

# Talent in the taxi: a model system for exploring expertise

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Review

## Talent in the taxi: a model system for exploring expertise

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While there is widespread interest in and admiration of individuals with exceptional talents, surprisingly little is known about the cognitive and neural mechanisms underpinning talent, and indeed how talent relates to expertise. Because many talents are first identified and nurtured in childhood, it can be difficult to determine whether talent is innate, can be acquired through extensive practice or can only be acquired in the presence of the developing brain. We sought to address some of these issues by studying healthy adults who acquired expertise in adulthood. We focused on the domain of memory and used licensed London taxi drivers as a model system. Taxi drivers have to learn the layout of 25 000 streets in London and the locations of thousands of places of interest, and pass stringent examinations in order to obtain an operating licence. Using neuropsychological assessment and structural and functional magnetic resonance imaging, we addressed a range of key questions: in the context of a fully developed brain and an average IQ, can people acquire expertise to an exceptional level; what are the neural signatures, both structural and functional, associated with the use of expertise; does expertise change the brain compared with unskilled control participants; does it confer any cognitive advantages, and similarly, does it come at a cost to other functions? By studying retired taxi drivers, we also consider what happens to their brains and behaviour when experts stop using their skill. Finally, we discuss how the expertise of taxi drivers might relate to the issue of talent and innate abilities. We suggest that exploring talent and expertise in this manner could have implications for education, rehabilitation of patients with cognitive impairments, understanding individual differences and possibly conditions such as autism where exceptional abilities can be a feature.

Keywords: taxi; magnetic resonance imaging; neuropsychology; expertise; hippocampus; plasticity

## **1. INTRODUCTION**

Talent is highly prized in human culture. 'Gifted' musicians, artists, mathematicians, chess grandmasters, the multi-lingual and those with exceptional memories are lauded for their talent. Despite our passion for seeking out and appreciating talent, we still know relatively little about the basis of talent, and, in particular, there is a paucity of knowledge concerning its neural substrates (Kalbfleisch 2004; Ericsson et al. 2006; Grafton 2008). Perhaps this is not surprising, given that even defining talent is not straightforward. According to Kalbfleisch (2004), 'Someone exhibits 'talent' when they perform in a certain capacity above the norm'. But is talent innate or can it be acquired? Is it the same as expertise or being highly skilled? For many people talent implies innateness. However, talents are often first identified and nurtured in childhood and thus development and talent are typically conflated, making it difficult to determine whether talent is innate, can be acquired through extensive practice or can only be

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acquired in the presence of a 'plastic' developing brain. In order to understand whether exceptional ability is innately determined or can be acquired, we suggest that in the first instance it is necessary to eschew development as an influencing factor and establish whether exceptional ability can develop in healthy adults. In this paper, we review a series of experiments where we investigated this issue. In doing so, we use the more general term expertise rather than talent in order to avoid connotations about the origin of exceptional abilities.

In addition to examining expertise acquired in adulthood, we also focused on individuals with average IQs, thus the need for enhanced intellectual capacity as a prerequisite for expertise was removed. The skill we selected for investigation is widely acknowledged to be impressive and, moreover, with each participant being tested in a similar fashion by an independent body, the acquisition of expertise was verifiable. By acquiring cognitive data, and structural and functional magnetic resonance imaging (MRI) scans on these experts, we could address a number of key questions relating to expertise: in the context of fully developed brains and an average IQ, can people acquire expertise to an exceptional level; what are the neural signatures, both

One contribution of 18 to a Discussion Meeting Issue 'Autism and talent'.

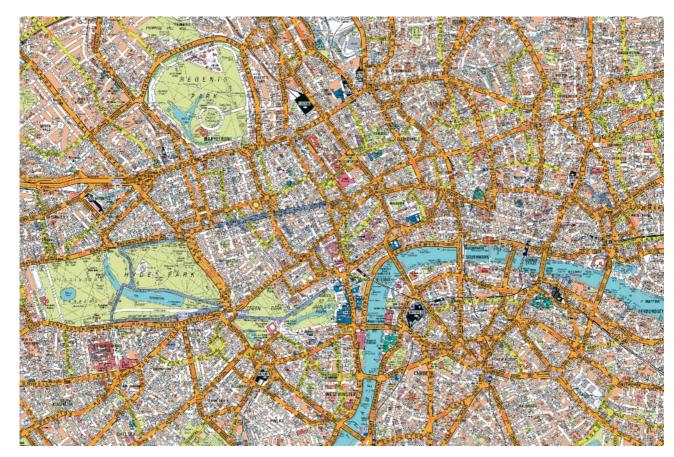


Figure 1. Central London, UK. Reproduced with the permission of Geographers' A–Z Map Co. Ltd. Crown Copyright 2005. All rights reserved. Licence number 100017302.



Figure 2. Virtual navigation around London. (*a*) An example view at Trafalgar Square from within the video game 'The Getaway' 2002 Sony Computer Entertainment Europe is shown. Image is reproduced with the kind permission of Sony Computer Entertainment Europe. (*b*) Some of the brain areas—including the hippocampus—activated when the taxi drivers navigated around virtual London during fMRI brain scanning are shown (data from Spiers & Maguire 2006).

structural and functional, associated with the use of expertise; does expertise change the brain compared with unskilled control participants; does it confer any added cognitive advantages, and, similarly, does expertise come at a cost to other functions; and what happens to their brains and behaviour when experts stop using their skills? Knowing the answers to these questions could be beneficial to those of us wishing to become skilled, for educationalists too, and for those involved in rehabilitation of patients with cognitive impairments. Furthermore, the data relating to expertise in average healthy individuals may aid in the interpretation of skills in clinical populations such as autism, where exceptional abilities are known to feature (Treffert 2009).

## 2. LICENSED LONDON TAXI DRIVERS

We chose to focus on the domain of memory, as we are all aware of the shortcomings of our own memories,

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covet exceptional memory and fear the devastating effects of pathologies such as Alzheimer's disease. Exceptional memory, sometimes for unusual material (e.g. bus routes, telephone directories—Pring 2008), is also displayed by some autistic savants. We made use of a unique learning situation in London (UK) and used licensed London taxi drivers as a model for exceptional memory. While the expertise of taxi drivers has been studied in Paris (Pailhous 1970, 1984; Peruch et al. 1989), Chicago (Chase 1982) and Helsinki (Kalakoski & Saariluoma 2001), only in London is their expertise truly exceptional and clearly defined. Training to become a taxi driver in London can take place only after the age of 21. Trainees undergo extensive training over a period of 2-4 years known as acquiring 'The Knowledge'. This involves the impressive feat of learning the layout of 25 000 streets in the city (figure 1) and thousands of places of interest, leading to a stringent set of examinations by the Public Carriage Office in order to obtain an operating licence. That there are 25 000 licensed London taxi drivers registered currently with the Public Carriage Office suggests that many people are able to acquire this expertise and our sampling of this population confirms an average level of IQ (Maguire et al. 2006a; Woollett & Maguire in press).

Key to the taxi drivers' skill is their ability to navigate. A wide body of evidence indicates that navigation is supported by a brain structure called the hippocampus (O'Keefe & Nadel 1978; Andersen *et al.* 2006; Bird & Burgess 2008). Lesions to the hippocampus impair navigation (Morris *et al.* 1982), and neurons within it exhibit location-specific firing creating a cognitive map of the environment (O'Keefe & Dostrovsky 1971; O'Keefe & Nadel 1978). The volume of the hippocampus in some non-human species can vary as a function of the demands placed on spatial memory, with food-caching species having greater hippocampal volume compared with those who do not cache food (Barnea & Nottebohm 1994; Smulders *et al.* 1995; Volman *et al.* 1997; Lee *et al.* 1998; Biegler *et al.* 2001).

In the first instance, we sought to ascertain whether taxi drivers use their hippocampus during navigation. Consequently, we scanned taxi drivers using functional MRI (fMRI) while they navigated in a highly accurate and interactive virtual reality (VR) simulation of central London (figure 2). This was developed as the backdrop for a commercial video game but enabled us to assess in situ navigation in a controlled manner. 'The Getaway' (Sony Computer Entertainment Europe) has over 110 km (70 miles) of London's driveable roads, accurately recreated from Ordinance Survey map data, covering 50 square kilometres (20 square miles) of the city centre. The one-way systems, working traffic lights, the busy London traffic and an abundance of Londoners going about their business are all included. Conveniently, one can simply navigate freely (with the usual game scenarios suspended) around the city using the game console, with a normal ground-level first-person perspective, in a car of one's choice. A distributed network of brain areas, including the hippocampus, was active in the brains of taxi drivers while they navigated around VR London (Spiers & Maguire 2006, 2007a,b; see figure 2). The same is true of non-taxi drivers when

they imagined navigating between the houses of friends in London (Kumaran & Maguire 2005), and when they navigated around various VR environments (Maguire *et al.* 1998; Hartley *et al.* 2003; Iaria *et al.* 2003). Given that taxi drivers and non-taxi drivers activate the hippocampus during navigation, are there identifiable neural or behavioural correlates of being an expert navigator that differentiate them from non-experts?

#### 3. NAVIGATION EXPERTISE: POSITIVE OUTCOMES

Unsurprisingly, relative to non-experts, taxi drivers have been found to be significantly more knowledgeable about London landmarks and their spatial relationships. This was true even when taxi drivers were compared with another group of navigators, London bus drivers (Maguire *et al.* 2006*a*; Woollett & Maguire in press; see figure 3a,b). Bus drivers also spend all day driving among the busy London traffic and dealing with customers, but unlike taxi drivers who navigate widely around the city, bus drivers operate along a constrained set of routes.

While their vastly superior London knowledge distinguished them, an examination of grey matter volume in the brains of taxi drivers revealed further differences. Structural MRI brain scans of taxi drivers and non-taxi driver control participants were analysed using voxel-based morphometry (VBM), a method that permits automatic whole-brain analysis of grey matter volume (Ashburner & Friston 2005; Mechelli et al. 2005). Compared with controls, taxi drivers had greater grey matter volume in the posterior hippocampi (Maguire et al. 2000). This finding was replicated when taxi drivers were compared with bus drivers (Maguire et al. 2006a-see figure 3c; see also Woollett & Maguire in press). On the basis of these results, we suggested that learning, representing and using a spatial representation of a highly complex and large-scale environment is a primary function of the posterior hippocampus in humans such that this brain region might adapt structurally to accommodate its elaboration. Evidence that this pattern of grey matter volume was acquired from the experience of learning and using the highly complex mental map of London comes from an additional finding. The number of years of navigation experience correlated with hippocampal grey matter volume only in taxi drivers (and not bus drivers who were matched for number of years navigating in London), with right posterior grey matter volume increasing with more navigation experience (figure 3d).

While the correlation of time taxing driving and grey matter volume suggests that the brain changes are acquired and not innate, it could still be argued that the difference in hippocampal volume is instead associated with innate navigational expertise, leading to an increased likelihood of becoming a taxi driver. To investigate this possibility, we used VBM to examine a group of non-taxi drivers who navigated in a VR environment (Maguire *et al.* 2003*a*). Despite this group showing a wide range of navigational expertise, there was no association between expertise and posterior hippocampal grey matter volume (or, indeed,

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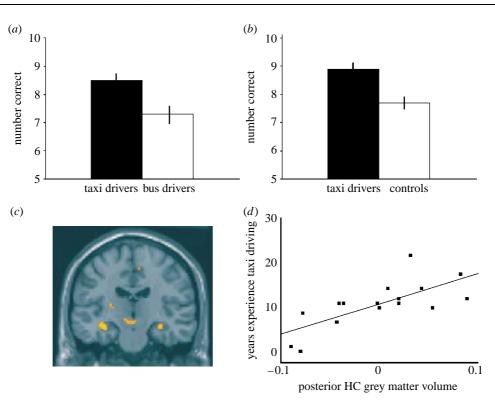


Figure 3. Navigation expertise: positive outcomes. (a) Taxi drivers (n=18) were significantly better at judging the relative locations of landmarks in London than bus drivers (n=17; mean scores  $\pm 1$  s.e., data from Maguire *et al.* 2006*a*). (*b*) This result was replicated in a different cohort of taxi drivers and a control group of non-taxi drivers (n=20 each group; data from Woollett & Maguire in press). (*c*) Taxi drivers had greater grey matter volume in the posterior hippocampus bilaterally compared with bus drivers (data from Maguire *et al.* 2006*a*). (*d*) Posterior hippocampal (HC) grey matter volume correlated positively with increasing navigation experience in taxi drivers (data from Maguire *et al.* 2006*a*).

grey matter volume throughout the brain). This failure to find an association between hippocampal volume and navigational expertise thus suggests that structural differences in the hippocampus of taxi drivers reflect the detail and/or duration of the use of the spatial representation acquired and not innate navigational expertise *per se*.

Clearly, taxi drivers in London have to learn a vast amount of information. Another question that naturally arises is whether intensive and extensive acquisition of knowledge in domains other than spatial navigation produces the same results (Terrazas & McNaughton 2000). In order to examine this issue, participants were required who were similar to taxi drivers in terms of how their knowledge acquisition occurs, but whose knowledge was less spatial. We focused on medical doctors as an appropriate group to test (Woollett et al. 2008). They also acquire their knowledge in adulthood over a number of years of initial intensive medical training. While our previous work has shown that taxi drivers and their control subjects generally have average IQs (Maguire *et al.* 2006*a*; Woollett & Maguire in press), the medical doctors had above-average IQs. Thus, we compared the medical doctors with control participants matched on IQ, but who had not undergone university education or periods of intense learning. VBM analysis failed to identify any differences in grey matter volume between the groups, including in the hippocampus. Moreover, the amount of medical experience, which ranged from 0.5 to 22.5 years, did not correlate with grey matter volume in the hippocampus or elsewhere in the brain. From this, we conclude that intensively

acquiring a large amount of knowledge over many years is not invariably associated with structural brain differences. Instead, it would seem that hippocampal grey matter volume effects are more likely to be observed when the knowledge acquired concerns a complex and detailed large-scale spatial layout.

This is supported by the findings from another group with exceptional memory, namely participants in the World Memory Championships, held in London every year. Their memory skills are wide ranging including the ability to memorize numerous decks of playing cards and long lists of random digits. Exceptional memory in these individuals was not found to be associated with higher IQ or any structural brain differences relative to control participants (Maguire et al. 2003b). However, fMRI scanning revealed that they activated brain areas associated with navigation, including the hippocampus, more than control participants. The expert memorizers in general used a mnemonic strategy known as the Method of Loci (Yates 1966). With extensive practice, this method is effective at enabling one to remember the order of stimuli by imagining familiar routes and placing the to-be-remembered items along the routes thus promoting deeper encoding of the stimuli with rich associations. Unlike taxi drivers, however, the restricted set of routes they employed was not sufficient to affect structural brain changes. This is concordant with the findings from bus drivers who also learn and use a constrained set of routes and show no structural brain changes (Maguire et al. 2006a).

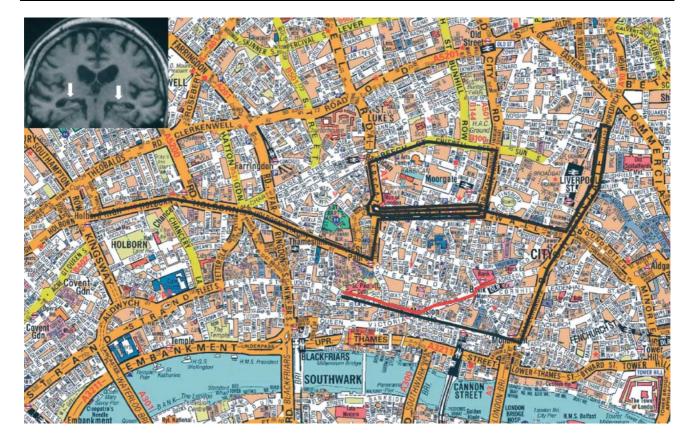


Figure 4. The sudden loss of expertise. Patient TT, with bilateral hippocampal lesions (see inset upper left), and control taxi drivers retired for a similar length of time as TT, navigated around the VR London. An example of their navigation performance for a route from St Paul's Cathedral to the Bank of England is shown. All 10 controls performed in an identical manner, shown in red on this map. TT's route is shown in black and was grossly impaired being mainly restricted to the A roads (shown in orange and yellow on the map) and he never reached the required destination (data from Maguire *et al.* 2006*b*). Map reproduced with the permission of Geographers' A–Z Map Co. Ltd. Crown Copyright 2005. All rights reserved. Licence number 100017302.

Thus, it would seem that intensive learning of a city's spatial layout is possible, and the effective use of mnemonics can facilitate memory for impressive amounts of information. This suggests that becoming an expert in the domain of memory may be attainable by any of us, with a great deal of time and effort as in the case of taxi drivers, and the use of mnemonics as employed by the memory champions. Structural brain changes associated with learning over a time scale of years, however, seem to be restricted to taxi drivers and the acquisition of a large, integrated and complex spatial layout (see Draganski et al. (2004, 2006) for effects relating to short time scales). Expertise in other domains has been associated with grey matter volume differences in various parts of the brain relative to control participants, for example in musicians (Munte et al. 2002; Sluming et al. 2002, 2007; Gaser & Schlaug 2003), mathematicians (Aydin et al. 2007) and bilinguals (Mechelli et al. 2004). Professional musicians were also 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, to our knowledge, there are no reports of adult-acquired expertise in these domains, thus grey matter and neuropsychological differences in these cases may be due to the interaction between practice and brain development.

## 4. NAVIGATION EXPERTISE: NEGATIVE OUTCOMES

Talent and expertise are typically viewed in a positive light. However, we would argue that the potential costs of expertise also warrant consideration. There have been several case reports of individuals whose memories are so good that it actually causes them great distress as they are unable to forget anything (Luria 1987; Parker et al. 2006). There can also be devastating effects when one suddenly loses expertise. Using the VR simulation of central London described above, we assessed the navigation ability of a licensed London taxi driver who had sustained bilateral hippocampal damage as a consequence of limbic encephalitis (Maguire et al. 2006b). In this test, patient TT and matched control taxi drivers drove a virtual London taxi along the streets they had first learned 40 years before. We found that the hippocampus is not required for general orientation in the city, detailed topographical knowledge of landmarks and their spatial relationships, or even for the navigation along some routes, all of which abilities were preserved. However, in his navigation, TT was very reliant on main artery or 'A' roads, and became lost when navigation depended instead on non-A roads (figure 4). The hippocampus in humans is therefore necessary for facilitating navigation even when the navigator is an expert of very longstanding. Thus expertise, while taking many years to

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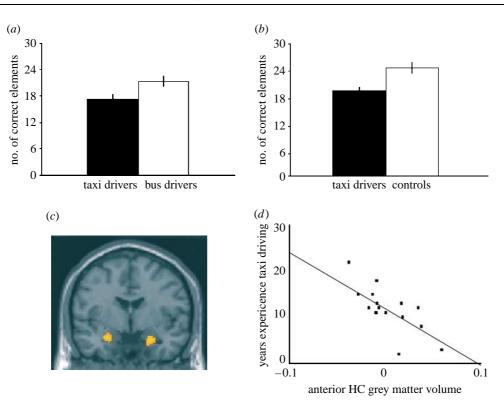


Figure 5. Navigation expertise: negative outcomes. (a) Taxi drivers (n=18) were significantly worse at recalling elements of the Rey–Osterrieth Complex Figure at delayed recall compared with bus drivers  $(n=17; \text{ mean scores} \pm 1 \text{ s.e.}, \text{ data from Maguire et al. 2006a}). (b)$  This result was replicated in a different cohort of taxi drivers and a control group of non-taxi drivers (n=20 each group; data from Woollett & Maguire in press). (c) Taxi drivers had less grey matter volume in the anterior hippocampus bilaterally compared with bus drivers (data from Maguire et al. 2006a). (d) Anterior hippocampal (HC) grey matter volume correlated negatively with increasing navigation experience in taxi drivers (data from Maguire et al. 2006a).

develop, can be vulnerable to sudden and focal brain insult, leading in this case to a loss of livelihood and independence.

Considered next is the question of whether expertise and its associated neuroanatomy result in broader cognitive costs. Of note, exceptional abilities in autism occur in the context of impairments in social cognition and executive functions (Frith & Happe 2005), and some expert musicians suffer focal dystonia, a loss of control and degradation of skilled hand movements (Munte et al. 2002). In taxi drivers, we noted above their enhanced knowledge of London. However, in two separate studies, the performance of taxi drivers was significantly poorer than both bus drivers (Maguire et al. 2006a) and control participants (Woollett & Maguire in press) on a widely used test of spatial memory, the delayed recall of the Rey-Osterrieth Complex Figure (Rey 1941; Osterrieth 1944; Corwin & Bylsma 1993; figure 5a,b). Furthermore, they were also deficient at acquiring and retaining other types of new information. Specifically, they were poorer at learning object-place and word-pair associations. After a delay they also recalled less of this associative information. This pattern of anterograde memory performance was in the context of learning and recognition memory for single items being comparable with control participants, as were retrograde memory for autobiographical and semantic information, executive and perceptual functions, working memory and levels of stress and anxiety.

Negative effects of navigation expertise were not only found behaviourally but also structurally in the

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brain. In comparison with the posterior hippocampus that had greater grey matter volume compared with control participants, the anterior hippocampus had reduced grey matter volume in taxi drivers (Maguire et al. 2000, 2006a; Woollett & Maguire in press; figure 5c). Moreover, anterior hippocampal grey matter volume decreased as navigation experience increased in taxi drivers (figure 5d). We suggest that the belowaverage scores observed in taxi drivers on tests of anterograde associative memory could be related to their reduced right anterior hippocampal grey matter volume. This accords with the findings across species that there may be functional differentiation along the anterior-posterior axis of the hippocampus (e.g. Jung et al. 1994; Colombo et al. 1998; Hock & Bunsey 1998; Moser & Moser 1998; Maguire et al. 2000; Bannerman et al. 2004; Gogtay et al. 2006). In humans, functional neuroimaging studies have linked anterior hippocampal activity with the detection of stimulus novelty and encoding, while the posterior hippocampus has been associated with retrieval and spatial memory (e.g. Lepage et al. 1998; Strange & Dolan 2001; Kumaran & Maguire 2005; Spiers & Maguire 2006; but see Small et al. 2001).

We have established that navigation expertise is associated with structural brain differences and behavioural consequences, both positive and negative. In particular, the correlations between time taxi driving and hippocampal grey matter volume suggest that experience drives the patterns observed. However, studies to date have been cross-sectional and we acknowledge that in order to categorically conclude this, a within-subject longitudinal study is required,

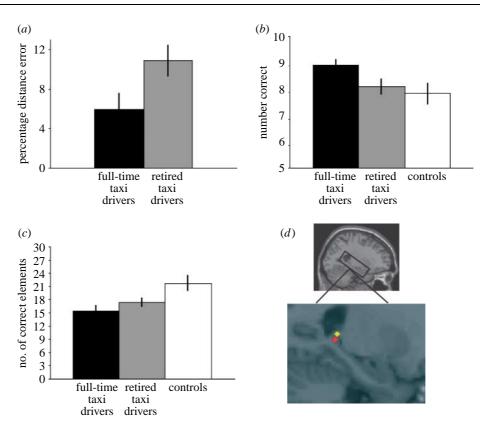


Figure 6. Ceasing to use a skill: preliminary data. Mean scores are shown  $\pm 1$  s.e. (a) The performance of elderly taxi drivers who were still working full-time was compared with retired taxi drivers on the VR London navigation test (n=8 each group). Consistently chosen legal routes were established for each trial, and the ideal minimum length of these routes was computed. The distance each participant drove and the ideal distance for each route were measured and the difference calculated as percentage distance error. The routes of the retired taxi drivers were longer and less ideal than those taxi drivers who were still working. (b) A group of elderly still-working taxi drivers, retired taxi drivers and retired control non-taxi drivers were compared on a range of neuropsychological measures. Groups (n=10 each group) were matched for age (mean age 66.1, 69.5, 66 years, respectively) and years experience taxi driving (full-timers 34.2 years, retired 36.2 years). Full-timers were significantly better on tests of London knowledge (landmark proximity judgements). (c) The reverse pattern was apparent on tests of new learning, with full-timers significantly worse on the delayed recall of the Rey–Osterrieth Complex Figure. (d) Full-time taxi drivers (n=10) had greater grey matter volume in the posterior hippocampus than retired taxi drivers (n=9; voxel of peak difference shown in yellow), while the retired taxi drivers had greater grey matter volume in this region than the retired control participants (n=10; voxel of peak difference shown in red). Data are shown at a threshold of p < 0.05 corrected for the volume of the hippocampus.

which permits the comparison before and after taxi driver training (such a study is ongoing). This longitudinal approach will also permit the examination of the characteristics of those who succeed at taxi driver training, and whether innate pre-training cognitive factors and/or hippocampal volume are predictive of subsequent successful qualification. This will provide vital information about brain plasticity and navigation expertise, and the factors that might affect or limit the ability to develop such expertise. Even then, further questions will remain, which must be addressed in future studies. Navigational accuracy can be supported by different types of representation, for example remembering individual routes versus a coherent map-like representation (O'Keefe & Nadel 1978; Hartley et al. 2003; Iaria et al. 2003; Bohbot et al. 2007). It may be that some individuals have an innate bias for using one type of representation, with successful taxi drivers perhaps more likely to use map-like strategies. Beyond representational biases, successful qualification might also depend on genetic factors, with perhaps the propensity for hippocampal plasticity more likely in individuals with a certain genetic profile (Egan et al. 2003; Hariri et al. 2003).

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#### 5. USE IT OR LOSE IT?

If, as the cross-sectional studies suggest, navigation expertise results in structural changes to the brain and positive and negative neuropsychological consequences, then what happens if one stops using this expertise? Anecdotally, it is suggested that skills can be lost if not practised-use it or lose it. If expertise and its expression are indeed plastic, then can the effects of expertise be reversed? We have started to examine this issue by comparing retired taxi drivers with taxi drivers who are still working full time. We hypothesized that the full-time taxi drivers would be better at navigation in London than the retired. We tested this by using the VR London navigation test described earlier (figure 2). Preliminary data show that the full-timers are indeed significantly better at navigation in London than the retired taxi drivers (figure 6a). Interestingly, this was also the case for performance on tests of London knowledge, such as making proximity judgements between landmarks. In figure 6b, it is clear that the still-working taxi drivers perform best while there is very little difference between the retired taxi drivers and a set of retired non-taxi driver control participants.

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Consideration of the negative outcomes is particularly interesting. If taxi drivers perform poorly on tests such as the delayed recall of the Rey Complex Figure, does performance improve in retired taxi drivers? Our preliminary data suggest that this may be the case. Figure 6c shows that, as in our previous studies (Maguire et al. 2006a, Woollett & Maguire in press), control non-taxi drivers were significantly better on the delayed recall of the Rey Figure than the fulltime taxi drivers. Interestingly, there was no significant difference between the controls and the retired taxi drivers. The intermediate performance of the retired taxi drivers, not as poor as the full-timers, and not as good as controls, is in line with the view that ceasing to use a skill might result in the normalization of expertise-related negative outcomes. On average, the taxi drivers in this preliminary sample had only been retired for 3.6 years. It may be that with a longer period of retirement, performance on tests such as the Rey Figure would normalize entirely.

In line with the pattern of behavioural tests, it seems that the structural brain changes observed in taxi drivers in our previous studies may also reverse in retired taxi drivers. Full-time taxi drivers had significantly greater grey matter volume in the posterior hippocampus than retired taxi drivers, who had greater volume in this region than the non-taxi driver retired control participants (figure 6d). Clearly, increased numbers of participants are required to confirm these findings. Nevertheless, the possibility of plasticity effects in both directions, i.e. during acquisition and use of expertise, and then again when use of the skill ceases, serves to highlight that expertise and its behavioural consequences may be plastic and, in the case of the hippocampus at least, so are the related structural brain changes. The improvement of performance on tests such as the Rey Figure by the retired taxi drivers is also interesting in that it may indicate that the 'elderly' hippocampus can support memory improvement, in contrast with the more traditional view of age-related memory decline.

#### 6. CONCLUSIONS

Understanding the cognitive and neural mechanisms underpinning talent and expertise is important for a number of reasons. First, this issue has universal relevance by informing what each of us can hope to achieve, and providing much-needed insights into the basis of individual differences, as well as having relevance in the realm of education. Second, understanding skill acquisition may have implications for patients with cognitive impairments. If we are to approach rehabilitation in a systematic and efficacious way, then it is vital to know, for example, whether the memory system has the propensity for plasticity in adulthood, the limiting factors on such plasticity and the time scales of any plastic change. Third, understanding exceptional abilities in the healthy brain may also offer benchmarks for interpreting talent and expertise in clinical populations, such as those with autism. Here we have focused on one type of expertise in the domain of memory, availing a unique learning situation in London known to engage the hippocampus,

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and by studying healthy average adults operating in a realworld setting over many years. From this, we conclude that the development of expertise is possible with extensive effort, and that this can be associated with neuropsychological and structural brain consequences. These effects can be positive and negative, with increased expertise and grey matter volume in some brain regions occurring in tandem with decreased performance on other tasks and decreased grey matter volume in neighbouring brain areas. Clearly, more work is required to establish whether the effects we have described here in relation to taxi drivers generalize beyond the domain of memory and the hippocampus. In particular, longitudinal studies will be crucial to explore the nature and consequences of skill acquisition. Finally, it will also be vital to consider whether expertise and its related effects can be expected to develop in any individual or whether they are genetically determined.

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All participants gave informed written consent to participation in accordance with the local research ethics committee.

#### REFERENCES

- Andersen, P., Morris, R. G. M., Amaral, D., Bliss, T. & O'Keefe, J. 2006 *The hippocampus book*. Oxford, UK: Oxford University Press.
- Ashburner, J. & Friston, K. J. 2005 Unified segmentation. *Neuroimage* 26, 839–851. (doi:10.1016/j.neuroimage. 2005.02.018)
- Aydin, K., Ucar, A., Oguz, K. K., Okur, O. O., Agayev, A., Unal, Z., Yilmaz, S. & Ozturk, C. 2007 Increased gray matter density in the parietal cortex of mathematicians: a voxel-based morphometry study. *Am. J. Neuroradiol.* 28, 1859–1864. (doi:10.3174/ajnr.A0696)
- Bannerman, D. M., Rawlins, J. N., McHugh, S. B., Deacon, R. M., Yee, B. K., Bast, T., Zhang, W. N., Pothuizen, H. H. & Feldon, J. 2004 Regional dissociations within the hippocampus: memory and anxiety. *Neurosci. Biobehav. Rev.* 28, 273–283. (doi:10.1016/j.neubiorev.2004.03.004)
- Barnea, A. & Nottebohm, F. 1994 Seasonal recruitment of hippocampal neurons in adult free-ranging black-capped chickadees. *Proc. Natl Acad. Sci. USA* 91, 11 217–11 221. (doi:10.1073/pnas.91.23.11217)
- Biegler, R., McGregor, A., Krebs, J. R. & Healy, S. D. 2001 A larger hippocampus is associated with longer-lasting spatial memory. *Proc. Natl Acad. Sci. USA* 98, 6941–6944. (doi:10.1073/pnas.121034798)
- Bird, C. M. & Burgess, N. 2008 The hippocampus and memory: insights from spatial processing. *Nat. Rev. Neurosci.* 9, 82–194. (doi:10.1038/nrn2335)
- Bohbot, V. D., Lerch, J., Thorndycraft, B., Iaria, G. & Zijdenbos, A. P. 2007 Gray matter differences correlate with spontaneous strategies in a human virtual navigation task. *J. Neurosci.* 27, 10 078–10 083. (doi:10.1523/ JNEUROSCI.1763-07.2007)
- Chase, W. G. 1982 Spatial representations of taxi drivers. In *Acquisition of symbolic skills* (eds D. Rogers & J. A. Sloboda), pp. 391–405. New York, NY: Plenum Press.
- Colombo, M., Fernandez, T., Nakamura, K. & Gross, C. G. 1998 Functional differentiation along the anterior–posterior axis of the hippocampus in monkeys. *J. Neurophysiol.* 80, 1002–1005.
- Corwin, J. & Bylsma, F. W. 1993 Translations of excerpts from Andre Rey's psychological examination of traumatic

encephalopathy and PA Osterrieth's the complex figure test. *Clin. Neuropsychol.* 7, 15–21. (doi:10.1080/1385404 9308401883)

- Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U. & May, A. 2004 Neuroplasticity: changes in grey matter induced by training. *Nature* **427**, 311–312. (doi:10.1038/ 427311a)
- Draganski, B., Gaser, C., Kempermann, G., Kuhn, H. G., Winkler, J., Buchel, C. & May, A. 2006 Temporal and spatial dynamics of brain structure changes during extensive learning. *J. Neurosci.* 26, 6314–6317. (doi:10. 1523/JNEUROSCI.4628-05.2006)
- Egan, M. F. *et al.* 2003 The BDNF val66met polymorphism affects activity-dependent secretion of BDNF and human memory and hippocampal function. *Cell* **112**, 257–269. (doi:10.1016/S0092-8674(03)00035-7)
- Ericsson, K. A., Charness, N., Hoffman, R. R. & Feltovich, P. J. 2006 *The Cambridge handbook of expertise and expert performance*. Cambridge, UK: Cambridge University Press. Frith, U. & Happe, F. 2005 Autism spectrum disorder. *Curr.*
- Biol. 15, R786–R790. (doi:10.1016/j.cub.2005.09.033)
- Gaser, C. & Schlaug, G. 2003 Gray matter differences between musicians and nonmusicians. *Ann. NYAcad. Sci.* 999, 514–517. (doi:10.1196/annals.1284.062)
- Gogtay, N. et al. 2006 Dynamic mapping of normal human hippocampal development. *Hippocampus* 16, 664–672. (doi:10.1002/hipo.20193)
- Grafton, S. 2008 Developing talent: expertise and the brain. In Your brain on cubs: inside the heads of players and fans (ed. D. Gordon), pp. 21-42. Washington, DC: Dana Press.
- Hariri, A. R., Goldberg, T., Mattay, V. S., Kolachana, B. S., Callicott, J. H., Egan, M. F. & Weinberger, D. R. 2003 Brain-derived neurotrophic factor val66met polymorphism affects human memory-related hippocampal activity and predicts memory performance. *J. Neurosci.* 23, 6690–6694.
- Hartley, T., Maguire, E. A., Spiers, H. J. & Burgess, N. 2003 The well-worn route and the path less traveled: distinct neural bases of route following and wayfinding in humans. *Neuron* 37, 877–888. (doi:10.1016/S0896-6273(03) 00095-3)
- Hock Jr, B. J. & Bunsey, M. D. 1998 Differential effects of dorsal and ventral hippocampal lesions. *J. Neurosci.* 18, 7027–7032.
- Iaria, G., Petrides, M., Dagher, A., Pike, B. & Bohbot, V. D. 2003 Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *J. Neurosci.* 23, 5945–5952.
- Jung, M. W., Wiener, S. I. & McNaughton, B. L. 1994 Comparison of spatial firing characteristics of units in dorsal and ventral hippocampus of the rat. J. Neurosci. 14, 7347–7356.
- Kalakoski, V. & Saariluoma, P. 2001 Taxi drivers' exceptional memory of street names. *Mem. Cogn.* 29, 634–638.
- Kalbfleisch, M. L. 2004 Functional neural anatomy of talent. Anat. Rec. 277B, 21–36. (doi:10.1002/ar.b.20010)
- Kumaran, D. & Maguire, E. A. 2005 The human hippocampus: cognitive maps or relational memory? *J. Neurosci.* 25, 7254–7259. (doi:10.1523/JNEUROSCI.1103-05.2005)
- Lee, D. W., Miyasato, L. E. & Clayton, N. S. 1998 Neurobiological bases of spatial learning in the natural environment: neurogenesis and growth in the avian and mammalian hippocampus. *Neuroreport* 9, R15–R27.
- Lepage, M., Habib, R. & Tulving, E. 1998 Hippocampal PET activations of memory encoding and retrieval: the HIPER model. *Hippocampus* **8**, 313–322. (doi:10.10 02/(SICI)1098-1063(1998)8:4<313::AID-HIPO1>3. 0.CO;2-I)

- Luria, A. R. 1987 *The mind of a mnemonist*. New York, NY: Harvard University Press.
- Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D. & O'Keefe, J. 1998 Knowing where, and getting there: a human navigation network. *Science* 280, 921–924. (doi:10.1126/science.280.5365.921)
- Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S. & Frith, C. D. 2000 Navigation-related structural change in the hippocampi of taxi drivers. *Proc. Natl Acad. Sci. USA* 97, 4398–4403. (doi:10.1073/pnas.070039597)
- Maguire, E. A., Spiers, H. J., Good, C. D., Hartley, T., Frackowiak, R. S. & Burgess, N. 2003a Navigation expertise and the human hippocampus: a structural brain imaging analysis. *Hippocampus* 13, 250–259. (doi:10.1002/hipo.10087)
- Maguire, E. A., Valentine, E. R., Wilding, J. M. & Kapur, N. 2003b Routes to remembering: the brains behind superior memory. Nat. Neurosci. 6, 90–95. (doi:10.1038/nn988)
- Maguire, E. A., Woollett, K. & Spiers, H. J. 2006a London taxi drivers and bus drivers: a structural MRI and neuropsychological analysis. *Hippocampus* 16, 1091–1101. (doi:10.1002/hipo.20233)
- Maguire, E. A., Nannery, R. & Spiers, H. J. 2006b Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain* 129, 2894–2907. (doi:10.1093/brain/awl286)
- Mechelli, A., Crinion, J. T., Noppeney, U., O'Doherty, J., Ashburner, J., Frackowiak, R. S. & Price, C. J. 2004 Neurolinguistics: structural plasticity in the bilingual brain. *Nature* 431, 757. (doi:10.1038/431757a)
- Mechelli, A., Price, C. J., Friston, K. J. & Ashburner, J. 2005 Voxel-based morphometry of the human brain: methods and applications. *Curr. Med. Imaging Rev.* 1, 105–113. (doi:10.2174/1573405054038726)
- Morris, R. G., Garrud, P., Rawlins, J. N. & O'Keefe, J. 1982 Place navigation impaired in rats with hippocampal lesions. *Nature* 297, 681–683. (doi:10.1038/297681a0)
- Moser, M. B. & Moser, E. I. 1998 Functional differentiation in the hippocampus. *Hippocampus* **8**, 608–619. (doi:10. 1002/(SICI)1098-1063(1998)8:6<608::AID-HIPO3>3. 0.CO;2-7)
- Munte, T. F., Altenmuller, E. & Jancke, L. 2002 The musician's brain as a model of neuroplasticity. *Nat. Rev. Neurosci.* 3, 473–478. (doi:10.1038/nrm866)
- O'Keefe, J. & Dostrovsky, J. 1971 The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res.* **34**, 171–175. (doi:10.1016/0006-8993(71)90358-1)
- O'Keefe, J. & Nadel, L. 1978 *The hippocampus as a cognitive map.* Oxford, UK: Oxford University Press.
- Osterrieth, P. A. 1944 Le test de copie d'une figure complexe. Archives de Psychologie **30**, 206–356.
- Pailhous, J. 1970 La representation de l'espace urbain: L'example du chauffeur de taxi. Paris, France: Presses Universitaires de France.
- Pailhous, J. 1984 The representation of urban space: its development and its role in the organisation of journeys. In *Social representation* (eds R. Farr & S. Moscovici), Cambridge, UK: Cambridge University Press.
- Parker, E. S., Cahill, L. & McGaugh, J. L. 2006 A case of unusual autobiographical remembering. *Neurocase* 12, 35–49. (doi:10.1080/13554790500473680)
- Peruch, P., Giraudo, M.-D. & Garling, T. 1989 Distance cognition by taxi drivers and the general public. *J. Environ. Psychol.* 9, 233–239. (doi:10.1016/S0272-4944(89) 80037-4)
- Pring, L. 2008 Memory characteristics in individuals with savant skills. In *Memory in autism: theory and evidence* (eds J. Boucher & D. Bowler), pp. 210–230. Cambridge, UK: Cambridge University Press.

**PHILOSOPHICAL TRANSACTIONS** 

0

- Rey, A. 1941 L'examen psychologique dans les cas d'encephalopathie traumatique. *Archives de Psychologie* 28, 286–340.
- Sluming, V., Barrick, T., Howard, M., Cezayirli, E., Mayes, A. & Roberts, N. 2002 Voxel-based morphometry reveals increased gray matter density in Broca's area in male symphony orchestra musicians. *Neuroimage* 17, 1613–1622. (doi:10.1006/nimg.2002.1288)
- Sluming, V., Brooks, J., Howard, M., Downes, J. J. & Roberts, N. 2007 Broca's area supports enhanced visuospatial cognition in orchestral musicians. *J. Neurosci.* 27, 3799–3806. (doi:10.1523/JNEUROSCI.0147-07.2007)
- Small, S. A., Nava, A. S., Perera, G. M., DeLaPaz, R., Mayeux, R. & Stern, Y. 2001 Circuit mechanisms underlying memory encoding and retrieval in the long axis of the hippocampal formation. *Nat. Neurosci.* 4, 442–449. (doi:10.1038/86115)
- Smulders, T. V., Sasson, A. D. & DeVoogd, T. J. 1995 Seasonal variation in hippocampal volume in a foodstoring bird, the black-capped chickadee. *J. Neurobiol.* 27, 15–25. (doi:10.1002/neu.480270103)
- Spiers, H. J. & Maguire, E. A. 2006 Thoughts, behaviour, and brain dynamics during navigation in the real world. *Neuroimage* **31**, 1826–1840. (doi:10.1016/j.neuroimage. 2006.01.037)

- Spiers, H. J. & Maguire, E. A. 2007a A navigational guidance system in the human brain. *Hippocampus* 17, 618–626. (doi:10.1002/hipo.20298)
- Spiers, H. J. & Maguire, E. A. 2007b The neuroscience of remote spatial memory: a tale of two cities. *Neuroscience* 149, 7–27. (doi:10.1016/j.neuroscience.2007.06.056)
- Strange, B. A. & Dolan, R. J. 2001 Adaptive anterior hippocampal responses to oddball stimuli. *Hippocampus* 11, 690–698. (doi:10.1002/hipo.1084)
- Terrazas, A. & McNaughton, B. L. 2000 Brain growth and the cognitive map. *Proc. Natl Acad. Sci. USA* 97, 4414–4416. (doi:10.1073/pnas.97.9.4414)
- Treffert, D. A. 2009 The savant syndrome: an extraordinary condition. A synopsis: past, present, future. *Phil. Trans. R. Soc. B* 364, 1351–1357. (doi:10.1098/rstb.2008.0326)
- Volman, S. F., Grubb Jr, T. C. & Schuett, K. C. 1997 Relative hippocampal volume in relation to food-storing behavior in four species of woodpeckers. *Brain Behav. Evol.* 49, 110–120. (doi:10.1159/000112985)
- Woollett, K. & Maguire, E. A. In press. The expertise of London taxi drivers compromises anterograde associative memory. *Neuropsychologia*.
- Woollett, K., Glensman, J. & Maguire, E. A. 2008 Non-spatial expertise and hippocampal gray matter volume in humans. *Hippocampus* 18, 981–984. (doi:10.1002/hipo.20465)
- Yates, F. A. 1966 The art of memory. London, UK: Pimlico.

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