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Navigational expertise may compromise anterograde associative memory

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ABSTRACT

Grey matter volume increases have been associated with expertise in a range of domains. Much less is known, however, about the broader cognitive advantages or costs associated with skills and their concomitant neuroanatomy. In this study we investigated a group of highly skilled navigators, licensed London taxi drivers. We replicated findings from previous studies by showing taxi drivers had greater grey matter volume in posterior hippocampus and less grey matter volume in anterior hippocampus compared to matched control subjects. We then employed an extensive battery of tests to investigate the neuropsychological consequences of being a skilled taxi driver. Their learning of and recognition memory for individual items was comparable with control subjects, as were working memory, retrograde memory, perceptual and executive functions. By contrast, taxi drivers were significantly more knowledgeable about London landmarks and their spatial relationships. However, they were significantly worse at forming and retaining new associations involving visual information. We consider possible reasons for this decreased performance including the reduced grey matter volume in the anterior hippocampus of taxi drivers, similarities with models of aging, and saturation of long-term potentiation which may reduce information-storage capacity.

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1. Introduction

Grey matter volume increases in various parts of the brain have been identified in a number of skilled groups such as musicians (Gaser and Schlaug (2003); Munte, Altenmuller, & Jancke, 2002; Sluming et al., 2002; Sluming, Brooks, Howard, Downes, & Roberts, 2007), mathematicians (Aydin et al., 2007), bilinguals (Mechelli et al., 2004), jugglers (Draganski et al., 2004), and medical students (Draganski et al., 2006). As well as exploring the grey matter substrates of a skill itself, a related and important question is whether a skill and its associated neuroanatomy confer broader cognitive advantages or indeed costs. This question has particular significance for the domains of rehabilitation and education. Only a limited number of studies have considered the neuropsychological consequences of expertise. Professional musicians with increased grey matter volume in Broca's area were found to show enhanced judgements of line orientation and three-dimensional mental rotation ability (Sluming et al., 2002, 2007). This was attributed to their musical sight-reading and motor sequencing expertise. However, this expertise can come at a cost, with some musicians suffering focal dystonia, a loss of control and degradation of skilled hand movements (Munte et al., 2002).

The consequences of skill acquisition have also been investigated in another group of experts, London taxi drivers, who must know the layout of 25,000 streets as well as thousands of landmarks and places of interest around the city (Maguire et al., 2000; Maguire, Woollett, & Spiers, 2006a). The volume of the hippocampus in some non-human species has been reported to vary as a function of the demands placed on spatial memory (Barnea & Nottebohm, 1994; Biegler, McGregor, Krebs, & Healy, 2001; Lee, Miyasato, & Clayton, 1998; Smulders, Sasson, & DeVoogd, 1995; Volman, Grubb, & Schuett, 1997). Similar effects were also found in licensed London taxi drivers, with greater grey matter volume in posterior hippocampi and less grey matter volume in anterior hippocampi compared with control subjects. In addition, posterior hippocampal grey matter volume correlated positively, and anterior hippocampal grey matter volume negatively, with the number of years spent taxi driving (Maguire et al., 2000, 2006a). It has been suggested that the greater volume of posterior hippocampal grey matter in taxi drivers may be related to the acquisition, storage and use of the 'mental map' of a large complex environment (Maguire et al., 2000, 2006a). Related to this, Maguire et al. (2006a) confirmed that London taxi drivers performed significantly better than control subjects (London bus drivers) on tests assessing knowledge of London landmarks and their spatial relationships. Interestingly, in the same study taxi drivers were found to be significantly worse than control subjects on the delayed recall of the Rey–Osterreith complex figure (Osterrieth, 1944; Rey, 1941), a test of anterograde visuo-spatial memory. It was suggested that this below average

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score could be related to their reduced anterior hippocampal grey matter volume.

Unlike many other experts such as professional musicians and bilinguals, London taxi drivers acquire their knowledge in adulthood. In addition, taxi drivers are the only group where expertise has been consistently associated with both increases and decreases in grey matter volume. When considered along with the preliminary evidence of positive and negative test performances associated with their navigational expertise (Maguire et al., 2006a), this makes taxi drivers a particularly interesting model for studying the effects of expertise on the brain. Moreover, given the focal nature of the grey matter volume changes in the taxi drivers, they offer another line of evidence to complement neuropsychological and functional neuroimaging studies in helping to understand the role of hippocampus in memory and navigation.

Whilst Maguire et al.'s (2006a) preliminary neuropsychological findings in taxi drivers are intriguing, the battery of tests they employed was brief and did not permit a wide-ranging examination of cognitive and memory functions. In the current study, therefore, we sought to replicate and extend the previous findings by undertaking a comprehensive neuropsychological evaluation of a new sample of taxi drivers and matched control subjects. As well as assessing basic cognitive and affective functions, 22 different memory measures were taken. These tasks assessed a broad range of memory types and processes including visual and verbal memory, recall and recognition, single item and associative memory, and anterograde and retrograde memory. Our aim was to examine the memory profile of taxi drivers in the context of their navigational expertise, and to investigate whether any specific memory type or process was affected, positively or negatively. In so doing we hoped to contribute new information to debates about the functions of the human hippocampus specifically, and the benefits and costs of skill acquisition more generally.

2. Methods

2.1. Participants

Forty healthy male volunteers participated in the study. Of these, 20 were licensed London taxi drivers, and 20 were control subjects. All participants gave informed written consent to participation in the study in accordance with the local research ethics committee. The background details of the two groups are shown in Table 1. All taxi drivers had completed "The Knowledge" training, had passed the necessary Public Carriage Office examinations, and obtained a full (green badge) licence. For more on London taxi drivers and why London (UK) is particularly useful for testing navigation and related brain changes, see Spiers and Maguire (2007). None of the control subjects had worked as licensed London taxi drivers or mini-cab drivers. None was training to be a licensed taxi driver or had ever been involved in such training. The taxi drivers and control subjects did not differ in terms of age ($t(38) = 1.81$; $p = 0.07$), handedness (laterality index as measured using the Edinburgh Handedness Inventory, Oldfield, 1971) ($t(38) = 0.90$; $p = 0.9$), or age at which they left school ($t(38) = 1.51$; $p = 0.1$). As all participants were native English speakers, an estimate of verbal IQ was obtained using the Wechsler Test of Adult Reading (Wechsler, 2001). IQ estimates for both groups were in the average range, and did not differ significantly ($t(38) = 0.57$; $p = 0.5$). Visual information processing and abstract reasoning skills were assessed using the Matrix Reasoning sub-test of the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999). The mean scaled scores for both groups were comparable and did not differ significantly ($t(38) = 0.36$; $p = 0.7$).

Table 1

Participant characteristics	Taxi drivers mean (S.D.)	Controls mean (S.D.)
Age (years)	43 (3.46)	40 (6.54)
Education (age left school, years)	16.30 (0.80)	16.70 (0.86)
Estimated verbal IQ (WTAR)	98 (5.10)	98.90 (4.59)
Matrix reasoning scaled score (WASI)	11.75 (1.68)	12 (2.55)
Handedness–laterality index[a]	78 (45.91)	79 (19.32)
Years experience taxi driving	12.35 (6.85)	–

WTAR = Wechsler Test of Adult Reading; WASI = Wechsler Abbreviated Scale of Intelligence

[a] Edinburgh Handedness Inventory.

Table 2

Basic cognitive measures	Taxi drivers mean (S.D.)	Controls mean (S.D.)
Digit span scaled score (WAIS-III)	12.25 (2.57)	11.45 (2.01)
Spatial span scaled score (WMS-III)	12.90 (2.67)	12 (2.40)
Verbal fluency—FAS (total score)	43.60 (10.01)	47.40 (12.43)
Block design scaled score (WASI)	8.85 (1.81)	9.45 (2.43)
Brixton test (6–7 = average–high average)	6.60 (1.14)	7.20 (1.19)
VOSP object decision (/20)	17.85 (1.78)	16.85 (1.72)
VOSP cube analysis (/10)	9.70 (0.51)	9.60 (0.59)
VOSP number location (/10)	9.65 (1.13)	9.75 (0.55)

WAIS-III = Wechsler Adult Intelligence Scale; WMS-III = Wechsler Memory Scale; WASI = Wechsler Abbreviated Scale of Intelligence; VOSP = Visual Object and Space Perception Battery.

2.2. MRI scan

Whole brain structural MRI scans were acquired on a 1.5 T Sonata whole body scanner (Siemens Medical Systems, Erlangen, Germany), with a whole-body coil for RF transmission and an 8-element phased-array head coil for signal reception, using a Modified Driven Equilibrium Fourier Transform (MDEFT) sequence (Ugurbil et al., 1993). Parameters were optimised as described in the literature (Deichmann, Schwarzbauer, & Turner, 2004; Howarth, Hutton, & Deichmann, 2005): for each volunteer, 176 sagittal partitions were acquired with an image matrix of 256 × 240 (Read × Phase). Twofold oversampling was performed in the read direction (head/foot direction) to prevent aliasing. The isotropic spatial resolution was 1 mm. Relevant imaging parameters were TR/TE/TI = 14.59 ms/3.4 ms/650 ms, BW = 96 Hz/Px, $\alpha = 20^{\circ}$. To increase the signal-to-noise ratio, an asymmetric position of the inversion pulse within the magnetisation preparation (duration TI) was chosen, and the delay between the initial saturation and the inversion amounted to 40% of TI (Deichmann et al., 2004). A fat saturation pulse was used to achieve fat suppression (see Howarth et al., 2005 for details). In addition, special RF excitation pulses were used to compensate for B1 inhomogeneities of the transmit coil (Deichmann, Good, & Turner, 2002). Images were reconstructed by performing a standard 3D Fourier Transform, followed by modulus calculation. No data filtering was applied either in k space or in the image domain. The total duration of the scan was 12 min.

2.3. Neuropsychological test battery

A test battery was employed to assess a range of cognitive, memory and affective functions, see Tables 2–4. The majority of tests were widely used standardised instruments and questionnaires with published normative data (see also, Maguire et al., 2006a; Maguire, Nannery, & Spiers, 2006b). A number of additional non-standard tests were also used and are detailed below.

2.3.1. Public events test

Retrograde memory for public events was evaluated using 28 black and white photographs of well known public events spanning four decades (1974–2005). Participants were required to name the event, give the date of the event (±3 years) and name the location where the event took place. Only events where all 3 details were correct achieved a score of 1.

2.3.2. London landmark recognition memory test

Recognition memory for London landmarks was assessed by showing subjects 48 colour photographs of landmarks one after another (see further details of this test in Maguire et al., 2006a, 2006b). Half of the pictures were of famous London landmarks and half were distractor landmarks that were neither famous nor in London, but were visually similar to the London landmarks. Target and distractor landmarks were randomly intermixed. The format was a yes/no recognition test where subjects were asked to state whether they recognised each landmark as a famous London

Table 3

Stress measures	Taxi drivers mean (S.D.)	Controls mean (S.D.)
Perceived Stress Scale	12.75 (7.30)	11.65 (7.13)
State-Trait Anxiety Inventory (State)	31.45 (9.13)	28.10 (5.49)
State-Trait Anxiety Inventory (Trait)	38.10 (10.33)	35.50 (11.98)
Life stress rating[a]	4.40 (1.75)	4.80 (2.41)
Job stress rating[a]	5 (1.91)	4.50 (2.03)

[a] Ratings from 1 (no stress) to 10 (very high stress).

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