

14 Studies of the Activation and Structural Changes of the Brain Associated with Expertise

Merim Bilalić

Department of Psychology, University of Northumbria
at Newcastle, UK

Guillermo Campitelli

School of Arts and Humanities, Edith Cowan University, Australia

Introduction

Experts' performance should actually not be possible. The contrasts between lesions and healthy tissue in radiological images are barely visible, yet experienced radiologists only need a split second to notice that something is wrong. Chess grand masters regularly find the best solution, often after a single glance and without much deliberation, in an environment where there are allegedly more possibilities than there are atoms in the universe (Shannon, 1950). Similarly, returning a tennis serve of over 150 mph should not be humanly possible but the best tennis players regularly start their own counterattacks with the return. Given the fascination that experts' performance usually elicits, it is not surprising that the scientific research on expertise is as old as scientific study of psychology (Binet, 1894). During that time there have been various methods of eliciting experts' performance and studying its underlying mechanisms. Recent technological advances enabled researchers to have direct access to experts' brains and tackle the question of the neural correlates behind experts' performance.

In this chapter we will review the research that shows how the brain accommodates the seemingly impossible feats of experts. We will first briefly consider the cognitive mechanisms behind experts' outstanding performance, as they will help us

understand the way in which the brain implements expertise. The main part of the chapter will focus on the neural implementation of expertise. We will follow the classical view of the human mind, which involves perception and the creation of a mental model of reality before acting. First we will deal with the neural changes associated with perceptual expertise domains, such as radiology, in which the main task is to rapidly detect relevant aspects of perceptual stimuli. In contrast, the crux of chess expertise is in the mental manipulation and simulation of the perceived stimuli. Chess experts are an example of cognitive expertise that we will review in the next section. Motor domains such as tennis feature the execution of movement sequences and will be dealt with in the section on motor expertise.

Cognitive Mechanisms of Expertise

Expertise is a prime example of how various cognitive processes, such as memory, attention, and perception, come together to enable a truly magnificent performance. Consider, for example, the opening example of skilled radiologists. Radiological images carry a wealth of information and one usually needs to carefully examine all of the tissue to make sure there are no abnormalities. Nevertheless, skilled radiologists can spot over 70 percent of pathologies even when the images are presented for only 200 milliseconds (Kundel &

Nodine, 1975). The short presentation precludes the search process commonly associated with radiological skill and the radiologists have to rely on their first impression of the image to make an educated guess. Experienced radiologists are able to perform so well in so little time because they have stored numerous instances of radiological images in their long-term memory (LTM). These stored knowledge structures are called by different names, from schemas to scripts (see Gobet et al., 2001), and their primary function is to make sense of the incoming new stimuli. When expert radiologists examine radiological images, related knowledge structures are inevitably activated in their LTM. Even if there is no perfect match between the incoming image and the existing ones, the chances are that the vast knowledge base of radiologists enables them to quickly form a good working hypothesis of the incoming images. Less experienced radiologists lack this knowledge and cannot form a quick impression of the incoming stimulus. They are essentially guessing when they are forced to decide in a split second.

The first impression based on the domain-specific knowledge stored in LTM has another consequence. It enables experts to attend to the most relevant aspects in the stimulus and disregard less informative features. The consequence is that expert radiologists need only a few fixations to locate the abnormality within a radiological image (Krupinski, 2000). Novices lack the domain-specific knowledge required to guide their attention and they consequently need to examine the stimulus in great detail, rarely distinguishing between more and less informative features.

The interplay between domain-specific memory, attention, and perception is the core of the theories on radiological expertise (Kundel, Nodine, Conant, & Weinstein, 2007; Swenson, 1980). A similar mechanism is found in a cognitive domain – chess. As in radiology, the domain-specific knowledge stored in chess experts' LTM enables them to quickly grasp the essence of chess positions. Experts not only have better recall of briefly

presented positions from unknown games (Chase & Simon, 1973; de Groot, 1978), but they are also faster at locating certain types of pieces in those positions (Bilalić, Langner, Erb, & Grodd, 2010). Just as in radiology (see Reingold & Sheridan, 2011), experts' strategies are vastly different from those of their less skilled peers – whereas novices need to examine every corner of the position to identify the pieces of interest, experts only need a few glances to perform the same task. The same efficiency is found when chess experts look for the best continuations. Experts do not necessarily look further ahead and simulate future situations in more depth than less skilled players, but they immediately examine solutions of high quality (de Groot, 1978; see also Gobet & Charness, Chapter 31, this volume). Their knowledge enables them to instantly orient themselves and concentrate on promising solutions to the problem at hand. Novices, on the other hand, do not have the luxury of the vast knowledge base that would guide their search. They need to examine numerous less promising paths before they stumble onto a promising solution.

Motor expertise also features a similar mechanism. Tennis experts do not wait to see the ball in the air before initiating their motor response because no matter how fast they are, they will not be able to execute the movement in time (see Abernethy, Mann, & Farrow, Chapter 35, this volume). Instead, they anticipate where the ball is going to land by extracting the kinetic information from the player who is serving. Obviously, tennis experts would not be able to perceive the informative aspects of complex movements such as tennis serves if they did not have similar movements stored in their LTM. The stored movements enable experts to pick up important information in the serve motion, mentally simulate the most likely scenario, and predict where the ball is heading before it has even made contact with the racket. Tennis novices lack this domain-specific knowledge and have to wait for the ball's trajectory to become apparent, when it is already too late to react.

Despite the differences between perceptual, cognitive, and motor expertise domains, the cognitive mechanisms responsible for experts' superior performance have been found to be remarkably similar. At the core of all types of expertise is domain-specific memory that has been acquired through prolonged exposure and practice within a domain of specialization. The content of memory may be different depending on the domain, a feature that is important to keep in mind when we talk about neural implementation of expertise. In all instances, however, the domain-specific knowledge enables quick orientation in a new situation by biasing the perceptual intake through guided attention. It is important to underline that the greater efficiency of experts is not caused by them performing more quickly the very same strategies as novices. Instead, domain-specific knowledge enables experts to employ qualitatively different strategies that draw on their vast knowledge base. Experts' strategies may be fast and even look effortless, but as we have seen, their efficiency is based on a complex interaction between numerous cognitive processes (Bilalić et al., 2010). As it turns out, this has a profound effect on the way the brain implements experts' performance.

How the Brain Accommodates Expertise

One of the exciting technical developments in recent years is the availability of neuroimaging techniques for research. The most commonly employed neuroimaging technique is arguably functional magnetic resonance imaging (fMRI), which will be featured in most of the research presented in the upcoming sections on functional brain changes associated with expertise. The structural brain changes, typically investigated with voxel based morphometry (VBM) for gray matter, and diffusion tensor imaging (DTI) for white matter, will be presented after the functional changes.

Perceptual Expertise

Functional Brain Changes in Perceptual Expertise

When we talk about expertise, we usually have in mind highly specialized domains such as radiology. However, we are all experts in many aspects of everyday life as we can easily and efficiently find our way in the environment. For example, we are particularly skilled at recognizing objects in our environment, with perception of faces arguably the pinnacle of our perceptual skill (for a different perspective, see Ericsson, Krampe, & Tesch-Römer 1993). Most of us need just a second to recognize a face, a skill which we have honed our whole life. The instant perception of faces is a consequence of the way the faces are processed in our system. Instead of individually parsing face elements such as eyes, nose, and mouth, most of us can perceive a face in a single glance as a whole without paying attention to its individual components. This perceptual processing of individual elements as a single unit is called holistic processing (Richler, Palmeri, & Gauthier, 2012), which is the opposite of analytical processing where components are individually perceived before they are made into a whole. Since experts' performance in many ways resembles holistic processing, the neural basis of face perception is of interest to expertise research.

There are a number of brain areas involved in the different components of face processing (Duchaine & Yovel, 2015), but most researchers identify the fusiform face area (FFA), in the inferior side of the temporal lobe, as the main engine of holistic processing. Not only is the FFA more responsive to faces than any other stimuli, but damage to the brain tissue in and around this area leads to prosopagnosia, a condition in which people have difficulty in perceiving faces. People suffering from prosopagnosia fail to perceive a face as a whole and instead revert to analytical strategies of examining individual

face components (Hadjikhani & de Gelder, 2002). The important finding here is that the FFA is more activated in experts than in novices when they observe objects within their domains of specialization (Bilalić, Grottenhaler, Nägele, & Lindig, 2016; Bilalić, Langner, Ulrich, & Grodd, 2011; Ross et al., 2015), which implies that the FFA is important for holistic processing, not just for perception of faces.

A holistic-like process is typical of radiological expertise and one recent study (Harley et al., 2009) looked into its connection with the FFA. The activation levels in the FFA did not differ among differently skilled radiologists when they had to indicate if the cued part of a thorax X-ray contained a pulmonary nodule. However, the FFA was modulated by the performance, as the better the radiologists were at identifying nodules, the more they engaged the FFA. In contrast, the lateral occipital complex (LOC), the first complex station of the ventral stream that responds to objects and their shape (Grill-Spector, Kourtzi, & Kanwisher, 2001), was negatively associated with radiological performance, indicating that only the less skilled radiologists engaged the LOC. The engagement of the FFA and disengagement of the LOC as radiological expertise develops fits well with the notion that radiological expertise relies more on holistic and less on analytic processes.

A recent study (Bilalić et al., 2016) extended these results by using a more sensitive multivariate voxel pattern analysis (MVPA). As can be seen in Figure 14.1, the activity patterns in and around the FFA of radiologists could reliably indicate whether the radiological images were presented or other neutral stimuli. There was no such differentiation in the FFA of medical students. The study further investigated one of the hallmarks of holistic processing, the inversion effect – experts perceive objects less well when they are inverted, that is upside-down, than when they are in their normal upright orientation (Thompson, 1980). The inverted stimuli impaired the performance of skilled radiologists, but it

was also reflected in their FFA activity, which could be used to reliably indicate when upright and inverted X-rays were being presented. In contrast, the FFA in medical students could not differentiate between different orientations of X-rays.

Another visual expertise that relies on processing wholes instead of individual parts is fingerprint matching. Unlike on TV shows where computers do all the work, in real life expert examiners are responsible for matching fingerprints from a crime scene with the fingerprints in a database. It turns out that that fingerprints are perceived as a whole too (Busey & Vanderkolk, 2005). If holistic processing is disabled, for example by turning the stimuli upside-down, experts' behavioral performance deteriorates. The struggle with inverted fingerprints has been reflected in the neural response as measured by electroencephalography (EEG). The negative amplitude produced from around the occipitotemporal areas, generally related to the FFA (Sadeh, Podlipsky, Zhdanov, & Yovel, 2010), reached a peak after 170 milliseconds of the fingerprint presentation. In expert examiners, the abovementioned N170 component was more pronounced for inverted than for upright fingerprints, the characteristic pattern in the inversion effect (Rossion & Jacques, 2008). In contrast, the amplitudes were almost identical for upright and inverted fingerprints in students with little fingerprint experience.

Visual expertise involves numerous cognitive processes, some of them unrelated to the FFA. A recent study (Harel, Gilaie-Dotan, Malach, & Bentin, 2010) demonstrated that visual expertise is not only an automatic bottom-up process, but that it also engages other top-down processes such as attention and domain-specific memory. Once the attention of (car) experts has been engaged, together with the access to all their knowledge about the stimuli from their domain of expertise, the neural differences become evident, not only in the FFA, but all over the cortex including not only

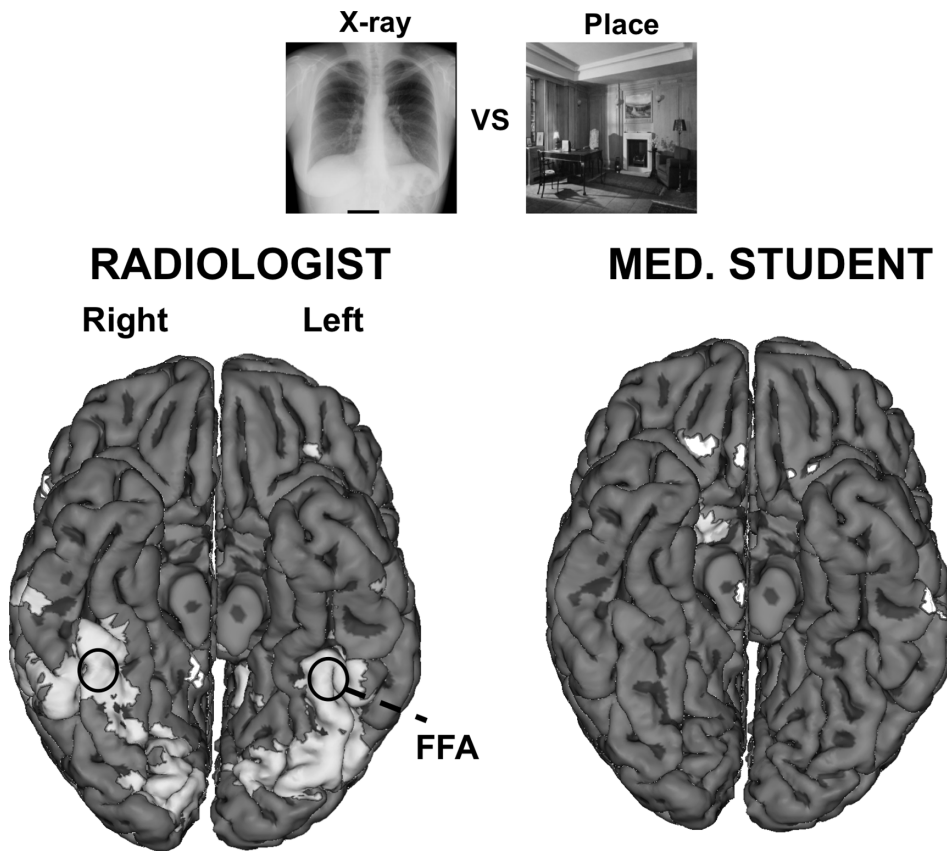


Figure 14.1 Radiological expertise. The brain areas that can reliably differentiate between radiological images and neutral stimuli in radiologists (left) and medical students (right). For more details, see Bilalić et al. (2016).

visual but also non-visual areas (for a review, see Harel, 2015). Expertise of any kind may involve many more cognitive processes than just the simple act of perception. Even face perception, a prime example of automatic holistic process, involves different aspects, from recognition of people, to judging their mood. Radiology is no different, and passive observing may also involve a number of other areas besides the FFA. For example, when radiologists look for inserted artificial modification in radiological images (blurred part of the image), they activate not only the middle and inferior temporal gyri but also the middle and superior frontal gyri (Haller & Radue, 2005), generally important for executive functions. Similarly, the left inferior frontal gyrus and the

posterior cingulate gyrus, typically associated with reasoning and decision-making, were more activated in skilled radiologists when they recognized pathologies within radiological images than when they had to recognize embedded animals and letters in the same images (Melo et al., 2011). The sight-reading of music notes, another visual skill, also engages a number of areas besides the FFA (Wong & Gauthier, 2010).

Besides the visual domains, auditory expertise is probably the most investigated perceptual expertise (see Lehman, Gruber, & Kopiez, Chapter 28, this volume; Altenmüller & Furuya, Chapter 29, this volume). Here we will review the expertise associated with other senses, such as the tactile, gustatory, and olfactory senses. One

of the reasons why these kinds of perceptual expertise are not as often investigated as visual and auditory is that they rarely come alone, isolated from information from the other senses. People rarely need to orient themselves by only relying on touching, smelling, and tasting. That is why there are not many tactile experts. Blind people, however, do not have the luxury of using visual information and often rely on touch for information about their environment. They also tend to be better than their sighted counterparts on tactile tasks involving recognition and fine discrimination of two surfaces (for a review, see Kupers & Ptito, 2014). Neuroimaging studies (Stilla, Deshpande, LaConte, Hu, & Sathian, 2007; Stilla & Sathian, 2008) regularly show that blind people involve the areas that are normally reserved for visual processing, such as the LOC, the primary visual cortex (V1), and the fusiform gyrus. It is now clear that the activation of LOC in blind people during tactile tasks is a consequence of bottom-up processing – tactile information from the somatosensory cortex is being forwarded for further processing to bilateral visual areas (Lucan, Foxe, Gomez-Ramirez, Sathian, & Molholm, 2010). This direct connection between somatosensory areas and nominally visual areas is not available in sighted persons (Stilla et al., 2007; Stilla & Sathian, 2008). In the case of sighted participants, the information from the somatosensory cortex goes to the right intraparietal sulcus (IPS). Indeed, the IPS predicts the performances on fine tactile discrimination tasks of people with intact vision but not those of blind people (Stilla et al., 2007). In contrast, the activation in the LOC, nominally a visual area, reliably predicts the tactile performance of blind people.

As with tactile stimuli, gustatory stimuli rarely come alone. The flavor of our favorite dish is a combination of not only its smell and taste, but also its visual characteristics. That might be one of the reasons why people are not particularly good at identifying taste when other visual and olfactory information is not present. Yet some

people compete in recognizing (and nicely verbalizing) the components of taste, for example wine experts. Wine expertise is probably exaggerated in wine tasting circles, as wine tasting is in many ways more an exercise in verbal description than perceptual skill (Morrot, Brochet, & Dubourdieu, 2001). Nevertheless, trained wine tasters are better able to distinguish the components in expensive wine than regular wine lovers lacking training (Goldstein et al., 2008). Neuroimaging studies on expertise in this domain are rare not only because of the dearth of gustatory experts, but also because of the difficulty of administering gustatory stimuli to participants inside neuroimaging devices such as MRI scanners. Two studies on wine experts (Castriota-Scanderbeg et al., 2005; Pazart, Comte, Magnin, Millot, & Moulin, 2014) indicated that the strategies of expert and novice wine tasters differ significantly. Experts analyze the taste components, since this is their main task, while naive participants perceive the taste in a global emotional manner. This is reflected in the neural implementation in which the expert wine tasters engaged the insula area, which extends antero-inferiorly into the caudal orbitofrontal cortex, as well as the dorsolateral prefrontal cortex (DLPFC). The first area is associated with the synthesis of gustatory and olfactory stimuli as well as with the judgment of taste quality, while the DLPFC is also probably related to the attention paid to the taste input and retrieval of verbal labels for the individual components. The analysis and identification of the taste components in experts inevitably activate the hippocampal and parahippocampal areas, which are responsible for memory processes. In contrast, novices engage more the amygdala, an area associated with pleasure and emotions.

As with tactile and gustatory performance, olfactory experts are rare. Blind people, however, seem to reliably outperform sighted people on tasks that require olfactory discrimination (Rombaix et al., 2010). A recent neuroimaging study (Kupers et al., 2011) demonstrated enhanced

activity in the primary olfactory areas (amygdala) and the secondary olfactory areas (orbitofrontal cortex and hippocampus) in people who lacked vision from birth, or lost it early in life, when they are compared to sighted participants on identifying odors. Another study (Renier et al., 2013) found that the activation in the posterior part of the right fusiform gyrus differentiated between skilled odor perceivers (mostly blind participants) and less skilled counterparts on categorization and discrimination of odors. Once the olfactory tasks were replaced by auditory tasks, the fusiform gyrus did not differentiate between the groups or their performance.

In the next section, on structural differences, we will see that the piriform cortex is enlarged in perfumers, people who undergo training to become professional makers of perfumes. The only functional study (Plailly, Delon-Martin, & Royet, 2012) that has examined the brain activity of the perfumers during passive exposure to odors, found activation in the piriform cortex in both hemispheres all the way to the anterior part of the neighboring amygdala.

Structural Brain Changes in Perceptual Expertise

Expertise, involving seemingly impossible performances, puts considerable demands on the brain. The brain reacts to these new demands with structural and functional reorganization. An example of this reaction is the brain plasticity that we have seen in blind people, where the connections between somatosensory and nominally visual areas have been reestablished following the absence of visual stimuli. The structural brain changes as a consequence of perceptual expertise are arguably most obvious in music experts (see Altenmüller & Furuya, Chapter 29, this volume). Here we will just briefly mention a few studies on the structural brain changes associated with olfactory expertise.

The size of the olfactory bulb, the most rostral part of the brain, is positively correlated with scent identification (Buschhüter et al., 2008; Rombaux et al., 2010). The cortical thickness of other areas important for olfactory perception, such as the medial orbitofrontal cortex and insula, was also positively associated with performance on differentiating and categorizing smells (Frasnelli et al., 2010). The olfactory areas seem to be differently specialized, as the volume of the olfactory bulb predicted the identification of odor but the fine differentiation between two odors was best predicted by the amount of gray matter in the orbitofrontal cortex and piriform gyrus (Seubert, Freiherr, Frasnelli, Hummel, & Lundstrom, 2013).

Cognitive Expertise

The importance of connecting incoming stimuli with the existing knowledge structures in LTM is arguably most obvious in cognitive expertise. We will start with the neural changes in expert memorizers, then move to the neural differences between two kinds of calculators: abacus experts and mental calculators. We will finish the section with board games and spatial experts, who need to find their way in complex environments such as large cities.

Functional Brain Changes in Cognitive Expertise

The way to remember new information is to connect it with the already existing information in LTM. That is the basis of a mnemonic called method of loci, in which highly familiar locations along a route are used for storing information by making associations between the locations and the information being stored. When memorizers need to retrieve that information, they visit the well-known locations along the route in their LTM and find the stored information. In the first neuroimaging study featuring a number of

exceptional memorizers (Maguire, Valentine, Wilding, & Kapur, 2003), a number of brain areas associated with spatial memory and navigation were more active during the encoding of information in memorizers than in the controls: the cerebellum, medial superior parietal gyrus, retrosplenial cortex (RSC), and posterior hippocampus.

In another study (Raz et al., 2009), a person who is capable of reciting 65,000 decimals of π using the method of loci was shown to activate only the medial frontal gyrus and partly the dorsolateral prefrontal cortex (DLPFC) when the retrieval of the first 500 digits of π was compared to the activity associated with counting to 100. When the same person was asked to encode a matrix of 100 digits presented in 10 rows of 10 digits, the activation was markedly different from that of the retrieval of highly learned material. Besides the visual association areas around the precuneus, lingual, and fusiform gyri, at the beginning of the process of encoding new material, the motor associative areas and insula were also active. Later during the encoding process, the activation in the visual associative areas disappeared while new activation in the DLPFC and the orbitofrontal cortex appeared. It seems that the memorizer employed visual associations at the beginning, which in turn activated visual and motor associate areas, but later when the memory load increased, the frontal areas responsible for working memory (DLPFC) were being employed.

In a recent study (Yin, Lou, Fan, Wang, & Hu, 2015), another expert memorizer, who used a storytelling method, was compared to a control group on a task where a series of two digits had to be remembered. The memorizer had more activation during encoding of the digits in areas that are important for episodic memory: left superior parietal gyrus (SPG), left DLPFC, left premotor cortex, and bilateral frontal pole. In contrast, the controls, who employed a rehearsal strategy, had more activation in the areas typical for rehearsal (left middle and inferior frontal gyri) and in the

occipital visual areas. A similar pattern of brain areas was involved when the recall phase was analyzed. As with other studies on expert memorizers, the memorizer in this study did not use working memory, which is reflected in the functional reorganization of his brain activity compared to control participants who do not employ mnemotechnics.

Expert calculators, who can quickly manipulate numbers mentally, represent another group of cognitive experts. Here we report the study on a mental calculator R. Gamm (Pesenti et al., 2001), who can quickly execute complicated calculations such as multiplying two two-digit numbers within a few seconds (see also Butterworth, Chapter 32, this volume). Besides the typical brain areas responsible for the visual working memory that control participants engage when they perform calculations, Gamm additionally activated the areas typically associated with episodic LTM regions important for encoding and retrieving: the parahippocampal gyrus (PHG), medial frontal cortex, and upper anterior cingulate gyrus. The controls did not engage these areas during their mental calculations, which confirms that their strategies did not involve storing intermediate results of complex calculation in LTM for later retrieval, as was the case with R. Gamm.

Abacus experts are a different kind of expert calculators because they employ an external device to deal with complex calculations. Unlike mental calculators who rely on LTM to store intermediate results and retrieve them later when they are needed, abacus experts use the visuospatial working memory they need for mental representation and manipulation of the abacus (Frank & Barner, 2012). Even a simple digit-span task (Tanaka, Michimata, Kaminaga, Honda, & Sadato, 2002) elicited a marked difference in the brain activations between abacus experts and control non-experts. Non-experts engaged the left Broca and the neighboring ventral prefrontal cortex, responsible for rehearsal typical in the digit-span performance. The abacus experts

engaged the superior and inferior part of the parietal lobe (IPL and SPL), visuospatial areas most likely involved in the generation of visuospatial images of the abacus, the manipulation of these, and the maintenance of abacus content. In addition, abacus experts engaged the upper dorsal parts of the premotor cortex (PMd), an area important for voluntary action and in this specific situation used for imagining the movements necessary for the manipulation of beads. The importance of PMd in abacus performance was confirmed in a case study of an abacus expert who lost her abacus skill after a stroke that also damaged her PMd (Tanaka et al., 2012).

Another study (Hanakawa, Honda, Okada, Fukuyama, & Shibasaki, 2003) employed a representative task of adding a series of numbers with abacus experts and found the same bilateral parietal-prefrontal network associated with their performance. Non-experts, on the other hand, activated predominantly the left frontoparietal areas responsible for rehearsal strategy. The study also featured a clever spatial control task, which required participants to mentally move an object on a grid. The task, not unlike the abacus task itself, produced essentially the same activations in both groups as the abacus task had elicited in abacus experts. Suddenly, even non-experts were using the right prefrontoparietal network.

A recent study (Ku, Hong, Zhou, Bodner, & Zhou, 2012) measuring simultaneously fMRI and EEG activity indicated that at the very beginning of the abacus calculation (*c.* 380 ms after stimulus presentation), experts engage the SPL and middle temporal gyrus. Later, around 440 ms, the PMd premotor areas become engaged in abacus experts. The study illustrates the temporal dissociation between the visuospatial and visuomotor processes in abacus expertise, as abacus experts need to build up their mental abacus before they start to manipulate it.

Board games also place a great burden on the brains of experts as they not only have to perceive numerous individual objects and retrieve their

functions, but also mentally transform the situation in order to find the right path in a jungle of solutions. Here we will focus on the game of chess, which has often been used in research on expertise (see Gobet & Charness, Chapter 31, this volume). We will demonstrate how the brain implements numerous advantages that experts have over novices, starting from relatively simple object perception and moving toward more complex pattern recognition and problem-solving processes.

A recent series of studies (Bilalić, Kiesel, Pohl, Erb, & Grodd, 2011; Bilalić et al., 2010; Bilalić, Turella, Campitelli, Erb, & Grodd, 2012; RENNIG, Bilalić, Huberle, Karnath, & Himmelbach, 2013) examined skilled object and pattern recognition in chess. Object recognition was investigated using a 3×3 miniature board with only two pieces on it, as depicted in Figure 14.2. Chess experts were faster at identifying chess pieces as well as at retrieving their function and connecting them to other pieces. The eye-movement recordings showed that the experts' advantage lies in greater familiarity with the pieces, as they do not have to fixate them directly to identify them. The advantage is even greater when they had to indicate whether two pieces form a check relationship, since, again, greater familiarity allows experts to encompass the whole constellation with a single glance. Figure 14.2 shows that there is a large overlap in the brain activation in experts and novices on such a simple check task. Many of these activated areas proved to be task-specific, as the same task involving the same board but geometrical shapes (e.g. square, diamond) instead of pieces, engaged many of the same areas. There were, however, also noticeable chess-specific task areas, and these areas were more activated in experts than novices: lateral temporal areas, including the bilateral posterior middle temporal gyrus (pMTG) and its neighboring occipito-temporal junction (OTJ), as well as the bilateral supramarginal gyri (SMG). These areas were partly activated in novices in the left hemisphere, but only the skilled players engaged its right-hand counterparts.

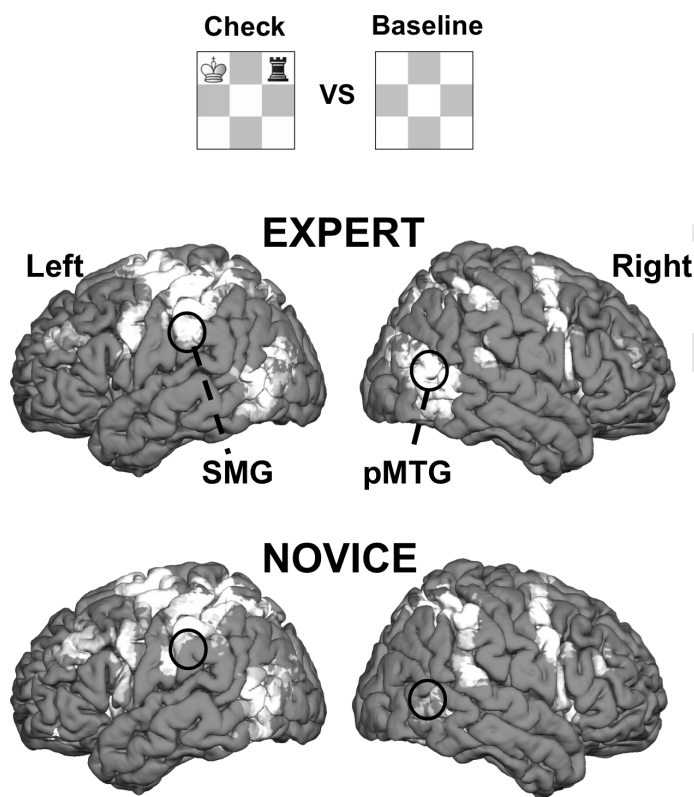


Figure 14.2 Skilled object perception in chess. The brain areas activated when chess experts (middle panel) and novices (bottom panel) had to indicate if there is a chess piece on a miniature chess board (top panel). For more details, see Bilalić, Kiesel, et al. (2011).

The other studies in the series employed the whole chessboard and chess-specific tasks of looking for certain types of pieces on the board and identifying threat relations between pieces. An additional manipulation was the randomization of chess positions, which tapped into pattern recognition processes. The same lateral areas as in the chess-specific object recognition were activated when experts were looking for specific pieces or threats: pMTG and SMG. These brain areas did not differentiate between normal and random positions, which is to be expected, as recognition of individual objects and their relations with other objects was present in both position types. The new activations were in the PHG, around the collateral sulcus (CoS), and the RSC.

Besides being modulated by expertise, the PHG and RSC were sensitive to the randomization manipulation. Normal positions, where experts could use their domain-specific knowledge, engaged the PHG and RSC more than random positions, where pattern recognition was difficult if not impossible. Novices, on the other hand, did not have much activation in these areas when compared to other control tasks, and the position type did not play an important role.

These areas were also found in other studies employing different paradigms. When the recall paradigm was used (Campitelli, Gobet, Head, Buckley, & Parker, 2007; Campitelli, Gobet, & Parker, 2005), experts had more activation in the vicinity of the PHG on the retrieval of normal

positions than on random ones. The novices displayed the same level of activation. A recent study (Bartlett, Boggan, & Krawczyk, 2013) used simple observation of normal and random positions and identified the posterior cingulate, the same region where the RSC is situated, as the region modulated by both expertise and randomization.

The lateral areas (pMTG and SMG) are important for perception of objects and their functions, especially manmade objects such as tools (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Chess pieces also possess characteristic functions rooted in movement, which may explain the activation of the dorsal stream area, SMG. The SMG is associated with explicit retrieval of the actions of tools. The distinct function of the pMTG and SMG may explain their involvement in the chess-specific task. The pMTG was activated both when a chess object was identified and when its function was retrieved, but the SMG was mainly engaged in the check task where the retrieval of the chess pieces' function was necessary. The involvement of these two lateral brain areas was confirmed in the pattern recognition experiments where identification of pieces on the board full of other pieces did not activate the SMG, but the identification of threats did (Bilalić, Kiesel, et al., 2011; Bilalić et al., 2012). The inferior (PHG) and medial (RSC) brain areas responsible for chess experts' quick orientation based on pattern recognition, are associated with scene perception and spatial navigation, respectively (Epstein, 2008). These findings indicate that chess experts' brains accommodate highly specialized cognitive processes. The PHG and RSC are important for forming an initial idea about the environment, based on matching of the incoming information with the stored chess patterns in LTM. Once the attention has been directed to the aspects of interest in the environment, the lateral areas (SMG and pMTG) take over for object identification and retrieval of their function.

A number of studies on chess investigate how people decide on the next move, the essence of

chess expertise. Unfortunately, many of them suffered from methodological problems where it is difficult to unpick the processes involved because of insufficient control (Amidzic, Riehle, Fehr, Wienbruch, & Elbert, 2001) or they simply did not investigate expert groups of participants (Atherton, Zhuang, Bart, Hu, & He, 2003; Nichelli et al., 1994). A recent study (Wan et al., 2011) used extensive control and expert shogi players to investigate the neural underpinning of the process of finding the best solution. First it was found that the similar areas involved in chess object and pattern recognition were also involved in shogi perception. The pMTG was engaged in both experts and novices, but the PHG and RSC were more activated in experts. The posterior cuneus at the medial side of the brain was also more engaged in experts, and this was also important for discrimination between normal and random positions in experts (the RSC and PHG were also sensitive to the randomization, but the differences did not quite reach the significance level). The posterior precuneus, together with premotor and motor areas, and the DLPF, was also engaged when both experts and novices had to find immediately a solution to a position presented for only a second. Experts, however, additionally engaged the head of the nucleus caudate, a part of the basal ganglia. The nucleus caudate did not respond in a number of control tasks, but its activation was positively associated with the performance of experts.

One of the functions of the basal ganglia is formation and execution of the stimulus-response associations and their caudate parts is responsible for cognitive responses (Poldrack, Prabhakaran, Seger, & Gabrieli, 1999). It is therefore possible that recognition of the well-known positions is carried out in the precuneus, an area involved in imagery of visuospatial stimuli and episodic memory retrieval (Wagner, Shannon, Kahn, & Buckner, 2005), as well as in the PHG and RSC. The information is then sent to the nucleus caudatus and triggers typical responses

to such constellations (Wan et al., 2011, 2012). This possibility gains further credence when we consider that the precuneus is directly connected to the nucleus caudatus as well as that their activations fluctuate in a similar manner – the more activation at a particular point in time in precuneus, the more activation there is in the nucleus caudatus (Wan et al., 2011).

An expertise of a more spatial nature is finding a way in a complex environment, a task at which taxi drivers excel. Similarly to chess players, taxi drivers have been used to investigate a number of issues. Here we will briefly review the functional studies that preceded the well-known structural studies we will consider in the next section. An early study on spatial expertise (Maguire, Frackowiak, & Frith, 1997) required taxi drivers and controls to find a particular destination using the shortest possible route. This topographical skill of taxi drivers engaged a number of areas in the medial temporal lobe: both hippocampi, both parahippocampal gyri (PHG), and both posterior parts of the cingulate, which we called the RSC (for a review, see Epstein, 2008). These areas were more activated in the typical topographical taxi-related activities than in other memory tasks.

Structural Brain Changes in Cognitive Expertise

The demands of cognitive expertise leave a profound effect on the functional organization of the brain. However, the study on exceptional memorizers (Maguire et al., 2003) could not find any structural differences between memorizers and the control group. In contrast, the expert who could recite 60,000 digits of π (Raz et al., 2009) had more cortical mass than the controls matched for gender and age in the right anterior region of the cingulate gyrus, an area important for mentalizing and emotional processing. The expert employed the method of loci that was based on vivid and emotionally laden images, unlike the exceptional memorizers in the other study

(Maguire et al., 2003), which may explain the inconsistency in the findings. A recent study (Kalamangalam & Ellmore, 2014) measured the cortical thickness in Hindu Vedic priests, who are required to learn a large amount of information. The Vedic priest had a thicker left orbitofrontal cortex and right infero-temporal gyrus, the areas involved in LTM, than the matched control participants.

Children who had more than three years of experience with the abacus have an overall higher degree of myelination than their peers with no experience with the abacus (Hu et al., 2011). This was particularly the case for motor and visuospatial pathways, which would mean that the information between these areas would be transferred more quickly in abacus than non-abacus children. Another intriguing finding is the difference in the corpus callosum, which connects the two brain hemispheres. Given that abacus experts engage both hemispheres for their calculation (Hanakawa et al., 2003), abacus expertise may enhance the connections between the left and right hemispheres as a result of extensive experience with generation and manipulation of the mental abacus.

Structural changes in board experts proved to be elusive. The described series of studies on skill object and pattern recognition (Bilalić, Kiesel, et al., 2011; Bilalić et al., 2010, 2012; Rennig et al., 2013) could not establish structural differences between experts and novices (Bilalić, 2017). The situation was no different in shogi experts, where neither the training study (Wan et al., 2012), nor the study involving experts playing for decades (Wan et al., 2011), could find any significant differences. Other studies involving more participants were more successful, but the pattern of results remains inconsistent. A structural study on the experts of the board game Baduk (also called Go) found that their caudate nucleus was larger than in novices (Jung et al., 2013), but another study on a similar board game (Chinese chess), found precisely the opposite pattern – the

nucleus caudatus was smaller in experts (Duan et al., 2012). Yet another study on chess expertise (Hänggi, Brüttsch, Siegel, & Jäncke, 2014), found no differences between the volume of the caudate nucleus in chess experts and that in matched controls who did not play chess. The same study found that the pMTG, an area implicated in skilled object recognition (Bilalić, Kiesel, et al., 2011; Wan et al., 2011), was smaller in chess experts than in non-players. The cortical thickness was also decreased in the pMTG in experts but also in the SMG and the posterior precuneus, both areas involved in skilled perception of objects and patterns (Bilalić, Kiesel, et al., 2011; Bilalić et al., 2010, 2012). The connections of the brain also differ in chess experts compared to non-playing matched controls (Hänggi et al., 2014). The superior longitudinal fasciculus, a pathway that connects the temporal lobe with the parietal and frontal lobes, was more dense and compact in chess experts.

The smaller volume and thinner cortex are consequences of microscopic changes in neurons and their connections as the brain purges unnecessary connections. This does not necessarily mean that the brain activation in these areas as measured by fMRI should also be smaller (Lu et al., 2009), but it most likely means that the efficiency has been increased through the pruning. For example, the studies investigating the overall activation patterns in Chinese chess experts and novices (Duan et al., 2012, 2014), found that experts' caudate nucleus was in much better synchrony with the infero-temporal and parietal areas implicated in skilled perception.

Another domain where experts rely on their memory is orientation, as we find in the case of taxi drivers. An intriguing finding about the importance of the right hippocampus in spatial expertise from an early study (Maguire et al., 1997), paved the way for one of the most imposing series of studies on structural changes in expertise. In a now seminal study (Maguire et al., 2000), taxi drivers in London were found to have a larger posterior part of the right hippocampus than the control

group. The volume of the posterior part was positively correlated with experience in the job. A later study (Maguire, Woollett, & Spiers, 2006) confirmed that bus drivers, who also had many years of driving experience, did not have a larger posterior hippocampus, thus ruling out driving as a possible cause of the structural change in the hippocampus. More direct evidence comes from a study that followed a group of people who enrolled in the official training program for becoming a taxi driver in London (Woollett & Maguire, 2011). Eventually, some of them obtained a taxi license after a couple of years of learning the locations of the London streets. When their post-training brain scan was compared to their pre-training scan, the posterior hippocampus was enlarged. The control group, who did not undergo the strenuous training, unsurprisingly did not display any change in the hippocampus. The really interesting question, however, is what happened to the trainees who started the program but dropped out. Again, their hippocampus did not show the change after they dropped out because they did not complete the training and acquire "the Knowledge," as the London taxi license is often called. Their pre-training scans were not, however, in any other way significantly different from those of the future taxi drivers who completed the training. What was different was the amount of time the two groups invested in training: the trainees who became licensed taxi drivers practiced for 35 hours every week, those who dropped out spent only 17 hours per week studying for the examination.

Motor Expertise

As in other expertise domains, memory plays a crucial role in motor expertise. The nature of this memory, however, is different as motor domains contain kinetic information. The kinetic information is stored at different brain areas compared to the perceptual kind of information we have encountered in the previous sections. The kinetic information is then used to anticipate

the course of action and prepare a response well in advance. The crucial neural component of motor expertise may be mirror neurons, a large subset of neurons located in premotor and parietal areas in primates (Rizzolatti & Craighero, 2004). Mirror neurons are responsible for movements but also become active if the same movements have only been observed in others. It may explain a range of different phenomena, but more importantly, it provides a plausible neural mechanism for experts' anticipation skills.

The following subsection provides an overview of the anticipation studies that involve evaluations of visual scenes within MRI scanners. This paradigm is by far the most common given the difficulty of executing actual movements in MRI scanners. Nevertheless, there are some neuroimaging studies that featured actual movements. These are covered in Altenmüller and Furuya's chapter on music (Chapter 29, this volume).

Functional Brain Changes in Motor Expertise

The human equivalent of mirror neurons is called the action observation network (AON), which encompasses premotor and parietal, and inferior frontal areas in humans (Turella, Wurm, Tucciarelli, & Lingnau, 2013). The most impressive series of studies on the AON in motor experts comes from dancing, a domain where a series of moves needs to be coordinated and executed. In the first studies (Calvo-Merino, 2004), ballet and capoeira experts and novices were shown videos of ballet and capoeira dancing. Experts had more activation than novices in the ventral premotor cortex and inferior parietal lobe, but the same areas also differentiated between the two groups of experts. Ballet dancers had more activation in the AON when they watched ballet than capoeira videos, while capoeira dancers' AON reacted more in the videos from their own domain of specialization. Subsequent studies found that the

premotor and parietal areas were more activated in modern (contemporary) dance experts when they watched actions that were a part of their movement repertoire than when they watched similar movements that they had not executed before (Cross, Hamilton, & Grafton, 2006).

The importance of the motor component as compared to the visual component is demonstrated in a study which compared female and male ballet dancers during the observation of female and male ballet dancing (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). Both genders spent a large amount of time observing the actions of the opposite gender, but the AON was less sensitive to the observation of movements performed by the opposite gender. A recent longitudinal study (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009) confirmed that the AON seems to be primarily influenced by motor and not visual experience. A group that trained a dance sequence only visually with video observation showed much less AON activation when observing a similar dance sequence than a group who received actual dance training involving movement. A similar conclusion is reached in a study in which basketball players were much better at predicting the fate of free throws than journalists and other expert watchers who had spent countless hours observing the game (Aglioti, Cesari, Romani, & Urgesi, 2008).

Other studies investigated motor anticipation in fast-moving sports such as football, basketball, or racket sports. The first study was on tennis (Wright, Bishop, Jackson, & Abernethy, 2010) and indicated that besides the frontal and parietal areas, parts of the AON, anticipation additionally activated the areas responsible for perception of body movements, the posterior middle and superior temporal lobe. The study on basketball (Abreu et al., 2012) involved experts and novices, who both activated the AON in a similar manner when they had to predict the direction of free throws. The differences were in the posterior temporo-occipital junction, also called the extrastriate

body area (EBA) because of its involvement in perception of body parts (Downing, Jiang, Shuman, & Kanwisher, 2001). The same AON areas and temporo-occipital areas important for body perception are found to be critical for the anticipation skill in hockey experts (Olsson & Lundström, 2013). The subsequent studies on tennis (Balser et al., 2014a, 2014b) found significantly more activation in experts' AON when they had to predict where different shots would land than in that of novices. As well as the AON, experts also activated more the cerebellum, and this area, together with the superior parietal lobe (SPL), successfully differentiated between successful (more activation) and unsuccessful predictions (less activation).

It does seem that all three main parts of the AON, the prefrontal, motor, and parietal cortex, underpin experts' anticipation. The parietal areas of the AON may, for example, integrate spatial information about different body parts. They can also receive information about the positioning of elements in the environment, such as players on a field. This information may then be sent to the (pre)motor cortex that is then simulating the most probable action that the person is going to perform. The information is most likely again exchanged with the parietal cortex, which in turn may exchange information with the prefrontal cortex to arrive at a possible course of action. Even the areas that are not nominally a part of the AON network, such as the pMTG, EBA, and cerebellum, may play a role in this interaction. The activated posterior MTG may send processed information about body motion to the parietal cortex. The cerebellum, on the other hand, is important for precise temporal sequencing of body movements, and, with its connection to both the motor and premotor areas, may provide another source for the premotor areas to simulate observed action.

A number of studies featured temporal occlusion, a standard paradigm on investigating anticipatory skill in motor experts (see Abernethy, Mann, & Farrow, Chapter 35, this volume).

It turns out that the anterior AON areas, the ventral and medial frontal areas as well as premotor areas, were activated more during early occlusion in tennis (Wright et al., 2010) and badminton experts (Wright, Bishop, Jackson, & Abernethy, 2011). In contrast, the AON areas at the back of the parietal lobe (SPL/IPL) were more activated in experts when they observed videos occluded late, than when watching the same videos occluded at an earlier point. Novices did not display this anterior–posterior differentiation between early and late occlusion activation. A helpful way to interpret these occlusion results would be to keep in mind that during the late occlusion the ball flight is available, whereas in the early occlusion there is no such information. The flight trajectory is most likely processed in the parietal areas, which would explain experts' reliance on the posterior AON areas. In contrast, such spatial information is lacking in the early occlusion condition and experts are forced to make predictions based on the observed kinetic information. They simulate the motion themselves, which would explain the activation of the motor and premotor areas. The frontal areas would then become engaged for the final decision.

If anticipation based on kinetic information is essential for understanding an opponent's next step in sports, then deception, such as covering up body cues with a series of other less obvious ones, is also an important part of the repertoire of a motor expert. A couple of studies (Bishop, Wright, Jackson, & Abernethy, 2013; Wright, Bishop, Jackson, & Abernethy, 2013) that featured a deception condition, came to the conclusion that besides the AON, the discovery of deception in the first place involves the insula and the posterior cingulate cortex, areas normally important for social interaction (Grafton, 2009). The prediction of the consequences of deception, such as where the ball is going to land, engaged more the anterior cingulate cortex (ACC), known to play an essential part in conflict resolution (Carter & van Veen, 2007), and the nucleus caudatus.

Structural Brain Changes in Motor Expertise

Some of the most drastic structural brain changes are associated with motor expertise, such as music (see Altenmüller & Furuya, Chapter 29, this volume). Studies involving other motor activities also found significant differences in experts' brain structure. Basketball players, for example, have increased gray matter in parts of the cerebellum and striatum (Park et al., 2009). Similarly, badminton players have a larger cerebellum as well as more pronounced connections between the frontal and parietal areas (Di et al., 2012). Golf players, who also require skilled hand and arm movements, have enlarged premotor areas as well as motor-related regions in the frontal and parietal lobes (Jäncke, Koeneke, Hoppe, Rominger, & Hänggi, 2009). Other motor activities like karate require skilled coordination between arms and legs. This is reflected in an increased cerebellum and primary motor cortex among karate specialists (Roberts, Bain, Day, & Husain, 2013). In the studies of typists, the more experienced they were (and thus the better they were at typing), the more gray matter they had in the SMA, prefrontal cortex, as well as cerebellum (Cannonieri, Bonilha, Fernandes, Cendes, & Li, 2007). Power athletes (e.g. sprinters and jumpers), who require quick foot movement for their performance, have a larger anterior part of the cerebellum, an area important for regulating motor speed performance, than endurance athletes, who do not require such quick foot movement (Wenzel, Taubert, Ragert, Krug, & Villringer, 2014).

Conclusions

We have seen that expertise changes the functional and structural properties of the brain. In all cases there is a close connection between the cognitive mechanisms that enable experts' outstanding performance and the way that the brain adapts to the cognitive demands of expertise. One of the main recurring themes is the importance of domain-

specific knowledge stored in LTM for experts' performance. The kind of knowledge that is employed for the performance dictates the brain areas involved in a particular kind of expertise. This may involve the infero-temporal areas in visual expertise, parietal areas in cognitive expertise, and (pre)frontal areas in motor expertise. The lack of domain-specific knowledge in novices is the main reason why their strategies are vastly different from those of experts who rely on such knowledge. Given the complexities associated with retrieval of this knowledge and its influence on other cognitive functions such as attention and perception, it is not surprising that associated neural changes in the brain are more extensive in experts than in novices. The demand and complexity that the brain is experiencing when implementing experts' strategies may also explain the common bilateral activation patterns in many expertise studies. The areas needed for the execution of certain cognitive processes are usually lateralized to one hemisphere, but the brain recruits the same areas on the opposite hemisphere when it needs to share the sudden increase in the computational burden (Weissman & Banich, 2000). The characteristic engagement of the additional brain areas in the opposite hemisphere by experts is dubbed the *double take of expertise* (Bilalić, 2016; 2017; Bilalić, Kiesel, et al., 2011; Bilalić et al., 2012). It is a hallmark of the neural implementation of expertise that reminds us that the brain changes associated with expertise are impossible to understand if the cognitive mechanisms involved in experts' strategies are not taken into account.

References

- Abreu, A. M., Macaluso, E., Azevedo, R. T., Cesari, P., Urgesi, C., & Aglioti, S. M. (2012). Action anticipation beyond the action observation network: A functional magnetic resonance imaging study in expert basketball players. *European Journal of Neuroscience*, 35, 1646–1654.

- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, 11, 1109–1116.
- Amidzic, O., Riehle, H. J., Fehr, T., Wienbruch, C., & Elbert, T. (2001). Pattern of focal gamma-bursts in chess players. *Nature*, 412, 603.
- Atherton, M., Zhuang, J., Bart, W. M., Hu, X., & He, S. (2003). A functional MRI study of high-level cognition. I. The game of chess. *Cognitive Brain Research*, 16, 26–31.
- Balser, N., Lorey, B., Pilgramm, S., Naumann, T., Kindermann, S., Stark, R., . . . & Munzert, J. (2014a). The influence of expertise on brain activation of the action observation network during anticipation of tennis and volleyball serves. *Frontiers in Human Neuroscience*, 8.
- Balser, N., Lorey, B., Pilgramm, S., Stark, R., Bischoff, M., Zentgraf, K., . . . & Munzert, J. (2014b). Prediction of human actions: Expertise and task-related effects on neural activation of the action observation network. *Human Brain Mapping*, 35, 4016–4034.
- Bartlett, J., Boggan, A. L., & Krawczyk, D. C. (2013). Expertise and processing distorted structure in chess. *Frontiers in Human Neuroscience*, 7, 825.
- Bilalić, M. (2016). Revisiting the role of the Fusiform Face Area (FFA) in expertise. *Journal of Cognitive Neuroscience*, 28, 1345–1357.
- Bilalić, M. (2017). *The neuroscience of expertise*. Cambridge University Press.
- Bilalić, M., Grottenhaler, T., Nägele, T., & Lindig, T. (2016). The faces in radiological images: Fusiform face area supports radiological expertise. *Cerebral Cortex*, 26, 1004–1014.
- Bilalić, M., Kiesel, A., Pohl, C., Erb, M., & Grodd, W. (2011). It takes two: Skilled recognition of objects engages lateral areas in both hemispheres. *PLoS ONE*, 6, e16202.
- Bilalić, M., Langner, R., Erb, M., & Grodd, W. (2010). Mechanisms and neural basis of object and pattern recognition: A study with chess experts. *Journal of Experimental Psychology: General*, 139, 728–742.
- Bilalić, M., Langner, R., Ulrich, R., & Grodd, W. (2011). Many faces of expertise: Fusiform face area in chess experts and novices. *Journal of Neuroscience*, 31, 10206–10214.
- Bilalić, M., Turella, L., Campitelli, G., Erb, M., & Grodd, W. (2012). Expertise modulates the neural basis of context dependent recognition of objects and their relations. *Human Brain Mapping*, 33, 2728–2740.
- Binet, A. (1894). *Psychologie des grands calculateurs et joiers d'échecs*. Paris: Hachette.
- Bishop, D. T., Wright, M. J., Jackson, R. C., & Abernethy, B. (2013). Neural bases for anticipation skill in soccer: An fMRI study. *Journal of Sport & Exercise Psychology*, 35, 98–109.
- Buschhüter, D., Smitka, M., Puschmann, S., Gerber, J. C., Witt, M., Abolmaali, N. D., & Hummel, T. (2008). Correlation between olfactory bulb volume and olfactory function. *NeuroImage*, 42, 498–502.
- Busey, T. A., & Vanderkolk, J. R. (2005). Behavioral and electrophysiological evidence for configural processing in fingerprint experts. *Vision Research*, 45, 431–448.
- Calvo-Merino, B. (2004). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, 15, 1243–1249.
- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, 16, 1905–1910.
- Campitelli, G., Gobet, F., Head, K., Buckley, M., & Parker, A. (2007). Brain localization of memory chunks in chessplayers. *International Journal of Neuroscience*, 117, 1641–1659.
- Campitelli, G., Gobet, F., & Parker, A. (2005). Structure and stimulus familiarity: A study of memory in chess-players with functional magnetic resonance imaging. *Spanish Journal of Psychology*, 8, 238–245.
- Cannonieri, G. C., Bonilha, L., Fernandes, P. T., Cendes, F., & Li, L. M. (2007). Practice and perfect: Length of training and structural brain changes in experienced typists. *Neuroreport*, 18, 1063–1066.
- Carter, C. S., & van Veen, V. (2007). Anterior cingulate cortex and conflict detection: An update of theory and data. *Cognitive, Affective & Behavioral Neuroscience*, 7, 367–379.

- Cagriota-Scanderbeg, A., Hagberg, G. E., Cerasa, A., Comitteri, G., Galati, G., Patria, F., . . . & Frackowiak, R. (2005). The appreciation of wine by sommeliers: A functional magnetic resonance study of sensory integration. *NeuroImage*, 25, 570–578.
- Chase, W. G., & Simon, H. A. (1973). Perception in chess. *Cognitive Psychology*, 4, 55–81.
- Cross, E. S., Hamilton, A. F. de C., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, 31, 1257–1267.
- Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. de C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex*, 19, 315–326.
- de Groot, A. (1978). *Thought and choice in chess* (2nd edn.). The Hague: Mouton. (Original work published 1946)
- Di, X., Zhu, S., Jin, H., Wang, P., Ye, Z., Zhou, K., . . . & Rao, H. (2012). Altered resting brain function and structure in professional badminton players. *Brain Connectivity*, 2, 225–233.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293, 2470–2473.
- Duan, X., He, S., Liao, W., Liang, D., Qiu, L., Wei, L., . . . & Chen, H. (2012). Reduced caudate volume and enhanced striatal-DMN integration in chess experts. *NeuroImage*, 60, 1280–1286.
- Duan, X., Long, Z., Chen, H., Liang, D., Qiu, L., Huang, X., . . . & Gong, Q. (2014). Functional organization of intrinsic connectivity networks in Chinese-chess experts. *Brain Research*, 1558, 33–43.
- Duchaine, B., & Yovel, G. (2015). A revised neural framework for face processing. *Annual Review of Vision Science*, 1, 393–416.
- Epstein, R. A. (2008). Parahippocampal and retrosplenial contributions to human spatial navigation. *Trends in Cognitive Sciences*, 12, 388–396.
- Ericsson, K. A., Krampe, R. T., & Tesch-Römer, C. (1993). The role of deliberate practice in the acquisition of expert performance. *Psychological Review*, 100, 363–406.
- Frank, M. C., & Barner, D. (2012). Representing exact number visually using mental abacus. *Journal of Experimental Psychology: General*, 141, 134–149.
- Frasnelli, J., Lundström, J. N., Boyle, J. A., Djordjevic, J., Zatorre, R. J., & Jones-Gotman, M. (2010). Neuroanatomical correlates of olfactory performance. *Experimental Brain Research*, 201, 1–11.
- Gobet, F., Lane, P. C. R., Croker, S., Cheng, P. C. H., Jones, G., Oliver, I., & Pine, J. M. (2001). Chunking mechanisms in human learning. *Trends in Cognitive Sciences*, 5, 236–243.
- Goldstein, R., Almenberg, J., Dreber, A., Emerson, J. W., Herschkowitsch, A., & Katz, J. (2008). Do more expensive wines taste better? Evidence from a large sample of blind tastings. *Journal of Wine Economics*, 3, 1–9.
- Grafton, S. T. (2009). Embodied cognition and the simulation of action to understand others. *Annals of the New York Academy of Sciences*, 1156, 97–117.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, 41, 1409–1422.
- Hadjikhani, N., & de Gelder, B. (2002). Neural basis of prosopagnosia: An fMRI study. *Human Brain Mapping*, 16, 176–182.
- Haller, S., & Radue, E. W. (2005). What is different about a radiologist's brain? *Radiology*, 236, 983–989.
- Hanakawa, T., Honda, M., Okada, T., Fukuyama, H., & Shibasaki, H. (2003). Neural correlates underlying mental calculation in abacus experts: A functional magnetic resonance imaging study. *NeuroImage*, 19, 296–307.
- Hänggi, J., Brütsch, K., Siegel, A. M., & Jäncke, L. (2014). The architecture of the chess player's brain. *Neuropsychologia*, 62, 152–162.
- Harel, A. (2015). What is special about expertise? Visual expertise reveals the interactive nature of real-world object recognition. *Neuropsychologia*, 83, 88–99.
- Harel, A., Gilaie-Dotan, S., Malach, R., & Bentin, S. (2010). Top-down engagement modulates the neural expressions of visual expertise. *Cerebral Cortex*, 20, 2304–2318.

- Harley, E. M., Pope, W. B., Villablanca, J. P., Mumford, J., Suh, R., Mazziotta, J. C., ... & Engel, S. A. (2009). Engagement of fusiform cortex and disengagement of lateral occipital cortex in the acquisition of radiological expertise. *Cerebral Cortex*, 19, 2746–2754.
- Hu, Y., Geng, F., Tao, L., Hu, N., Du, F., Fu, K., & Chen, F. (2011). Enhanced white matter tracts integrity in children with abacus training. *Human Brain Mapping*, 32, 10–21.
- Jäncke, L., Koenke, S., Hoppe, A., Rominger, C., & Hänggi, J. (2009). The architecture of the golfer's brain. *PLoS ONE*, 4, e4785.
- Jung, W. H., Kim, S. N., Lee, T. Y., Jang, J. H., Choi, C.-H., Kang, D.-H., & Kwon, J. S. (2013). Exploring the brains of Baduk (Go) experts: Gray matter morphometry, resting-state functional connectivity, and graph theoretical analysis. *Frontiers in Human Neuroscience*, 7.
- Kalamangalam, G. P., & Ellmore, T. M. (2014). Focal cortical thickness correlates of exceptional memory training in Vedic priests. *Frontiers in Human Neuroscience*, 8.
- Krupinski, E. A. (2000). The importance of perception research in medical imaging. *Radiation Medicine*, 18, 329–334.
- Ku, Y., Hong, B., Zhou, W., Bodner, M., & Zhou, Y.-D. (2012). Sequential neural processes in abacus mental addition: An EEG and fMRI case study. *PLoS ONE*, 7, e36410.
- Kundel, H. L., & Nodine, C. F. (1975). Interpreting chest radiographs without visual search. *Radiology*, 116, 527–532.
- Kundel, H. L., Nodine, C. F., Conant, E. F., & Weinstein, S. P. (2007). Holistic component of image perception in mammogram interpretation: Gaze-tracking study. *Radiology*, 242, 396–402.
- Kupers, R., Beaulieu-Lefebvre, M., Schneider, F. C., Kassuba, T., Paulson, O. B., Siebner, H. R., & Ptito, M. (2011). Neural correlates of olfactory processing in congenital blindness. *Neuropsychologia*, 49, 2037–2044.
- Kupers, R., & Ptito, M. (2014). Compensatory plasticity and cross-modal reorganization following early visual deprivation. *Neuroscience & Biobehavioral Reviews*, 41, 36–52.
- Lu, L. H., Dapretto, M., O'Hare, E. D., Kan, E., McCourt, S. T., Thompson, P. M., ... & Sowell, E. R. (2009). Relationships between brain activation and brain structure in normally developing children. *Cerebral Cortex*, 19, 2595–2604.
- Lucan, J. N., Foxe, J. J., Gomez-Ramirez, M., Sathian, K., & Molholm, S. (2010). Tactile shape discrimination recruits human lateral occipital complex during early perceptual processing. *Human Brain Mapping*, 31, 1813–1821.
- Maguire, E. A., Frackowiak, R. S., & Frith, C. D. (1997). Recalling routes around London: Activation of the right hippocampus in taxi drivers. *Journal of Neuroscience*, 17, 7103–7110.
- 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. *Proceedings of the National Academy of Sciences USA*, 97, 4398–4403.
- Maguire, E. A., Valentine, E. R., Wilding, J. M., & Kapur, N. (2003). Routes to remembering: The brains behind superior memory. *Nature Neuroscience*, 6, 90–95.
- Maguire, E. A., Woollett, K., & Spiers, H. J. (2006). London taxi drivers and bus drivers: A structural MRI and neuropsychological analysis. *Hippocampus*, 16, 1091–1101.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, 270, 102–105.
- Melo, M., Scarpin, D. J., Amaro, E., Passos, R. B., Sato, J. R., Friston, K. J., & Price, C. J. (2011). How doctors generate diagnostic hypotheses: A study of radiological diagnosis with functional magnetic resonance imaging. *PLoS ONE*, 6, e28752.
- Morrot, G., Brochet, F., & Dubourdieu, D. (2001). The color of odors. *Brain and Language*, 79, 309–320.
- Nichelli, P., Grafman, J., Pietrini, P., Alway, D., Carton, J. C., & Miletich, R. (1994). Brain activity in chess playing. *Nature*, 369, 191.
- Olsson, C.-J., & Lundström, P. (2013). Using action observation to study superior motor performance: A pilot fMRI study. *Frontiers in Human Neuroscience*, 7, 819.

- Park, I. S., Lee, K. J., Han, J. W., Lee, N. J., Lee, W. T., Park, K. A., & Rhyu, I. J. (2009). Experience-dependent plasticity of cerebellar vermis in basketball players. *The Cerebellum*, 8, 334–339.
- Pazart, L., Comte, A., Magnin, E., Millot, J.-L., & Moulin, T. (2014). An fMRI study on the influence of sommeliers' expertise on the integration of flavor. *Frontiers in Behavioral Neuroscience*, 8.
- Pesenti, M., Zago, L., Crivello, F., Mellet, E., Samson, D., Duroux, B., . . . & Tzourio-Mazoyer, N. (2001). Mental calculation in a prodigy is sustained by right prefrontal and medial temporal areas. *Nature Neuroscience*, 4, 103–107.
- Plailly, J., Delon-Martin, C., & Royet, J.-P. (2012). Experience induces functional reorganization in brain regions involved in odor imagery in perfumers. *Human Brain Mapping*, 33, 224–234.
- Poldrack, R. A., Prabhakaran, V., Seger, C. A., & Gabrieli, J. D. (1999). Striatal activation during acquisition of a cognitive skill. *Neuropsychology*, 13, 564–574.
- Raz, A., Packard, M. G., Alexander, G. M., Buhle, J. T., Zhu, H., Yu, S., & Peterson, B. S. (2009). A slice of π : An exploratory neuroimaging study of digit encoding and retrieval in a superior memorist. *Neurocase*, 15, 361–372.
- Reingold, E. M., & Sheridan, H. (2011). Eye movements and visual expertise in chess and medicine. In S. P. Liversedge, I. D. Gilchrist, & S. Everling (eds.), *The Oxford Handbook of Eye Movements* (pp. 523–550). Oxford: University Press.
- Renier, L., Cuevas, I., Grandin, C. B., Dricot, L., Plaza, P., Lerens, E., . . . & De Volder, A. G. (2013). Right occipital cortex activation correlates with superior odor processing performance in the early blind. *PLoS ONE*, 8, e71907.
- Rennig, J., Bilalić, M., Huberle, E., Karnath, H.-O., & Himmelbach, M. (2013). The temporo-parietal junction contributes to global gestalt perception: Evidence from studies in chess experts. *Frontiers in Human Neuroscience*, 7, 513.
- Richler, J., Palmeri, T. J., & Gauthier, I. (2012). Meanings, mechanisms, and measures of holistic processing. *Frontiers in Psychology*, 3, 553.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Roberts, R. E., Bain, P. G., Day, B. L., & Husain, M. (2013). Individual differences in expert motor coordination associated with white matter microstructure in the cerebellum. *Cerebral Cortex*, 23, 2282–2292.
- Rombaux, P., Huart, C., De Volder, A. G., Cuevas, I., Renier, L., Duprez, T., & Grandin, C. (2010). Increased olfactory bulb volume and olfactory function in early blind subjects. *NeuroReport*, 21, 1069–1073.
- Ross, D., Tamber-Rosenau, B., Palmeri, T., Zhang, J., Xu, Y., & Gauthier, I. (2015). High resolution fMRI reveals holistic car representations in the anterior FFA of car experts. *Journal of Vision*, 15, 614.
- Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *NeuroImage*, 39, 1959–1979.
- Sadeh, B., Podlipsky, I., Zhdanov, A., & Yovel, G. (2010). Event-related potential and functional MRI measures of face-selectivity are highly correlated: A simultaneous ERP-fMRI investigation. *Human Brain Mapping*, 31, 1490–1501.
- Seubert, J., Freiherr, J., Frasnelli, J., Hummel, T., & Lundstrom, J. N. (2013). Orbitofrontal cortex and olfactory bulb volume predict distinct aspects of olfactory performance in healthy subjects. *Cerebral Cortex*, 23, 2448–2456.
- Shannon, C. F. (1950). Programming a computer for playing chess. *Philosophical Magazine*, 41. http://archive.computerhistory.org/projects/chess/related_materials/text/2-0%20and%202-1.Programming_a_computer_for_playing_chess.shanon/2-0%20and%202-1.Programming_a_computer_for_playing_chess.shanon.062303002.pdf.
- Stilla, R., Deshpande, G., LaConte, S., Hu, X., & Sathian, K. (2007). Posteromedial parietal cortical activity and inputs predict tactile spatial acuity. *Journal of Neuroscience*, 27, 11091–11102.

- Stilla, R., & Sathian, K. (2008). Selective visuo-haptic processing of shape and texture. *Human Brain Mapping*, 29, 1123–1138.
- Swenson, R. G. (1980). A two-stage detection model applied to skilled visual search by radiologists. *Attention, Perception, & Psychophysics*, 27, 11–16.
- Tanaka, S., Michimata, C., Kaminaga, T., Honda, M., & Sadato, N. (2002). Superior digit memory of abacus experts: An event-related functional MRI study. *Neuroreport*, 13, 2187.
- Tanaka, S., Seki, K., Hanakawa, T., Harada, M., Sugawara, S. K., Sadato, N., . . . & Honda, M. (2012). Abacus in the brain: A longitudinal functional MRI study of a skilled abacus user with a right hemispheric lesion. *Frontiers in Psychology*, 3.
- Thompson, P. (1980). Margaret Thatcher: A new illusion. *Perception*, 9, 483–484.
- Turella, L., Wurm, M. F., Tucciarelli, R., & Lingnau, A. (2013). Expertise in action observation: Recent neuroimaging findings and future perspectives. *Frontiers in Human Neuroscience*, 7, 637.
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9, 445–453.
- Wan, X., Nakatani, H., Ueno, K., Asamizuya, T., Cheng, K., & Tanaka, K. (2011). The neural basis of intuitive best next-move generation in board game experts. *Science*, 331, 341–346.
- Wan, X., Takano, D., Asamizuya, T., Suzuki, C., Ueno, K., Cheng, K., . . . & Tanaka, K. (2012). Developing intuition: Neural correlates of cognitive-skill learning in caudate nucleus. *Journal of Neuroscience*, 32, 17492–17501.
- Weissman, D. H., & Banich, M. T. (2000). The cerebral hemispheres cooperate to perform complex but not simple tasks. *Neuropsychology*, 14, 41–59.
- Wenzel, U., Taubert, M., Ragert, P., Krug, J., & Villringer, A. (2014). Functional and structural correlates of motor speed in the cerebellar anterior lobe. *PLoS ONE*, 9, e96871.
- Wong, Y. K., & Gauthier, I. (2010). A multimodal neural network recruited by expertise with musical notation. *Journal of Cognitive Neuroscience*, 22, 695–713.
- Woollett, K., & Maguire, E. A. (2011). Acquiring “the knowledge” of London’s layout drives structural brain changes. *Current Biology*, 21, 2109–2114.
- Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2010). Functional MRI reveals expert–novice differences during sport-related anticipation. *Neuroreport*, 21, 94–98.
- Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2011). Cortical fMRI activation to opponents’ body kinematics in sport-related anticipation: Expert–novice differences with normal and point-light video. *Neuroscience Letters*, 500, 216–221.
- Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2013). Brain regions concerned with the identification of deceptive soccer moves by higher-skilled and lower-skilled players. *Frontiers in Human Neuroscience*, 7, 851.
- Yin, L.-J., Lou, Y.-T., Fan, M.-X., Wang, Z.-X., & Hu, Y. (2015). Neural evidence for the use of digit-image mnemonic in a superior memorist: An fMRI study. *Frontiers in Human Neuroscience*, 9.

PROOF