Exploring anterograde associative memory in London taxi drivers

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London taxi drivers are renowned for their navigation ability, spending a number of years acquiring 'The Knowledge' of London's complex layout and having to pass stringent examinations to obtain an operating licence. In several studies, this navigation skill has been associated with increased posterior but also decreased anterior hippocampal grey matter volume. Neuropsychologically, gain and loss has also been documented in taxi drivers; while very skilled at navigation in London, they are significantly poorer than controls at learning and recalling new object–location associations. Here we tested a group of London taxi drivers and matched control participants on this object–location associations task, while also subjecting them to a battery of challenging anterograde associative memory tests involving verbal, visual and auditory material both within and across modalities. Our aim was to assess whether their difficulty in previous studies reflected a general problem with associative memory, or was restricted to the spatial domain. We replicated previous findings of poor learning and memory of object–location associations. By contrast, their performance on the other anterograde associative memory tasks was comparable with controls. This resolves an outstanding question in the memory profile of London taxi drivers following hippocampal plasticity, and underlines the close relationship between space and the hippocampus. ***NeuroReport*** **23:885–888 © 2012 Wolters Kluwer Health | Lippincott Williams & Wilkins.**

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Introduction

To be licensed to operate, taxi drivers in London, UK, must learn the layout of 25 000 streets and the locations of thousands of places of interest. This process takes about 3–4 years, and is colloquially known as acquiring 'The Knowledge' [1]. A number of cross-sectional studies of London taxi drivers [2–4] and a recent within-subjects longitudinal study [5] confirmed their navigational superiority and also documented increased posterior hippocampal grey matter volume compared with matched control participants. Interestingly, the taxi driver story is one of loss as well as gain. Decreased grey matter volume in the anterior hippocampus [2–4] and poor performance compared with controls on several memory tests have been consistently observed [3–5]. Specifically, taxi drivers were significantly worse than control participants on the delayed recall of the Rey-Osterreith complex figure [3–5], a widely used test of anterograde visuospatial memory [6,7]. In addition, they were poorer at learning new object–location associations on a table-top array and recalled less of this information after a delay [4,5].

Given that taxi drivers continually deal with spatial information, decrements on these visuospatial tasks seem surprising; and several potential explanations have been offered to account for these findings [4]. The Rey-Osterreith complex figure and the object–location associations test clearly require spatial memory to recall the positions of lines (Rey) and objects in spatial arrays. It may be that hippocampal involvement in supporting the complex spatial representation of London limits its capacity for acquiring and storing new, specifically spatial, information [4,8,9]. Alternatively, both of these tasks can also be viewed as associative in nature, involving the association of items with locations. As such, the basic problem in the taxi drivers might be with forming new associations in general, and not merely to do with space [4,10,11].

To try and resolve the precise nature of anterograde memory in taxi drivers and gain further insight into information processing in the hippocampus and the consequences of plasticity, we set out to probe this issue further in a new cohort of London taxi drivers and matched control participants. We tested them on the object–location associations task [4,5], and also on additional tests that assessed associative learning and memory more generally. These tasks examined associative memory within the visual domain, across modalities (e.g. vision–sound), and in the verbal domain. If the taxi drivers had an underlying problem with associative memory *per se* then they should have difficulty on all of these tasks. However, if their primary problem concerned the processing of new spatial information then they should only show poor performance on the object–location associations test.

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Methods

Participants

There were 38 healthy male participants, 20 licensed London taxi drivers and 18 control participants. All gave informed written consent to participation in accordance with the approval of the National Hospital for Neurology and Neurosurgery and Institute of Neurology Joint Research Ethics Committee. All taxi drivers had completed 'The Knowledge' training and obtained a licence (mean years taxi driving experience 13.67 years, SD 7.86). None of the control participants had worked as taxi drivers or minicab drivers. Taxi drivers and control participants did not differ in terms of age [mean age of taxi drivers 42.1 years, SD 5.37; controls 38.72 years, SD 5.85; $t(36) = 1.85$; $P = 0.07$], handedness (laterality index [12]; mean of taxi drivers 87.05, SD 40.36; controls 83.83, SD 39.18; $t(36) = 0.24$; $P = 0.8$), or school-leaving age [mean of taxi drivers 16.45 years, SD 0.94; controls 16.72 years, SD 1.22; $t(36) = 0.7$; $P = 0.4$]. Visual information processing and abstract reasoning skills were assessed using the matrix reasoning subtest of the Wechsler Abbreviated Scale of Intelligence [13]. The mean scaled scores for the groups did not differ significantly [taxi drivers 8.9, SD 1.88; controls 8.38, SD 2.54; $t(36) = 0.7$; $P = 0.4$]. An estimate of verbal IQ was obtained using the Wechsler Test of Adult Reading [14] (mean of taxi drivers 98.66, SD 3.91; controls 100.3, SD 5.17), and did not differ significantly between the groups [$t(32) = 1.05$; $P = 0.3$].

Tasks

Six tests of anterograde associative memory were conducted. The first was the object–location associations test used in previous studies [4,5]. This comprised 16 coloured photographs of single objects placed on a white board measuring 64 cm × 48 cm (Fig. 1a). Participants had 60 s to name each object and study their locations. The array was then removed and a blank board of equal dimensions was introduced. Participants were given the 16 object photographs and asked to place them in the correct locations. Performance was recorded before the next learning trial. Subsequent study periods lasted 30 s and after each one, participants were asked to reproduce the array. The study-recall procedure was repeated until a criterion of 100% correct object placements was reached. Participants were also asked to reproduce the array after a 30 min delay. A score of 1 was given to objects placed within 3 cm in any direction of their original place on the board (see [4] for details). Two measures were derived, the number of learning trials required to reach criterion and the number of correct object–location associations recalled following the delay.

The other five tests followed a standard procedure for associative memory tests. For each task this involved seeing/hearing 16 pairs of stimuli (eight pairs for the verbal paired associates test, which was taken from the Wechsler Memory Scale III [15]), for 3 s/pair. After exposure to the stimulus pairs, memory was assessed by presenting one item from the pair and asking the participant to recall the associated item. In each test there were six learning-retrieval trials of this type (four for the verbal paired associates test). In the visual paired associates test, the stimuli were unrelated pairs of objects on a white background (Fig. 1b). The visual paired associates with a relevant context also involved pairs of objects, but this time superimposed onto a scene background (Fig. 1c); on any one trial both objects were related to the background context but not to each other. In another test, objects were paired with sounds, with each stimulus comprising an object shown on a white background and an unrelated sound that was played simultaneously (Fig. 1d). During retrieval, the sounds were played and participants had to recall the associated objects. In the face–name associations test, each stimulus contained a male forward-looking face with neutral expression and a person's name in text underneath (Fig. 1e). During retrieval, the faces were shown and the participant had to recall the associated names. In the final test, participants heard pairs of words during learning (Fig. 1f). During retrieval one word from each pair was provided auditorily and participants had to recall the associated word. Stimuli did not appear in more than one test. Overall, two scores were derived for each test, the sum of correctly recalled items across the learning trials, and the number of correctly recalled items after the 30 min delay.

Procedure

Each participant was tested individually during two sessions on two separate days. The order of tests within and across sessions was balanced to ensure tests involving similar types of material (e.g. the two visual paired associates tests) were not administered in close proximity.

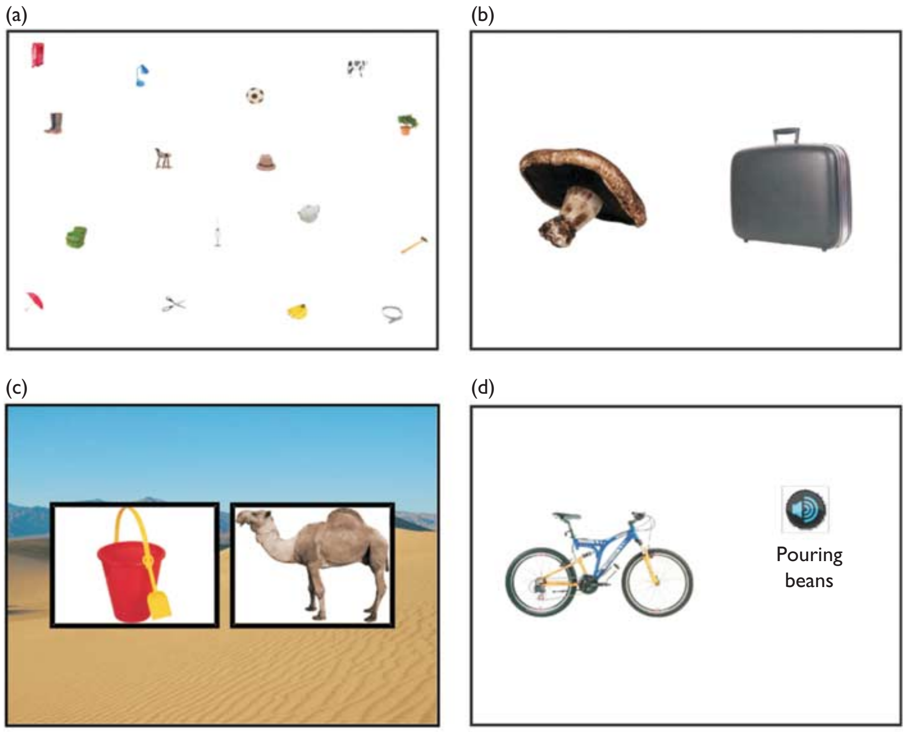
Data analysis

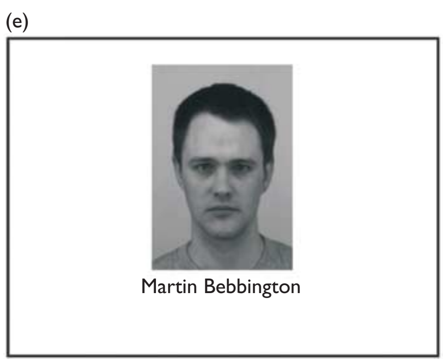
Group comparisons for participant characteristics were made using two-tailed t-tests. For the main associative memory tasks, data were screened for outliers, homogeneity of variance, and to ascertain whether the data were normally distributed. Multivariate analysis of variance (MANOVA; Hotelling's trace multivariate test) was carried out using the general linear model with the significance threshold set at P value less than 0.05. Group (taxi drivers, control participants) was the independent variable and the 12 associative memory measures (Table 1) were the dependent variables. Where MANOVA indicated a significant effect, the between-subjects tests were used to ascertain the source with a threshold of P value less than 0.05.

Results

Mean scores for the two groups on the associative memory measures are shown in Table 1. A MANOVA showed a significant difference between the two groups [$F(12,25) = 2.33$; $P = 0.03$]. The source of this difference

Fig. 1





(f)

List A	Recall (response)	
Truck-Arrow	1 Bank (Cartoon)	
Insect-Acorn	2 Reptile (Clown)	
Reptile-Clown	3 Star (Ladder)	
Bank-Cartoon	4 Rose (Bag)	
Star-Ladder	5 Elephant (Glass)	
Badger-Paper	6 Truck (Arrow)	
Rose-Bag	7 Insect (Acorn)	
Elephant-Glass	8 Badger (Paper)	

Examples of the stimuli. (a) The table-top array from the object–location associations test; (b) example stimulus from the visual paired associates task; (c) from the visual paired associates with context task; (d) from the object–sound associations task – note that for each stimulus in this test participants saw an object presented centrally on the screen and simultaneously heard an unrelated sound (no text was shown, and is provided here merely to aid clarity); (e) example stimulus from the face–name associations test; and (f) from the verbal paired associates test.

was investigated using the tests of between-subjects effects produced by MANOVA. There were two main effects; taxi drivers took significantly longer to reach criterion on the object–location associations test [$F(1,36) = 9.70$; $P = 0.004$] and recalled fewer of the object–location associations after a 30 min delay [$F(1,36) = 7.25$; $P = 0.01$]. The two groups did not differ significantly on any other associative memory measure.

Discussion

In line with previous studies [4,5], we found that licensed London taxi drivers took significantly longer to learn the locations of objects on a table-top array and recalled fewer of them after a delay than control participants. In contrast, there was no difference between the groups when learning and recalling a range of other associations, including those between objects pairs, between objects and sounds, faces and names, and pairs of words.

The object–location associations test on which taxi drivers here and in previous studies [4,5] showed poor performance concerned items in the visual domain. We therefore included in our associative memory battery two other tests that involved visual associations, one with stimuli comprised of two unrelated objects presented centrally on a white background, and the other involving pairs of objects, unrelated to each other, presented

Table 1 Scores for the associative memory tests

Measures	Taxi drivers [mean (SD)]	Controls [mean (SD)]
Object–location associations, number of trials to criterion[a]	2.95 (0.82)	2.11 (0.83)
Object–location associations DR (/16)[a]	12.65 (1.53)	14.27 (1.84)
Visual paired associates IR (Σ for 6 trials/96)	87.55 (5.09)	85.22 (6.55)
Visual paired associates DR (/16)	14.75 (0.91)	15.11 (0.96)
Visual paired associates with context IR (Σ for 6 trials/96)	91.85 (3.93)	90.05 (3.45)
Visual paired associates with context DR (/16)	15.30 (1.03)	15.33 (0.90)
Object–sound associations IR (Σ for 6 trials/96)	80.95 (6.77)	79.22 (10.69)
Object–sound associations DR (/16)	13.65 (1.53)	14.22 (1.66)
Face–name associations IR (Σ for 6 trials/288)	110 (52.07)	125.44 (55.64)
Face–name associations DR (/48)	27.10 (12.80)	30.22 (10.66)
Verbal paired associates IR (Σ for 4 trials/32)	25.25 (5.98)	24.05 (6.04)
Verbal paired associates DR (/8)	7.25 (1.20)	7.27 (1.31)

For the face–name associations test, 1 point was awarded for recalling the correct first name, 1 for the correct surname or 3 points if both were recalled correctly.
Σ, sum of scores; DR, delayed recall after 30 min; IR, immediate recall; /X, total possible score for a test.
[a]Control participants significantly better than taxi drivers.

centrally on related background contexts. The taxi drivers were unimpaired on both tasks, suggesting that the ability to form associations between visual stimuli was intact. The object–location associations test could also be viewed as spanning two domains – the visual and the spatial. To investigate whether taxi drivers might have a problem when stimuli straddle more than one domain, we included the face–name and the object–sound associations tests in our compendium. In neither case was the taxi driver group impaired, suggesting that a general difficulty with between-domain associative memory was not the issue. Their performance on the verbal paired associates test confirmed that memory for associations that were devoid of visual objects was also intact.

Our findings allow us to rule out one potential explanation for the anterograde memory profile in taxi drivers. They do not appear to have a general problem with making associations between items. Instead, acquiring new information with a spatial component (the object–location task) seems to be specifically constrained in the context of their navigational expertise. Several theoretical frameworks propose that spatial processing is the fundamental concern of the hippocampus [8,9], even underpinning its acknowledged role in episodic memory and imagining the future [16]. Perhaps it is not surprising, therefore, that gain and loss within the same spatial hippocampal system should be observed.

While this study resolves one issue, a number of key questions remain that should be targeted in future research. For instance we still lack a clear understanding of why acquiring new visuospatial information is compromised in a context of general navigation expertise. Is it simply a capacity issue – too much existing spatial information in the hippocampus that reduces resources for dealing with incoming spatial information? Table-top tasks such as the Rey-Osterreith complex figure and the object–locations task seem distinct from the type of spatial processing involved in navigating through a large-scale environment like London. Why is it that one impacts adversely upon the other? Finally, how does the pattern of neuropsychological gain and loss in taxi drivers map onto the pattern of grey matter changes observed in their posterior and anterior hippocampus [4,5]?

Conclusion

London taxi drivers offer a unique opportunity to study information processing in the hippocampus, hippocampal plasticity and its neuropsychological consequences. Our finding of intact anterograde associative memory but specifically compromised anterograde visuospatial memory adds to this evolving story and helps highlight topics for further investigation.

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Conflicts of interest

There are no conflicts of interest.

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