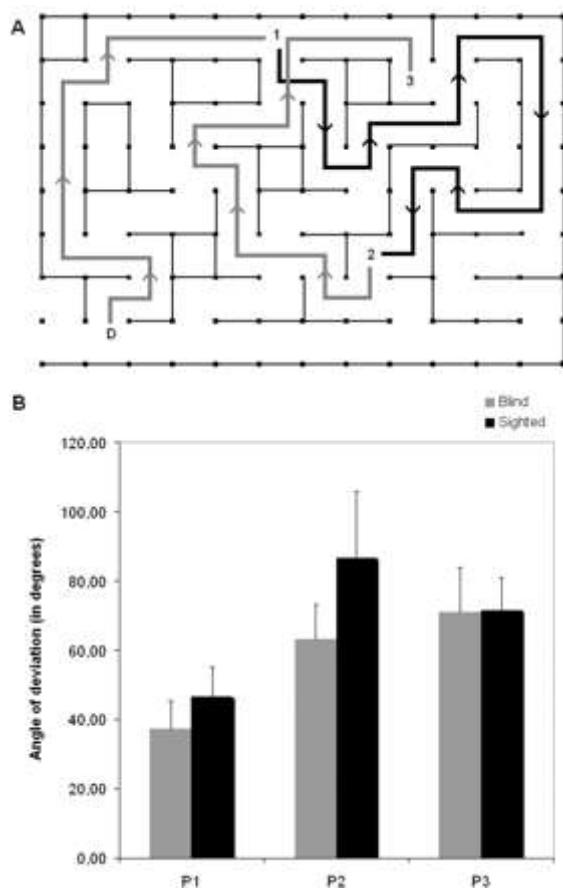


Effect of learning. Learning curves for both the blind and sighted participants across the five trials for all four paths. It can be seen that both groups show similar learning rates for all paths.

In the ‘pointing’ task, the participants were guided to three different locations in the labyrinth. At each new location, they had to point as precisely as possible towards the starting point or towards the last

revealed no significant effects between the two groups of blind participants [ $F(1,17) = 0.86; P > 0.05$ ]. There was a pointing location effect [ $F(2,34) = 4.02; P \leq 0.05$ ], the degree of errors generally increasing for each new pointing location. There were no significant interactions between the groups (early and late blind) and the different pointing location ( $P > 0.05$ ). Again, the blind participants were pooled together for comparison with the sighted controls. A two (blind versus sighted) by three (pointing locations) repeated measures ANOVA was carried out. As was the case for the analysis involving only the blind participants, there was a pointing location effect [ $F(2,72) = 7.355; P \leq 0.001$ ], the number of errors generally increasing for each new pointing location. The analysis revealed no significant effect [ $F(1,36) = 0.702; P = 0.408$ ] between the blind (mean = 57.09 errors, SE = 8.21) and the sighted (mean = 68.18 errors, SE = 10.38) and no significant interactions between the groups (blind and sighted) and the different pointing location ( $P > 0.05$ ) (see graph of Fig. 3).

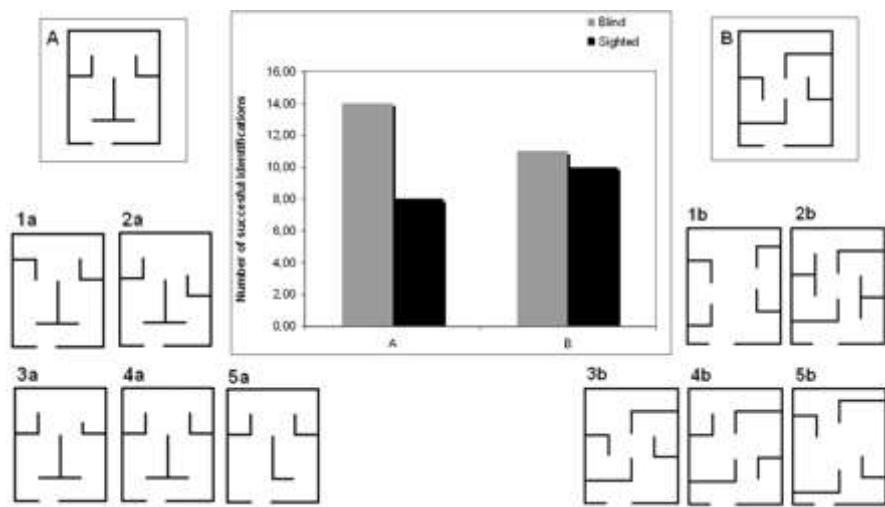
**Fig. 3**



The pointing task. (A) The subjects were guided from the departure point **D** to the first pointing position **1** and were then asked to point towards the departure point **D**. They were then guided to the second pointing position **2** and asked to point towards the first pointing position **1**. Finally, they were guided to the third pointing position **3** and were asked to point towards the second pointing position **2**. (B) Shows the performance of the sighted and the blind.

In the ‘spatial layout’ task, the participants were told to freely explore the spatial layout of a small maze in order to familiarize themselves with its spatial organization (Fig. 4). Following this exploration, the participants had to choose the correct model out of five small-scale models representing the layout they had just explored. There were two different configurations with different degrees of complexity. The difference between each erroneous small-scale model and the good one was limited to only one cue for the complex configuration

**Fig. 4**



The spatial layout task. The left portion of the figure shows the axial symmetrical layout of the complex configuration (**A**) along with the five small-scale models from which the participants had to choose the correct representation (in this case **4a**). In the right portion of the figure is shown the central symmetrical layout of the simple configuration (**B**) along with the different configurations from which the subjects had to choose the correct response (in this case **3b**). In the middle graph, the performance of the sighted and the blind is shown.

For the complex configuration (one cue), a chi-square analysis showed that significantly more blind participants succeeded in performing the task in comparison to the sighted subjects ( $\chi^2_{(1)} = 3,89; P \leq 0.05$ ). However, there was no difference between the number of blind and sighted participants who succeeded in the simple configuration task where more cues were available ( $\chi^2_{(1)} = 0.11, P > 0.05$ ) (see graph of Fig. 4).

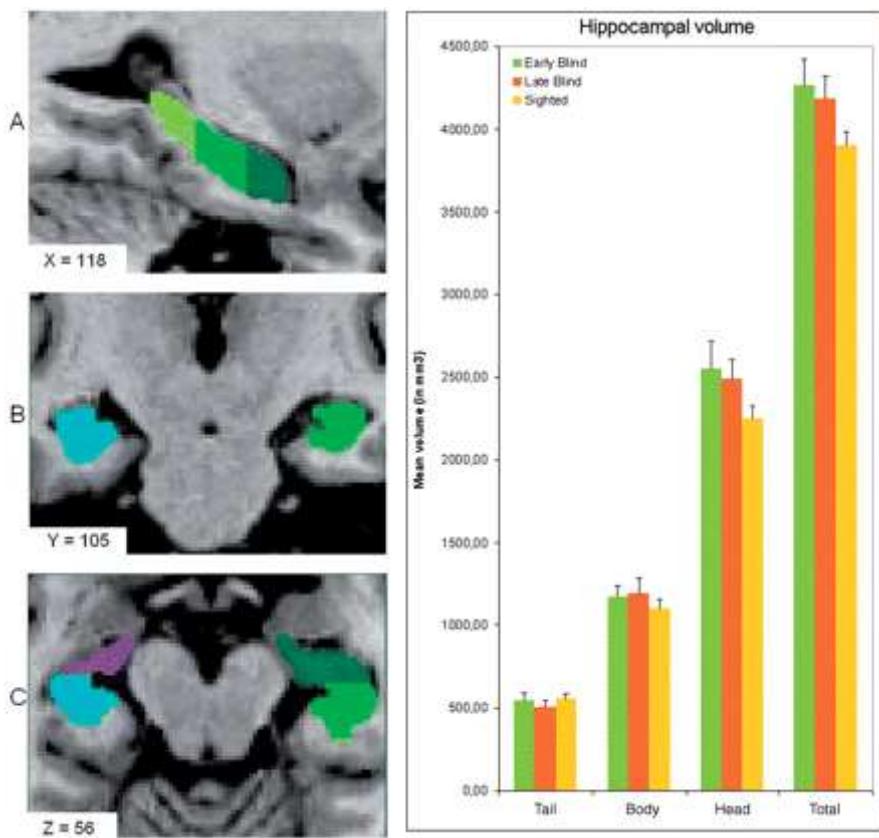
The type of strategy used by the subjects from the two groups was compared. Generally, they used one of two strategies: they either simply moved along the perimeter of the room to which were attached the panels (border evaluation) or they also tried to understand the general layout by touching the different panels and establish some relationship between them (border and layout evaluation). Based on previous experiments with the apparatus the

their preferred strategy for exploring the set of panels making up the space ( $\chi^2_{(1)} = 1.42$ ,  $P > 0.05$ ).

## Anatomical data

Grey matter volume of the hippocampus was first examined for difference as a function of whether the blindness occurred early or later in life. For these participants, a two (early blind and late blind) by two (hemisphere) by three (structure: head, body and tail of the hippocampus) repeated measures ANOVA revealed no significant effects between the early and the late blind [ $F(1,17) = 0.133$ ;  $P > 0.05$ ]. There was a structure effect [ $F(2,34) = 148.001$ ;  $P \leq 0.001$ ], the head of the hippocampus being larger than the body ( $P < 0.001$ ) which in turn was larger than the tail ( $P < 0.001$ ). There were no significant interactions between group (early versus late blind) and structure [ $F(2,34) = 0.058$ ;  $P > 0.05$ ] (Fig. 5). The lack of differences between the early- and late-blind group could not be attributable to the age or the sex of the participants since they did not differ for these characteristics [Age:  $t_{(17)} = -1.130$ ,  $P > 0.05$ ; Sex:  $\chi^2$  Fisher's Exact Test (two sided)  $P > 0.05$ ].

**Fig. 5**



Segmented hippocampus. In (A) the sagittal, (B) coronal and (C) horizontal plane. The yellow-green scale corresponds to the right hippocampus and the blue-purple scale to the left hippocampus. The head (dark green) can clearly be distinguished from both the body (light green) and tail (yellow-green) in the sagittal slice. The mean total and partial hippocampal volumes for both the early blind (green), the late blind (orange) and the sighted (yellow) are shown in the graph.

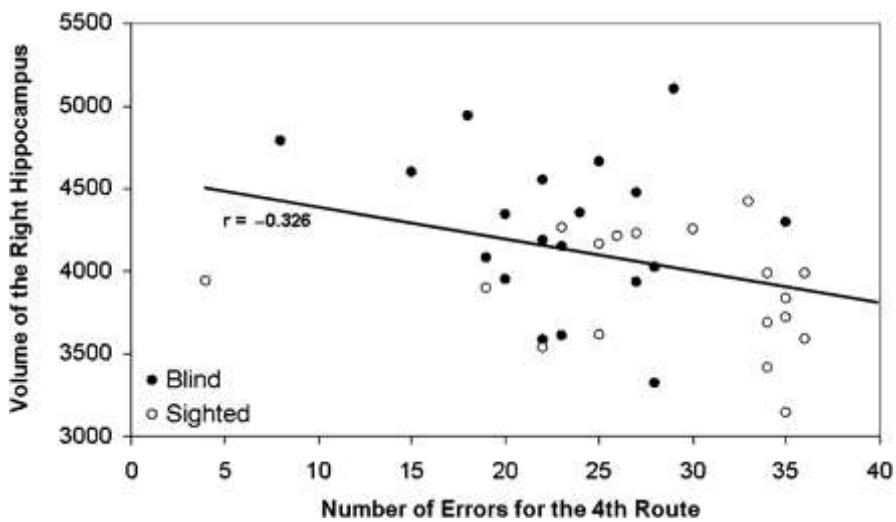
Hence, the blind participants were pooled together for comparison with the sighted controls. A two (blind versus sighted) by two (hemisphere) by three (structure: head, body and tail of the hippocampus) repeated measures ANOVA revealed a significant effect between the blind and the sighted [ $F(1,36) = 6.314; P \leq 0.01$ ], with the blind showing a larger hippocampal volume than the sighted (blind: mean =  $4237.00 \text{ mm}^3$ , SE = 107.53; sighted: mean =  $3905.74 \text{ mm}^3$ , SE = 76.27).

structure and hemisphere was found [ $F(2,72) = 8.358; P \leq 0.001$ ], with the body being larger in the left hemisphere ( $P = 0.006$ ) and the head being larger in the right hemisphere ( $P = 0.008$ ) while the tail volume did not differ between hemispheres for both blind and sighted participants ( $P > 0.05$ ) (Fig. 4). A trend was also found for the interaction between structure and visual experience (blind versus sighted) [ $F(2,72) = 2.354; P < 0.1$ ]. A contrast analysis was conducted in order to determine which part of the hippocampus differed between the blind and sighted. This analysis showed that the overall head volume (left and right hemisphere combined) was larger in the blind individuals [ $P \leq 0.05$  (blind: mean =  $2527.08 \text{ mm}^3$ , SE = 111.27; sighted: mean =  $2250.76 \text{ mm}^3$ , SE = 73.32)], while there was no significant difference between the blind and the sighted for the hippocampus body ( $P > 0.05$ ) and the hippocampus tail ( $P > 0.05$ ).

## Correlational analyses

Given the significant differences between groups observed both for the maze task as well as for the hippocampal volume, it is only natural to see if both data sets correlated with one another. Although the volume of the right head of the hippocampus did not significantly correlate with the overall results of each of the routes ( $P > 0.05$ ), the total volume of the right hippocampus did correlate with the data from the fourth route, the most difficult one ( $r = -0.326; P = 0.046$ ). The negative relationship simply implies that the larger the volume of the right hippocampus, the less errors a subject committed (Fig. 6). In addition, we found no significant correlation between the age of the onset of blindness with the volume of the right head ( $r = 0.073; P = 0.766$ ), the right hippocampus ( $0.106; P = 0.665$ ) and the total hippocampal volume ( $r = 0.055; P = 0.823$ ), thus supporting our decision to pool both blind groups together for our analyses.

**Fig. 6**



Brain-behaviour correlation. Seen here is the right hippocampus volume plotted against the error scores on the fourth learned route for both blind and sighted subjects. When both groups were pooled together, a significant correlation was observed between the above-mentioned variables. The sighted subjects tended to have smaller right hippocampal volumes associated with poorer performance on the behavioural task as opposed to the blind subjects in which the opposite pattern was observed.

## Discussion

The results presented above provide clear evidence of structural differences between blind and sighted individuals. Indeed, there was a significant difference in the overall volume of the hippocampus between the blind and the sighted. The involvement of this structure in spatial tasks has been demonstrated in many studies. For instance, structural differences in taxi drivers in comparison to controls concerned the hippocampus (Maguire *et al.*, 2000). More generally, imaging studies have demonstrated the activation of this structure in association with navigational tasks (Maguire *et al.*, 1997; Mellet *et al.*, 2000; Hartley *et al.*, 2003; Iaria *et al.*, 2003). Furthermore, the importance of the temporal lobe as a whole for path integration has been clearly established by studies in humans with temporal

hippocampus head. Although it is not known for its implication in spatial processing, Maguire and colleagues (2006) have shown a possible link between the head of the hippocampus and visuo-spatial memory. The head of the hippocampus has also been typically associated with verbal memory (Hackert *et al.*, 2002). Keeping this in mind, it is possible that during the ‘learning a route’ task, subjects were simply verbally storing path information as a string of right and left turns as opposed to learning an allocentric representation of the space. Thus, a volume increase of this part of the structure could also be related to an enhanced use of memory by blind individuals, as observed in previous studies (Röder *et al.*, 2001; Amedi *et al.*, 2003, 2004; Raz *et al.*, 2005). Although the aforementioned studies related performance in verbal memory tasks to primary visual cortex activation, it remains nonetheless possible that an additional contribution came from the hippocampus head.

A very recent study also examined hippocampal volume differences between blind and sighted individuals (Chebat *et al.*, 2007). They found that the volume of the right posterior hippocampus was significantly reduced compared to sighted controls. Although their findings appear at odds with the ones presented here, they are not entirely incompatible. In fact, another recent study found both sets of differences between blind and sighted hippocampal volumes: a larger anterior and a smaller posterior region in the right hippocampus (Lepore *et al.*, 2008). The latter study used a new surface mapping algorithm (see Shi *et al.*, 2007), suggesting that the differences between the studies could have a methodological basis. Moreover, Chebat *et al.* (2007) used predefined cut-offs to segment the hippocampus (with the most anterior quarter of the slices being counted as the head, the posterior quarter of the slices as the tail, leaving the intermediate slices as the body), which could explain the discrepancies between the results of both studies. Nevertheless, both the findings of Chebat *et al.* (2007) and the current findings presented here are supported by the data provided by Lepore *et al.* (2008),

Because of the global enhancement in hippocampal volume in blind participants, a structure involved in spatial navigation, we wanted to investigate whether this would lead to behavioral enhancements in these individuals with respect to spatial tasks. A recent study also examined the effects of visual deprivation on spatial cognition and showed that blind individuals can perform better than sighted ones across a series of spatial tasks (Tinti *et al.*, 2006). While some of their tasks were quite similar to ours, they did not evaluate navigational skills during route learning *per se*, which was the primary objective in the current study. Our results show that blind individuals are indeed better at learning complex paths within a maze compared to blindfolded sighted subjects. These results extend previous findings regarding spatial navigation and the blind (Passini *et al.*, 1990) where no difference between blind and blindfolded sighted subjects was found when learning a new route in the labyrinth. However, the routes used were relatively easy with only 3 and 5 decision points (compared with 6, 8, 10 and 12 for the current study).

Consistent with their results, our easier routes produced very little difference between groups, with the exception of the first route. One explanation for this might be that since the 6-decision point route was the first task performed by all subjects, it is possible that the sighted subjects, who suddenly had to navigate in unfamiliar territory without eyesight for the first time, committed more errors than they would have had if they had more experience with the maze setting or if they had been blindfolded for a longer period of time. After completing the first route and consequently familiarizing themselves better with the maze, their performance increased and reached a level similar to that of the blind for the following two routes (routes 2 and 3). Therefore, it would seem that tasks with few decision points may be too easy for both the blind and the sighted and that the lack of difference between groups is simply result of a ceiling effect. The superior abilities of the blind became more apparent as task difficulty increased (especially notable for 12 decision points), which is

that this is the first study to show a link between a cerebral structure and spatial abilities in blind individuals. Finally, it is noteworthy to mention that while both groups showed learning effects (albeit slight) across the five trials for each route, they did not differ in terms of their learning rates.

A significant difference was also found when comparing the number of blind individuals and paired control participants who successfully identified the correct small scale model corresponding to the spatial layout they had previously explored when only one cue was available. This suggests that blind individuals are better than the sighted at understanding and encoding spatial information when only idiothetic cues are available. It has been argued that blind individuals tend to be better when they use an idiothetic frame of reference when encoding spatial information in large scale environments (Noordzij *et al.*, 2006) and especially if they have lost sight at an early age (Millar, 1994; Thinus-Blanc and Gaunet, 1997). The present results do not seem to support the latter part of this statement because no difference was found between the early and late blind group on the different spatial tasks. It is worth noting that blind subjects have more experience in dealing with tactile stimuli, and therefore might be better at extracting information about shapes from touch as opposed to simply a superior spatial memory. Perhaps the actual answers lie in the form of some combination of the two mechanisms.

As far as the pointing task is concerned, there was no significant difference between the performance of blind and sighted individuals. While this could be explained by the fact that pointing in a specific direction is not a behaviour used often by blind persons since such behaviour relies more on allocentric-based knowledge of the environment, our blind subjects did on average perform better although the difference did not reach statistical significance (mostly attributable to large variances). In addition, Tinti *et al.* (2006) also had their blind subjects perform a similar pointing task and showed that they were significantly better than the sighted subjects. This

difficult to enable the observation of any substantial differences between our groups. Taking these facts into account, it would nonetheless seem that blind individuals are better able to situate themselves in their environment with respect to a specific reference point.

The absence of structural differences in the posterior portion of the hippocampus (hippocampal tail) and the finding that blind individuals perform better than sighted individuals on different spatial tasks are not incompatible. In fact, in the general population, variations in navigational skills alone are not associated with structural differences (Maguire *et al.*, 2003). Maguire and collaborators submitted participants to different spatial tasks, including navigation in a virtual reality town, recognition of an environmental scene from the visited town, construction of a map of the town and a standardized topographical memory test. None of those tasks were related to the grey matter volume of the hippocampus. Furthermore, the posterior part of the hippocampus has been related to the use of allocentric information (Millet *et al.*, 2000). It has also been argued that taxi drivers and controls differ on the kind of spatial representation they use. Taxi drivers tend to use a more integrated representation of space (allocentric) than normal controls (Maguire *et al.*, 2000). Therefore, it is possible that the enhancement of grey matter volume in the posterior part of the hippocampus of taxi drivers is linked to their increased use of an allocentric frame of reference. In marked contrast, however, it has been hypothesized that blind individuals rely mostly on an egocentric frame of reference to process spatial information (Thinus-Blanc and Gaunet, 1997), which could explain why no volume difference was found in the posterior portion of the hippocampus.

Worthy of mention is the fact that we did not measure volumes elsewhere in the brain nor did we have a control structure. This leaves open the possibility that other structural changes may exist in the adult brain of blind individuals. Moreover, the hippocampal changes

In summary, the present results revealed larger volumes of the anterior (head) portions of the hippocampus in blind individuals compared with sighted controls. These hippocampal volume differences were paralleled by multiple behavioural enhancements in the former. These individuals did in fact show superior navigational skills when learning new paths in a maze setting and also demonstrated superior recognition of small-scale tactile layouts representing spatial environments they had previously explored. Further research is required to better understand the role of the anterior hippocampus in spatial navigation in the blind. The reported difference might not be the result of altered spatial navigational abilities, but rather the result of increased use of memory functions, albeit for spatial tasks, in the blind.

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