Brain Localisation of Memory Chunks in Chessplayers

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Abstract

Chess experts store domain-specific representations in their long-term memory; due to the activation of such representations, they perform with high accuracy in tasks that require the maintenance of previously seen information. Chunk-based theories of expertise (chunking theory: Chase & Simon, 1973; template theory: Gobet & Simon, 1996) state that expertise is acquired mainly by the acquisition and storage in long-term memory of familiar chunks that allow quick recognition. We tested some predictions of these theories by using fMRI while chessplayers performed a recognition memory task. These theories predict that chessplayers access long-term memory chunks of domain-specific information, which are presumably stored in the temporal lobes. We also predicted that the recognition memory tasks would activate working memory areas in the frontal and parietal lobes. These predictions were supported by the data.

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Brain Localisation of Memory Chunks in Chessplayers

Chase and Simon's (1973) seminal study of cognitive processes in chessplayers has had a strong impact in cognitive psychology. Their research spawned several studies in which chess was used successfully as a research tool for studying cognitive processes such as perception, memory and decision making (see Charness, 1992; Gobet, De Voogt, & Retschitzki, 2004, and Saariluoma, 1995 for reviews).

One of the paradigmatic results obtained in this line of research is that chess experts are able to reconstruct with high accuracy a game position that had been shown for only a few seconds (Chase & Simon, 1973; Gobet & Simon, 2000). However, when the pieces are randomly placed throughout the board, experts perform only slightly better than novices (Gobet & Simon, 2000). Chunk-based theories of expertise (chunking theory: Chase & Simon, 1973; template theory: Gobet & Simon, 1996) account for these results by proposing that, during study and practice, experts store domain-specific "chunks" (perceptual patterns that can be used as units of meaning) in their long-term memory. When this practice becomes serious and continuous, some of the chunks evolve into more complex structures called "templates," consisting of core information supplemented with slots in which more information (perceptual or abstract) can be added (Gobet & Simon, 1996). Evidence for chunks and templates stored in long-term memory as the building blocks of chess expertise originates from behavioural studies (Chase & Simon, 1973; Gobet & Simon, 1996) and computational simulations (Gobet & Simon, 2000). Chunk-based theories of expertise are generalizable to other domains of expertise such as computer programming, medical diagnosis and engineering (Gobet et al., 20001; Simon & Gobet, 2000).

Since chess has proven to be successful as a research tool to study cognitive processes, it is surprising that only a handful of studies have been done in cognitive neuroimaging with this game. Nichelli et al. (1994) asked chessplayers to perform simple chess tasks while brain activity was monitored with a PET scanner; Onofrj (1995) performed a SPECT study in which they asked players to solve a chess problem; Amizdic, Riehle, Fehr, Wienbruch and Elbert (2001) asked participants, ranging from strong grandmasters to class B players (see Methods for an explanation of chess skill levels), to play a game against a computer while they were scanned using a gamma burst technique; and Atherton, Zhuang, Bart, Hu and Sheng (2003) carried out an fMRI study in which players had to solve a chess problem. The results of these studies suggest that, when players had to solve a problem or play a game, they activated frontal and parietal areas. Finally, Campitelli, Gobet and Parker (2005) used fMRI in order to compare chessplayers with non-chessplayers in a memory task using chess positions and displays made of geometrical shapes.

In the present study, we used chess as a tool to investigate the neural substrates of working and long-term memory, and, more specifically, the localisation of domain-specific chunks in long-term memory. We did this by performing two types of comparisons. First, we compared the brain activity of chessplayers performing a recognition memory task with chess stimuli to that of the same players performing a similar task with unfamiliar non-chess stimuli (in order to identify long-term domain-specific chunks). Second, we compared the brain activity of players performing a recognition memory task with chess stimuli to that of the same players performing a perceptual-motor control task with the same chess stimuli (in order to identify brain activity related to working memory). It is well established (Britton & Tesser, 1982; Chase & Simon, 1973; Gobet, 1998) that chessplayers automatically

activate chunks in long-term memory when perceiving familiar positions. Therefore, the added value of using chessplayers to study memory is that we can be confident that the players are using their long-term memory chunks, whereas in normal studies the use of long-term memory or working memory is assumed by the researcher as a function of the task used. For example, chessplayers can perform a so-called "working memory task" such as a delayed-match-to-sample task and a so-called "long-term memory task" such as a recall task, and in both they would access chunks that have been stored for a long time (i.e., long-term memory chunks). This is well established because their performance diminishes when non-domain-specific stimuli are used, regardless of the task. To our knowledge, this is the first study that investigates the brain localisation of long-term memory chunks in experts.

Previous studies both in cognitive neuroimaging in humans and single-cell recording in non-human primates have investigated the brain areas involved in working memory and long-term memory. There is evidence supporting the hypothesis that the ventral areas of the temporal lobe (fusiform gyrus and parahippocampal gyrus) are involved in the storage of familiar patterns in long-term memory (Desimone, Albright, Gross, & Bruce, 1984; Gross, 1992; Logothetis, Pauls & Poggio, 1995; Stark & Squire, 2000; Tanaka, 1993) whilst substantial evidence supports the role of the dorso-lateral prefrontal cortex and parietal lobes in working memory (Fuster, 1998, 2000; Goldman-Rakic, 1998). (But see Cabeza & Nyberg, 2000, for studies relating the dorso-lateral prefrontal cortex and parietal lobes to other memory processes, including episodic memory processes such as storage and retrieval.)

We submitted 5 skilled chessplayers to a recognition memory task while brain images were obtained using fMRI.[1] We hypothesized that players would access their long-term memory chunks automatically when chess stimuli were presented, and that this would activate long-term memory areas in the fusiform gyrus and parahippocampal gyrus.

Methods

Participants

Five right-handed healthy chessplayers with normal vision participated in the experiment. Informed consent was obtained from each subject. The mean age of the participants was 24.6 years (sd = 8.0). The players were recruited from Nottinghamshire chess clubs and from the University of Nottingham chess club. The mean in Elo rating points (Elo, 1978) was 1971 (range 1750-2200). The Elo system rates chessplayers from intermediate to world-champion level. Players with more than 2200 points are considered masters; players between 2000 and 2200 are classified as candidate masters; players between 1800 and 2000 are considered class A level players; chessplayers between 1600 and 1800 are considered class B level players, etc. The World Chess Federation awards players with titles; usually players with more than 2400 are international masters and players with more than 2500 are grandmasters.

Originally, seven players took part in the experiment; the data of two of the players were discarded because of failure to fulfil the motion criterion (see below). Ethical approval was obtained from the School of Psychology, University of

[1] We did not include a control group made of non-chess players, as their lack of knowledge of the game implies that they do not have chess chunks, which would make comparisons with chess players difficult to interpret.

Nottingham ethics committee. Regulations of the Sir Peter Mansfield Magnetic Resonance Centre, University of Nottingham, were followed.

Task and stimuli

All the blocks of all the conditions had the same structure (see Figure 1). Each block started with a fixation cross which remained on screen for 12.5 s. Following the fixation cross, a sample stimulus was presented for 6.5 s. After a 2-s delay, a series of 7 test stimuli of the same type appeared sequentially (i.e., if the sample stimulus was a scene, all the test stimuli were scenes). Each of the seven test stimuli was presented for 3 s with an inter-stimulus interval of 1 s. The task consisted of deciding whether the test stimuli matched the sample stimulus or not, by pressing the left and right buttons, respectively. The participants had to respond within the 3 seconds during which the test stimuli were on the screen.

INSERT FIGURE 1 ABOUT HERE

INSERT FIGURE 2 ABOUT HERE

There were 4 conditions: game, random, scene and dot (see Figure 2). In the first three conditions, the task was the one explained above, the only difference between the conditions being the type of stimuli. The dot condition was a perceptual-motor control for the game condition. In the dot condition the block structure was the same as that of the other conditions, but the task was different. The sample stimulus consisted of a chess position with a black dot in one of the middle squares of the board. The test stimuli were also chess positions; some of them had a black dot and some others did not. The task consisted of pressing the left button of the button box if

there was a black dot and the right button if there was no black dot. Note that we deliberately chose simple tasks so that the conditions are of similar difficulty.

In the game and dot conditions, the stimuli were the right half of a grey-scale chessboard (4 x 8 squares) with black and white chess pieces forming a pattern resembling that of a game position. Half boards, instead of full boards, were used in order to restrict the number of eye movements. Saariluoma (1994) has shown that players can recognize chunks within a quadrant of the board even when the location of the pieces on the adjacent quadrants has been randomised; thus, it is unlikely that the use of half boards negatively affected the access to LTM chunks. In the random condition, the pieces were haphazardly distributed throughout the board. All the positions in these conditions contained 16 pieces (8 ± 1 white and 8 ± 1 black). In the scene condition, the stimuli were a grey-scale background with ellipses and different types of black and white shapes (2 triangles, 2 squares, 2 rhombuses, and 2 circles).

Forty-four blocks (11 blocks of each condition) were pseudo-randomly presented. The number of test stimuli matching the sample within each block varied from 2 to 4, with an average of 3. The test stimuli that did not match the sample had the same number of pieces (or shapes) as the sample stimulus, the only difference being their location. Twelve stimuli were used for each condition, each taking the role of sample stimulus only once. The chess positions consisted of middle game positions with familiar configurations of pieces.

fMRI imaging parameters and analyses

The experiment was carried out in a 3-Tesla scanner with a TEM Nova medical head-coil at the University of Nottingham Sir Peter Mansfield Magnetic Resonance Centre. The stimuli had a vertical visual angle of 16º and a horizontal visual angle of 8º. Participants wore prism glasses in order to see the stimuli.

Images of the whole brain were obtained. Twenty-two coronal slices were obtained at a rate of 136 ms each, hence the TR was 2,992 ms. The images were T2* weighted Echo-Planar images (EPIs). The size of the images was 64 x 64 voxels. The voxel size was 3 mm x 3 mm in-plane, and the slice thickness was 9 mm. The experimental paradigm started 12 s after the scanner started recording, in order to allow for magnetic saturation effects. The 4 volumes obtained during these 12 s were discarded.

The processing of the data was carried out with Statistical Parametric Mapping (SPM99) developed by Friston et al. (1995). The software Talairach Daemon (Lancaster, Summerln, Rainey, Freitas, & Fox, 1997) was used to obtain Brodmann areas given Talairach coordinates as input. Realignment, spatial normalization and spatial smoothing were performed in SPM99. The data from subjects who translated their heads more than 5 mm in any direction or rotated their heads more than 5º in any of the axes were discarded from further analysis. For the spatial smoothing, an 8 mm x 8 mm x 8 mm Gaussian kernel was utilized. A high-pass temporal filter of 131 s. was used and the hemodynamic response function was chosen as a low-pass temporal filter. Since the accuracy rate was above 90% we used all the epochs for the analysis.

We performed a fixed-effects analysis. A box-car function convolved with a hemodynamic response function was used to model the data. Three contrasts were planned: game > dot, game > scene and game > random. SPM maps of *t* values were obtained after correction for multiple comparisons, showing $p < .05$. Only the clusters of more than 5 voxels were reported.

Game was the key condition, and the other three conditions controlled for different aspects of the task in the game condition. In the principal task, participants were supposed to perceive the stimulus; recognise it as a chess pattern; encode it;

maintain a representation of it in memory during the delay and during the presentation of the test stimuli; match the test stimuli to this representation; decide whether they are the same or not; and finally press a button. In the dot condition, participants were required to carry out only the perceptual and motor aspects of the task explained above; therefore, the subtraction game > dot captures the working-memory components of the task. In the scene condition, participants were required to carry out the same processes as in the game condition, but the type of stimuli differed. The subtraction of brain activity in the scene condition from that in the game condition would show the brain activity due to access to long-term memory areas. The random condition included the same type of task and stimuli as the game condition, but the meaningfulness and the typicality of the stimuli varied. Thus, the contrast game > random afforded us the possibility of investigating the brain location of familiar perceptual patterns. Because we had specific theoretical predictions, we limited the analysis to uni-directional contrasts; this also had the advantage of keeping the number of comparisons reasonably low.

Results

Behavioural data

The players performed very accurately (above 90% correct). The mean percentage correct and standard error (±) were: 97.1 ± 2.6. The mean percentage correct and the standard error for the four conditions were the following: game, 94.4 ± 1.3; random, 98.4 ± 0.8; scene, 97.6 ± 0.8; and dot, 98.2 ± 0.9. We carried out a one-way ANOVA for related samples and there was a significant effect ($F(3,12) = 4.25$; $p < .05$). The only significant post-hoc difference was that between game and random.

The overall mean reaction time (in milliseconds) and standard error were the following: 1164 ± 40. The mean reaction time and standard error for the four

conditions were the following: game, 1274 ± 80; random, 1202 ± 77; scene, 1149 ± 69; and dot, 1031 ± 75. A one-way ANOVA for related samples showed a significant effect ($F(3,12) = 12.1$; $p < .001$). The post-hoc comparisons indicated that players were faster in the dot condition than in both the game and random conditions, and that they were slower in the game condition than in the scene condition.

The effect of condition in accuracy, although significant, is quite small (a difference of only 4% between the game and random conditions). However, the differences in reaction time were considerable. It is not surprising that the dot condition was performed faster because it was computationally simpler than the other conditions. The difference between the game and scene conditions may be explained by the fact that players may automatically think of moves in the chess positions, moves that are not relevant for the task at hand, which may have slowed down the response. In support for this hypothesis, De Groot and Gobet (1996) report that, in a memory recall task, players often mentioned possible moves and plans, although the task was specifically presented as a memory task. In addition, Britton and Tesser (1982) have shown that engagemenf of chess knowledge slows down performance in a simultaneous reaction task.

Brain imaging data

Statistical parametrical maps were obtained of the contrasts game > dot, game > scene, and game > random. The first contrast assessed differences in working memory processes and the last two contrasts showed the activations due to different aspects of long-term memory.

Contrast game > dot: Working Memory.

The contrast game > dot (see Figure 3 and Table 1) reveals the brain activity due to the working-memory aspects of the game condition. A strong prediction of

chunk-based theories for this contrast is that it would activate working memory areas (i.e., dorso-lateral prefrontal and parietal areas) but not temporal areas. The access to domain-specific long-term memory patterns in the temporal lobe would occur in the game but also in the dot condition, due to the automatic character of pattern recognition (Britton & Tesser, 1982; Chase & Simon, 1973; Gobet, 1998); therefore, no activation should be found in the temporal lobe. However, the game condition requires the maintenance of the sample stimulus that would cause the activation of working-memory areas. The results support this prediction by showing the main activation in the dorso-lateral prefrontal and parietal lobes and little activation in the temporal lobes.

INSERT FIGURE 3 ABOUT HERE

INSERT TABLE 1 ABOUT HERE

There were 576 voxels activated in the players. Activations were found in BA37 (left occipital and bilateral temporal fusiform gyri), BA19 (bilateral superior occipital gyri), and BA7 (right superior parietal lobule and precunei). In the prefrontal lobes the activations were in BA46 (left middle frontal gyrus), BA45 (right middle frontal gyrus) and BA9 (inferior frontal gyrus). (In all cases, $p < .05$ with correction for multiple comparisons.)

Contrast game > scene: Long-term memory.

The contrast game > scene (see Table 2 and Figure 4) reveals the activations due to chess-specific features (i.e., chess pieces and board, and typical patterns of pieces). Chunk-based theories predict activation in areas that store long-term memory patterns (i.e., fusiform gyrus and parahippocampal gyrus) in chessplayers (because the

representations of the typical chess configurations will be activated) but not in working-memory areas (because in both conditions working-memory areas would be activated). Following our prediction, players showed activity in temporal lobe areas including the fusiform gyrus, the parahippocampal gyrus, and inferior temporal gyrus. On the other hand, they also showed unexpected activations in the precunei, the posterior cingulate, and the supramarginal gyrus.

INSERT FIGURE 4 ABOUT HERE

INSERT TABLE 2 ABOUT HERE

Contrast game > random: Long-term memory.

In the contrast game > random, chunk-based theories predict activity in areas that store long-term memory patterns (hence, in fusiform and parahippocampal gyri), but to a lesser extent than the contrast game > scene. This is because in the present contrast, only the typicality of the positions differs between conditions. We found activation only in BA37 (left parahippocampal gyrus, -28 -44 -7, $t = 5.31$).

Discussion

We investigated the neural substrates of working and long-term memory in a recognition memory task with chessplayers. The rationale of our study was that, given that chessplayers possess domain-specific chunks stored in long-term memory, the comparison of brain activity between a condition with chess stimuli and another condition with non-chess stimuli (but the same task), would be in the area where these chunks are stored. Following chunk-based theories of expertise and previous neuroscientific literature, we proposed that chessplayers would activate long-term memory chunks in the temporal lobe (i.e., fusiform and parahippocampal gyri) when presented with chess stimuli. Moreover, following the literature showing the

engagement of the dorso-lateral prefrontal and parietal lobes in working memory tasks, we expected activation in those areas in the conditions with a memory task. In terms of the contrasts of interest, we predicted brain activity in the fusiform and parahippocampal gyri in the game > scene contrast and in the game > random contrast (though, to a lesser degree in the latter), as well as activity in the dorso-lateral prefrontal, ventro-lateral prefrontal and parietal (but not temporal) lobes in the game > dot contrast.

The results supported our hypotheses. The game > dot contrast showed brain activity in the dorso-lateral prefrontal and parietal lobes and very little activation in the temporal lobes. Furthermore, the game > scene contrast showed activation in the temporal lobe and the game > random contrast showed a small cluster of brain activity in the temporal lobe. However, some results were not expected. First, given the large differences in performance found in memory recall tasks between the game and random conditions (e.g., Gobet & Simon, 2000), we expected more activation in the game > random contrast. However, we have to remember that the differences in performance between the game and random conditions were typically observed in *recall* tasks, whereas our experiment used a *recognition* task. In fact, previous experiments have shown that differences are much smaller in recognition tasks, Saariluoma (1984) finding a difference of 10% in favour of game positions and Goldin (1979) even finding a 2% advantage with random positions. Moreover, it is well known from the literature on verbal memory that, in recognition tasks, better performance is obtained with atypical words than with typical words (Kintsch, 1970). A natural continuation of our study would be to use the traditional recall task, although this may be difficult in a brain-imaging setting due to the necessity of

moving the computer mouse for placing pieces on the board, which requires numerous finger and hand movements.

Second, in the game > scene contrast, we found unexpected bilateral activation in the precunei and posterior cingulate, as well as activation in the right supramarginal gyrus. We suggest the following explanation. It is well known that there exist two visual pathways in the cortex: both start in the occipital lobe and then divide in the "where" dorsal pathway in the parietal lobe and the "what" ventral pathway in the temporal lobe (Ungerleider & Mishkin, 1982). We hypothesize that all conditions activated these pathways because of the visual nature of the task, and that they also activated motor areas due to the necessary motor response. Since all these areas were common for all the conditions, no activity was expected in these areas in the contrasts. We also hypothesize that in the game and the random conditions the activation of domain-specific long-term memory chunks in the temporal lobes was followed by the activation of the working memory areas of the dorso-lateral prefrontal and parietal lobes that, in turn, generated a feedback activation to the temporal lobes. This is similar to a proposal by Fuster (1998, 2000), who explained working memory by the feedback activation from the prefrontal lobes to the temporal lobes. This would allow a link to be generated between the domain-specific chunks already stored in long-term memory and the information held in working memory. On the other hand, we hypothesize that in the scene condition players activated the long-term memory patterns related to geometrical figures but they did not need to make a link between these patterns and areas involved in working memory; hence, the feedback mechanism just described did not take place in this case. This explanation accounts for the activation of parietal areas in the game > scene contrast, because in the game

condition (but not in the scene condition) the parietal areas generated a feedback activation to the temporal lobe.

In the present study, the network of areas recruited by chessplayers included dorso-lateral prefrontal areas BA46 (left middle frontal gyrus), and a cluster of dorsolateral and ventrolateral prefrontal areas containing BA45 and BA9 (right middle and inferior frontal gyri). In a review of brain imaging studies (Cabeza & Nyberg, 2000), BA9 was shown to be bilaterally involved in all types of working memory and in sustained attention in the right hemisphere, and BA46 was also bilaterally recruited by all kinds of working memory tasks, with emphasis on spatial working memory. Moreover, prefrontal areas were also involved in planning and executive control (Newman, Carpenter, Varma, & Just, 2003; Smith & Jonides, 1999). The pattern of activation seen in posterior areas includes a cluster in the right hemisphere in BA7 (superior parietal lobule and precuneus) and another in BA19 (superior occipital gyrus) emerged. The same was found in the left hemisphere. BA19 has been involved bilaterally in spatial working memory and problem solving tasks (Cabeza & Nyberg, 2000). Brodmann area 7 (especially the precuneus) has been shown to be involved in visual imagery (Andreasen et al., 1995) and matching targets to templates (Herath, Kinomura, & Roland, 2001). A number of voxels within BA37 were also active bilaterally: left occipital and temporal fusiform gyrus, and right temporal fusiform gyrus. The fusiform gyrus has been shown to be activated by the presentation of faces (Kanwisher, Tong, & Nakayama, 1998), and its activation increases with expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Tarr & Gauthier, 2000). Finally, supramarginal gyrus (BA39) activation was found in autobiographical memory

experiments (see Levine, 2004, for a review), and it has been suggested that this activation should reflect the imaging of movements (Levine, 2004).

We now analyze the relationship between our results and previous neuroimaging studies using chessplayers. In Amizdic et al.'s (2001) study, players ranging from intermediate players to grandmasters played a chess game against a computer while brain activity was measured. The strong players showed more activation in parietal and frontal areas relative to activation in medial temporal structures (i.e., perirhinal, entorhinal cortex and hippocampus). The intermediate players showed an equally distributed pattern of activation in the same areas. Our results also showed activation of frontal, parietal and temporal areas. Since the players who participated in our study are comparable with the average intermediate players in Amizdic et al.'s (2001) study, our results are consistent with theirs.

Onofrj et al.'s (1995) study found middle temporal and frontal activation in a problem solving and imagery task. The pattern of activation was similar to our study with the difference that Onofrj et al. did not find activity in the parietal lobe. As the authors pointed out, the fact that no parietal activation was observed was surprising due to the imagery nature of the task. One possible explanation is that they used a well-known chess position that may have been familiar to some of the players. Hence, finding the winning combination required more activation of LTM knowledge than online maintenance of information. Nichelli et al.'s (1994) study is in accord with our results in the activations found in lateral and medial parts of the occipital and parietal cortices, and also in inferior, lateral and medial parts of the left temporal lobe. Nichelli et al.'s tasks addressed colour and spatial discrimination, rule retrieval, and checkmate judgement.

Atherton et al. (2003) studied chess novices. They found a pattern of activation of parietal and prefrontal areas when they subtracted the brain activity due to a simple counting task from the brain activity due to a problem-solving task. Consistent with our explanation, when required, chessplayers use their working memory; therefore, activity in prefrontal and parietal areas is expected. Atherton et al. (2003) also investigated a hypothesis put forward by Cranberg and Albert (1988), according to which the visuospatial nature of chess suggests that it should predominantly engage the right hemisphere. However, Atherton et al. (2003) did not find any lateralization. Visual inspection of Figures 3 and 4 show that there was no lateralization in the game > dot contrast, and only a marginal right lateralization in the game > scene contrast; moreover, the game > random contrast showed a small area activated in the left hemisphere. Therefore, consistent with Atherton et al.'s (2003) study, our results do not support Cranberg and Albert's (1988) hypothesis.

Atherton et al. (2003) also investigated whether the general intelligence area (i.e., BA 45) identified by Duncan et al. (2000) was activated in their participants. They did not find activation in this area and, therefore, concluded that chess is a visuo-spatial task and not one that requires general abilities. Although we did find activation in BA45, we also think that chess is mainly a visuo-spatial ability. Indeed, Gobet, Campitelli and Waters (2003) showed that the link between chess and general intelligence is not clear-cut. In general, Duncan et al.'s (2000) claim that BA45 is the seat of general intelligence is difficult to reconcile with previous literature showing brain activity in this area in tasks that are not specifically engaging general intelligence (see Cabeza & Nyberg, 2000). Campitelli, Parker and Gobet (2005) found that non-chessplayers activated more frontal areas when they performed a memory task with chess stimuli than when they performed a memory task in which the chess

symbols were changed by geometric figures. By contrast, chessplayers did not show any differences.

In conclusion, our study aimed to find the brain localisation of experts' memory chunks. We compared chessplayers' brain activity using chess stimuli and non-chess stimuli in the same task. Moreover, we investigated working memory by comparing players' brain activity in a recognition memory task and a perceptual-motor control task. We found two clear results: activation of the frontal and parietal areas in the contrast that reflected working memory processes, and activation of temporal areas (fusiform and parahippocampal gyri) in the contrast that reflected long-term memory chunks. In addition, we found activation in the parietal lobe in the latter contrast; we explained this result in terms of feedback activation from the parietal to the temporal lobe.

The use of experts as participants is an important tool in brain imaging. Not only does it afford the possibility to study the acquisition of expertise—which is a relevant psychological phenomenon *per se*—but it also allows researchers to investigate the role of memory chunks in cognition. There is substantial evidence that chunking mechanisms play a key role in cognition in general, and in expertise in particular (Gobet et al., 2001). Understanding the biological basis of chunking is an important goal for neuroscience, and our study contributes to this goal by suggesting possible brain locations where long-term memory chunks are stored.

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Figure captions

Figure 1. Block structure.

Each block started with a fixation cross, which was displayed for 12.5 seconds; this was followed by a target stimulus, which remained on the screen for 6.5 seconds. After a 2-second delay, a series of 7 test stimuli was presented. Each stimulus remained visible for 3 seconds, with an inter-stimuli delay of 1 second. On average, 3 of the 7 test stimuli matched the target stimulus.

Figure 2. Experimental conditions.

(a) game, **(b)** random, **(c)** scene and **(d)** dot conditions. For the conditions **(a)**, **(b)** and **(c)**, after seeing a target stimulus for 6.5 seconds, the participants were presented with a series of 7 stimuli during 3 seconds each and had to decide whether each stimulus matched the target. Condition **(d)** was a perceptual-motor control condition, in which the block structure was the same as with the other conditions. Participants had to indicate whether there was a dot in each stimulus. There was no memory component in this task.

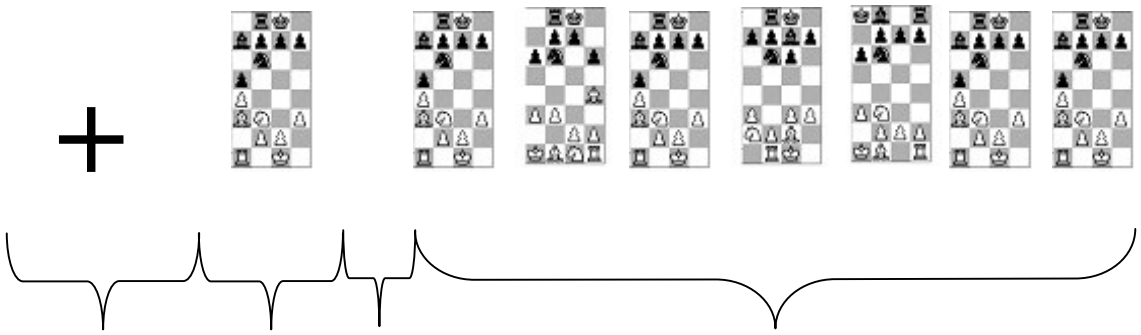
Figure 3. Brain activity of the contrast game > dot: Working memory.

The top-left image is a medial view of the left hemisphere, the top-right image is a medial view of the right hemisphere, the bottom-left image is a lateral view of the right hemisphere, and the bottom-right image is a lateral view of the left hemisphere. For more details of brain areas activated in this contrast, see **Table 1**.

Figure 4. Brain activity of the contrast game > scene: Long-term memory.

The top-left image is a medial view of the left hemisphere, the top-right image is a medial view of the right hemisphere, the bottom-left image is a lateral view of the right hemisphere, and the bottom-right image is a lateral view of the left hemisphere. For more details of brain areas activated in this contrast, see **Table 2**.

Figure 1. Block structure



FIXATION SAMPLE DELAY TEST STIMULI

12.5s 6.5s 2s (each stimulus = 3s; inter-stimulus interval = 1s)

Figure 2. Experimental conditions.

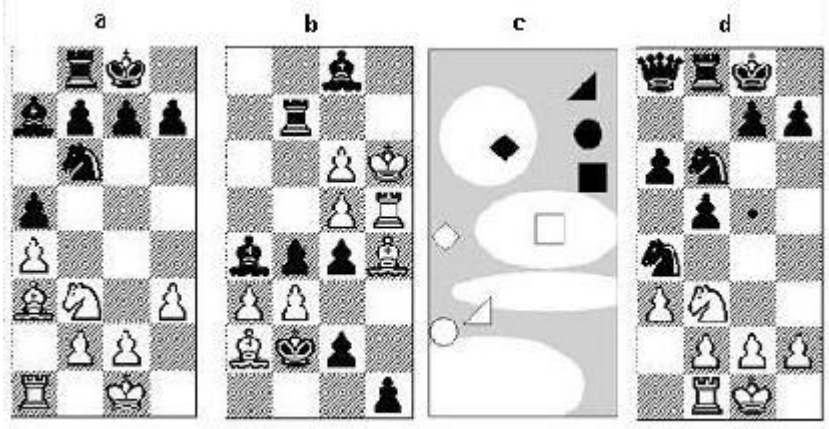


Figure 3. Contrast game > dot: Working Memory.

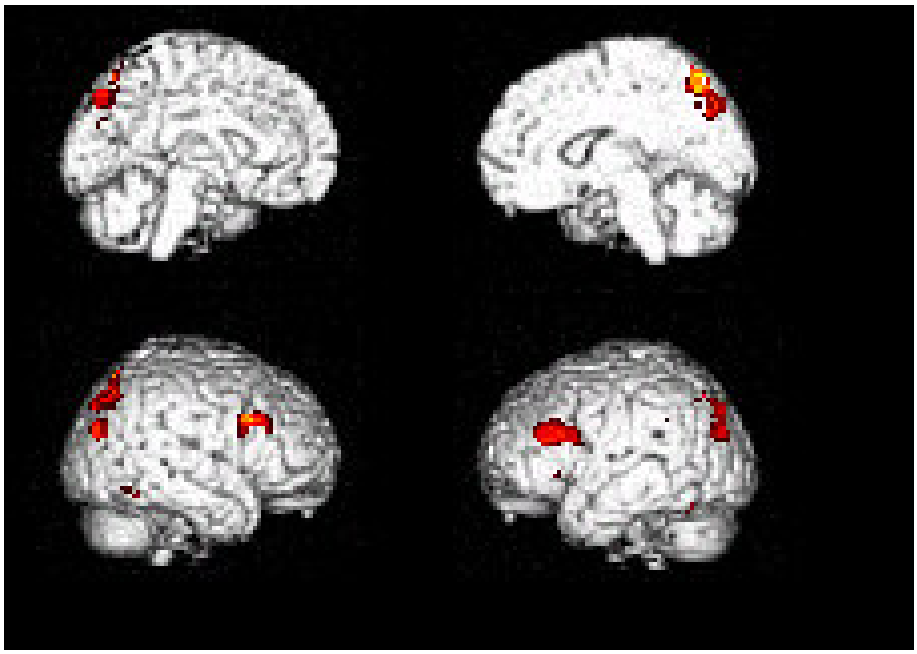


Figure 4. Contrast game > scene: Long-term memory.

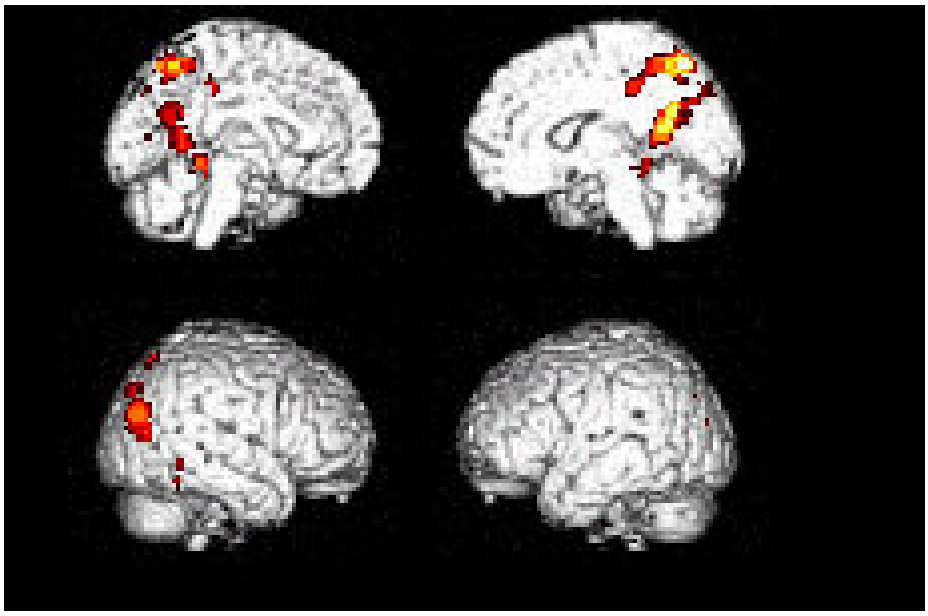


Table 1. Foci of activation of the contrast game > dot: Working memory

Vox	Hem.	Brain region	BA	t-value	Talairach		
					X	y	Z
28	L	Occipital fusiform gyrus	37	5.88	-33	-44	-10
36	R	Superior occipital gyrus	19	5.56	39	-74	26
149	L	Superior occipital gyrus	19	5.91	-27	-74	28
	L	Precuneus	7	5.48	-21	-71	37
	L	Precuneus	7	5.3	-12	-73	45
243	R	Superior parietal lobule	7	7.49	12	-64	56
	R	Precuneus	7	6.38	24	-68	42
7	L	Temporal fusiform gyrus	37	5.24	-47	-59	-17
6	R	Temporal fusiform gyrus	37	4.85	47	-53	-12
107	L	Middle frontal gyrus	46	6.07	-47	30	21
115	R	Middle frontal gyrus	45	6.76	53	22	26
	R	Inferior frontal gyrus	9	6.19	41	10	22

Note. Vox.= number of voxels in the cluster reported; Hem.= Hemisphere; BA= Brodmann area.

Table 2. Foci of activation of the contrast game > scene: Long-term memory

Vox.	Hem.	Brain region	BA	t-value	Talairach coordinates		
					x	y	Z
313	R	Precuneus	7	7.4	8	-61	55
	R	Precuneus	7	6.06	6	-44	52
	L	Precuneus	7	5.66	-6	-53	52
349	R	Posterior cingulate	31	6.88	15	-48	19
	R	Posterior cingulate	30	5.99	9	-49	11
	L	Lingual gyrus	18	6.09	-12	-52	5
7	R	Temporal fusiform gyrus	37	5.14	47	-50	-13
7	R	Inferior temporal gyrus	37	4.79	50	-47	-5
113	R	Supramarginal gyrus	39	7.8	44	-75	23
50	R	Parahippocampal gyrus	36	6.92	27	-38	-6
174	L	Parahippocampal gyrus	37	10.44	-29	-44	-8

Note. Vox.= number of voxels in the cluster reported; Hem.= Hemisphere; BA= Brodmann area.