Revisiting the Role of the Fusiform Face Area in Expertise

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Abstract

■ The fusiform face area (FFA) is considered to be a highly specialized brain module because of its central importance for face perception. However, many researchers claim that the FFA is a general visual expertise module that distinguishes between individual examples within a single category. Here, I circumvent the shortcomings of some previous studies on the FFA controversy by using chess stimuli, which do not visually resemble faces, together with more sensitive methods of analysis such as multivariate pattern analysis. I also extend the previous research by presenting chess positions, complex scenes with multiple objects, and their interrelations to chess experts and novices as well as isolated chess objects. The first experiment demonstrates that chess expertise modulated the FFA activation when chess positions were presented. In contrast, single chess objects did not produce different activation patterns among experts and novices even when the multivariate pattern analysis was used. The second experiment focused on the single chess objects and featured an explicit task of identifying the chess objects but failed to demonstrate expertise effects in the FFA. The experiments provide support for the general expertise view of the FFA function but also extend the scope of our understanding about the function of the FFA. The FFA does not merely distinguish between different exemplars within the same category of stimuli. More likely, it parses complex multiobject stimuli that contain numerous functional and spatial relations. ■

INTRODUCTION

The fusiform face area (FFA), a region in the inferotemporal cortex, plays an important role in face perception (Duchaine & Yovel, 2015; Kanwisher, McDermott, & Chun, 1997). The exact function of this brain region is however debated. On one side of the debate, there is the view that the FFA is exclusively a face-specific brain module. This view reflects the immense importance of face perception in our lives (Kanwisher & Yovel, 2006) and builds on the evolutionary assumption that a brain area can evolve to reflect exclusively the importance of a single stimulus category (Fodor, 1983). However, faces are not only crucial in our lives but also constitute one of the most often encountered, and consequently most often practiced, categories. This fact has led to the view that the FFA is in fact a general visual expertise module, not necessarily specific to faces (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). According to this expertise hypothesis, the FFA is responsible for visual individuation, that is, the ability to differentiate between different objects within any single category of stimuli. Here, I use the game of chess as a model for visual expertise to demonstrate that the FFA is indeed a general expertise module but that its function may extend beyond individuation and encompass parsing relations between elements of a complex stimulus.

There is no denying the importance of the FFA in face perception. Damage to and around the FFA results in the inability to perceive faces (Barton, 2008; Mayer & Rossion, 2007; Barton, Press, Keenan, & O'Connor, 2002), and faces commonly activate the FFA twice as much as any other stimuli (Kanwisher & Yovel, 2006). However, the heightened response to faces in the FFA could also be a consequence of our extensive experience and expertise in dealing with faces. This is the essence of the expertise hypothesis. One way to investigate this possibility is to compare the FFA response in people who have experience with certain nonface stimuli with the response in people who have less experience with the particular stimulus category. The expertise hypothesis has been tested with a number of nonface stimuli, ranging from birds (Gauthier et al., 2000), to cars (McGugin, Van Gulick, Tamber-Rosenau, Ross, & Gauthier, 2015; McGugin, Newton, Gore, & Gauthier, 2014; Gilaie-Dotan, Harel, Bentin, Kanai, & Rees, 2012; McGugin, Gatenby, Gore, & Gauthier, 2012; Xu, 2005; Grill-Spector, Knouf, & Kanwisher, 2004; Gauthier et al., 2000), butterflies (Rhodes, Byatt, Michie, & Puce, 2004), Pokémon characters (James & James, 2013), and novel object types (Gauthier et al., 1999). The results have been mixed, and their interpretation has been the focus of an extensive debate (Op de Beeck & Baker, 2010; Bukach, Gauthier, & Tarr, 2006; Kanwisher & Yovel, 2006). A factor that further complicates the interpretation is the visual similarity of the investigated stimuli with faces: Cars, birds, and even butterflies have face-like features (Kanwisher & Yovel, 2006).

An obvious way around the resemblance problem is to find stimuli that do not look like faces. Radiological

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stimuli, such as thorax x-rays, would fit the not-face-like description. Harley and colleagues (2009) demonstrated that expert and novice radiologists have similar activation levels when quickly examining x-rays for abnormalities. The experts' behavioral performance, however, was reliably correlated with the activation in the FFA, whereas the FFA activation in novices was not predictive of how well they identified abnormalities within the x-rays. Together with my colleagues (Bilalić, Grottenthaler, Nägele, & Lindig, 2016), I have recently shown that there were indeed no differences in the FFA activation between experienced radiologists and medical students during the perception of radiological stimuli when the classical univariate analysis was performed. However, when we employed the more sensitive multivariate pattern analysis (MVPA), the FFA could differentiate between radiological images and other neutral stimuli in radiologists, but the FFA in medical students was still not sensitive enough to differentiate between the stimuli within and outside specialization.

Here, I employ the MVPA on an expertise domain where the stimuli do not resemble faces—the game of chess. When looking at the chessboard, one processes both individual objects (the chess pieces) and the chess positions composed of these individual objects. Chess is particularly suitable for testing FFA's expertise hypothesis not only because hardly anyone would mistake either chess positions or chess objects for faces but also because it enables us to further extend the expertise hypothesis. Individual chess objects can, however, be differentiated, as there are six different chess object categories (see Figure 1: king, queen, bishop, knight, rook, and pawn). Because of accumulated domain-specific knowledge, expert chess players are quicker than their less-skilled peers at individualizing chess objects as well as retrieving their function (Bilalić, Kiesel, Pohl, Erb, & Grodd, 2011; Kiesel, Kunde, Pohl, Berner, & Hoffmann, 2009; Saariluoma, 1995). The real chess expertise, however, lies in using knowledge to quickly assess the gist of chess positions (Bilalić, Turella, Campitelli, Erb, & Grodd, 2012; Bilalić, Langner, Erb, & Grodd, 2010; Gobet & Simon, 1996). Unlike novices, experts do not perceive numerous chess objects as individual objects but rather as meaningful units of objects and their relations called chunks (Chase & Simon, 1973) and templates (Gobet & Simon, 1996). Given that they have previously acquired and stored numerous chunks and templates, experts can quickly perceive them in new chess positions. In this way, the previously acquired knowledge enables experts to quickly orient themselves when confronted by unfamiliar chess positions often consisting of over 20 individual objects (Bilalić, McLeod, & Gobet, 2009).

These aspects make chess an ideal domain for investigation of the FFA expertise hypothesis. Not only can we check whether the FFA is sensitive to chess expertise in the individuation process by presenting single chess objects, but also we can investigate whether perception of chess positions, considered to be the essence of chess expertise, also modulates the FFA. This would enable us to differentiate between two versions of the expertise hypothesis: one that involves recognition of individual members within a category (individuation) and another that involves perceptual processes that integrate multiple features and the relations between them. The perceptual process of automatically parsing complex multiobject environments, which is a characteristic of chess experts, bears a similarity to that found in face perception. Both processes are automatic, quick, and efficient in binding individual features into meaningful units. Indeed, our previous study (Bilalić, Langner, Ulrich, & Grodd, 2011) indicated that the FFA is expertise modulated when chess positions were presented. Although some studies confirmed the FFA's involvement in the perception of chess positions (Righi, Tarr, & Kingon, 2013), other studies

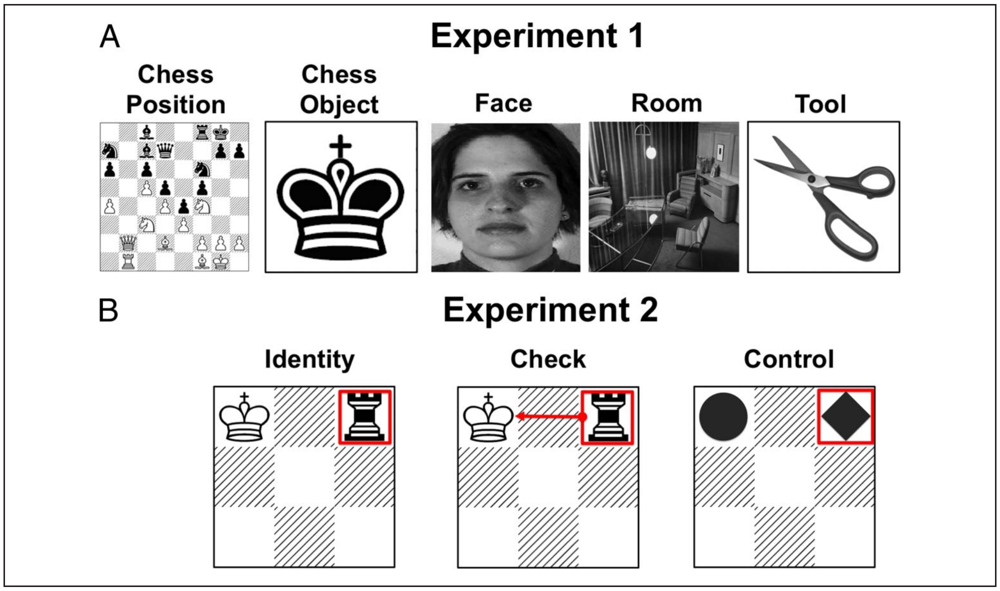

Figure 1. Stimuli. (A) Experiment 1 presented chess positions, chess objects, faces, rooms, and tools to participants who needed to identify direct repetition of two stimuli (1-back task). (B) Experiment 2 used explicit individuation task asking participants what was the presented chess object (identity), if there was check (check), and what is the geometrical shape present (control). The red color indicates the nature of the task and was not presented to the participants.

could find no differences between experts and novices when they checked their FFA responses to chess positions (Bartlett, Boggan, & Krawczyk, 2013; Krawczyk, Boggan, McClelland, & Bartlett, 2011).

Here, I extend the previous research by employing both the classical univariate fMRI analysis and the MVPA to see whether the FFA is indeed sensitive to chess expertise. I also introduce a novel manipulation, as I present not only chess positions, as was done in previous studies (Bilalić, Langner, et al., 2011), but also individual chess objects. The first experiment, in which participants passively observed the chess stimuli, demonstrates FFA modulation with respect to chess positions and an absence of modulation with respect to chess objects. In the second experiment, the FFA could not distinguish responses between chess experts and novices when they were explicitly involved in an individuation task of individual chess objects, even when the more sensitive technique MVPA was employed.

METHODS

Participants

In the first experiment, there were 16 chess experts (*M* = 25.9, *SE* = 1.6) and 19 chess novices (*M* = 29, *SE* = 1.1). The second experiment involved 12 experts (*M* = 27.2, *SE* = 1.9) and 13 novices (*M* = 28.8, *SE* = 1.2). Chess skill is measured on an interval scale called Elo (Elo, 1978) with a theoretical mean of 1500 and a standard deviation of 200. The players above 2000 rating points are considered experts, whereas the very best players in the world, grandmasters, have a rating around 2500. The experts in the first experiment had an average rating of 2061 Elo (*SE* = 133), whereas the experts in the second experiment had an average of 2140 Elo (*SE* = 119). Novice players were competent hobby players who played chess occasionally and would beat beginners without any problems. Although novices were not rated, because they did not play chess regularly (and not in chess clubs and tournaments), it is obvious that their chess skills are vastly inferior to experts. The experts were recruited in local chess clubs through the author's personal contacts. The novices were recruited via university's electronic mailing lists as well as announcements on the blackboard list. The experts were paid €30 and novices were paid €15 per hour for their participation in the experiments. All participants were right-handed. Four of the experts and one of the novices participated in other chess-related experiments (see Bilalić et al., 2012; Bilalić et al., 2010; Bilalić, Kiesel, et al., 2011; Bilalić, Langner, et al., 2011). One expert and two novices were female in the first and second experiments. There were six experts and eight novices who participated in both experiments (in different sessions conducted on different days). Written informed consent was obtained in line with the study protocol as approved by the ethics committee of Tübingen University.

Design and Procedure

Experiment 1 directly tested responses to individual chess objects and chess positions. The participants had to indicate if the current stimulus was the same as the previous one (1-back task). There were five classes of stimuli: faces, chess positions, chess objects, rooms, and tools. The face stimuli were black and white pictures of students not previously used in the localizer task (Leube, Erb, Grodd, Bartels, & Kircher, 2001). The chess stimuli were full-board positions taken from a database of four million chess games (ChessBase Mega Base 2007; ChessBase GmbH, Hamburg, Germany; www.chessbase.com) and individual chess objects taken from the same graphical software (chess positions were made out of individual pieces). Rooms were interior pictures taken from the Internet. Tools depicted single isolated everyday objects with a clear-cut function (e.g., hammer, screwdriver). The pictures of tools were taken from Brodeur, Dionne-Dostie, Montreuil, and Lepage (2010).

In Experiment 1, I presented face or chess stimuli (always upright) in blocks of five stimuli (Figure 1B). A single stimulus lasted for 2.75 sec and was followed by a mask. A baseline (gray screen with a center cross) was presented at the beginning, after each block, and at the end of the experiment for 14 sec. All four conditions were presented in each of the three runs four times (12 blocks of each condition in all runs). The physical dimensions of each stimulus were 336 × 336 mm.

Experiment 2 tested explicitly for individuation and featured four tasks. In the check task, participants indicated if the white king was attacked (i.e., placed in check) by the only black piece present. There were four different stimuli with two pieces on a 3 × 3 miniature chessboard (see Figure 1B). The white king was always on the first square of the upper left corner, whereas the identity of the other piece (knight or rook) and its location (center of the lower row or the end of the upper row) were varied. In the identity task, participants were presented with the same stimuli as in the check task, but this time, they were asked to identify the black piece presented (the white king was also presented to keep the two chess tasks visually identical). In the nonchess control task, chess pieces had been replaced by gray-colored geometrical shapes (a circle for the king; a diamond and square for the knight and rook, respectively). As in the two chess tasks, the identity (diamond or square) and position (center of the lower row or the end of the upper row) of the target stimulus were varied, and participants were asked to indicate its shape. The second control task required participants to take into account not only the shape of the geometrical figures but also whether they were on the white or black square. This control task will not be presented here because its results are essentially identical to those of the first control task. A part of the experiment was reported elsewhere (Bilalić, Kiesel, et al., 2011). The experiment reported here includes additional participants (four experts and five novices), and the individual ROI and MVPA analyses presented here are completely new and have not been reported elsewhere. The experiment employed a block design. There were four runs and 12 blocks in each run (four blocks for each condition in a single run). The runs were block-randomized and counterbalanced across participants. The experiment started with an empty 3 × 3 board (baseline) for 13.5 sec and was followed by a written instruction for 3 sec indicating the task type (check, identity, or control). After the instruction, there was a gap (an empty 3 × 3 board) with a black center cross appearing on it after one second. The cross lasted for 0.5 sec and was used to warn participants of the upcoming stimulus. The stimulus lasted for 2 sec, after which the gap and cross were repeated as a warning for the next stimulus. There were four trials (stimuli) in a block, and after each block, the baseline was presented. The stimuli in the second experiment were 126 × 126 mm for the whole stimulus.

Localizer Task

The face recognition paradigm was a localizer task used to isolate individual FFAs by having participants passively watch pictures of faces and objects. The pictures of faces were taken from students of Tübingen University (see Leube et al., 2001) and were not later used in Experiment 1. The stimuli in the localizer were the same as in the first experiment: 336 × 336 mm for the whole stimulus.

In all experiments, the stimuli were projected onto a screen above the head of the participant via a video projector in the adjacent room. The setup resulted in a visual field of 14.6° for the whole scene (face or chess board). Participants saw the stimuli through a mirror mounted on the head coil and indicated their decision by pressing one of two buttons of an MRI-compatible response device held in their right hand (the left button was for "yes"; and the right button, for "no").

MRI Acquisition

A 3-T scanner (Siemens Trio; Siemens, Erlangen, Germany) with a 12-channel head coil was used to acquire all neuroimaging data. The measurement covered the whole brain using a standard EPI sequence with the following parameters: repetition time = 2.5 sec, field of view = 192 × 192, echo time = 35 msec, matrix size = 64 × 64, 36 slices with thickness of 3.2 mm + 0.8 mm gap resulting in voxels with a resolution of $3 \times 3 \times 4\ \text{mm}^3$. The anatomical images covering the whole brain with 176 sagittal slices were obtained after the functional runs employing a magnetization prepared rapid gradient echo sequence with a voxel resolution of $1 \times 1 \times 1\ \text{mm}^3$ (repetition time = 2.3 sec, inversion time = 1.1 sec, echo time = 2.92 msec).

Univariate fMRI Data Analysis

I used the SPM software package (SPM8; Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk/spm) for all fMRI analysis. The preprocessing involved spatial realignment to the mean image including unwarping and coregistration of the mean EPI to the anatomical image for each participant separately. The images were neither normalized nor smoothed because we wanted to employ the unstandardized individual data in the univariate pattern analysis and MVPA later. In all experiments and the localizer, the blocks of stimuli were modeled explicitly in a general linear model (GLM) together with an implicitly modeled baseline (the modeling of the hemodynamic activation relied on a canonical response function, autocorrelation corrected with a first-order autoregressive model, and a 128 high-pass filter). The movement parameters were also added in the GLM to account for the variance introduced through head movements. The mean percent signal change for each task for each participant individually was extracted from all the voxels within the selected region of the ROI using Marsbar SPM Toolbox (Brett, Anton, Valabregue, & Poline, 2002).

The goal of the study was to check whether experts and novices differ in the percent signal change in the FFA and posterior STS (see below) when presented with different stimuli. That is why I compared them directly on each of the five categories (chess positions, chess objects, faces, rooms, and tools) using a *t* test. In each instance, I corrected for multiple comparisons using the Bonferroni correction. In the first experiment, the significance level was $p < .01$ because dividing .05 by 5 (the number of multiple comparisons) gives the threshold of .01. In the second experiment, the employed threshold was $p < .017$ because there were three comparisons (check, identity, and control—dividing .05 by 3 gives .017).

MVPA

The MVPA analyses were performed using the Decoding Toolbox (Hebart, Görgen, & Haynes, 2014). The toolbox uses the support vector machine (SVM) method of MVPA to ascertain whether the defined ROIs can distinguish between different stimuli among chess experts and novices. All comparisons were binary SVM classifications and focused on the comparisons between chess stimuli on the one hand and the neutral stimuli on the other. In the first experiment, chess positions were compared with rooms and with tools. Chess objects were also compared with the same neutral categories (rooms and tools), but I also compared chess positions and chess objects. In the second experiment, I compared the individuation task with the control task and the check task with the control task as well as the individuation task with the check task. For all classifications, I used a linear SVM with standard cost parameter, $c = 1$, as implemented in the LIBSVM 3.0 library (Chang & Lin, 2011). The classification was based on the β values previously obtained by the GLM and all voxels within an ROI. A leave-one-trial-out method (e.g., Sterzer, Haynes, & Rees, 2008) where the data set was divided into (1) a training set of N pattern vectors (vector length = number of voxels) and (2) a test set of two pattern vectors, one from each stimulus type, was employed. The β is then scaled in all training sets (0–1) as well as in test sets to ensure that one does not duplicate the univariate analysis. I trained iteratively the SVM classifier on the training data sets (N) and tested on an independent test data set, not used in the training. These training and testing procedures were repeated 100 times. The percentage of successful categorization of test items based on the previous independent training data was obtained for each comparison and for each participant. At the group level, I tested with one-sample, one-sided t tests to find out whether the average classification accuracy among the participants for the binary comparison in question was significantly greater than the chance level (50%). Because there were five binary comparisons in the first experiment, I adjusted the significance level from $p = .05$ to $p = .01$ ($.05 / 5 = .01$). In the second experiment, we had three binary comparisons and have adjusted the significance level to $p = .017$ ($.05 / 3 = .017$). The comparisons between groups were performed using two-sided t tests, but here, I used the same adjusted significance levels (.01 for the first experiment and .017 for the second experiment).

Cross-categorization MVPA

I performed a stronger test for shared processes in processing faces and chess stimuli in the FFA. I first trained the binary classifier on all possible faces-versus-rooms comparisons and tested on completely different stimuli–chess positions versus rooms as well as chess objects versus rooms. If face and chess perception share similar processes and play a role in the FFA's functioning, then the FFA should be sensitive even if the learned patterns are tested on different comparisons involving face and chess stimuli. The same procedure was performed on the second neutral stimuli—tools.

Localizer Analysis

The right FFA was identified in each participant as the activated area in the right lateral part of the mid-fusiform gyrus when I subtracted activation while passively watching faces from that while passively watching objects. In most participants, I was able to apply a stringent criterion including only voxels significant at the $p < .0001$ level. In two experts and three novices in the first experiment and in one expert and one novice in the second experiment, I used a less stringent threshold ($p < .001$) to identify the right FFA. The size of the FFA was no different in experts ($M = 386$ mm^3, $SE = 56$ mm^3) from that in novices ($M = 348$ mm^3, $SE = 42$ mm^3) in the first experiment ($t(33) = 0.55$, $p = .59$). The difference in the size of the FFA was also not significant between the groups in the second experiments (experts: $M = 434$ mm^3, $SE = 58$ mm^3; novices: $M = 403$ mm^3, $SE = 50$ mm^3; $t(23) = 0.42$, $p = .68$). Adding the size of the FFA as a covariate in the analyses reported in the Results section did not change the pattern of the results presented in the main text.

In addition to the right FFA, I also identified another face area, the pSTS (Campanella & Belin, 2007). In all participants, only voxels that were significantly more active when viewing faces than objects at $p < .0001$ in the localizer task were included. Two of the experts and two of the novices in the first experiments had their pSTS identified using a more liberal significance threshold of $p < .001$. In the second experiment, in all participants, the pSTS could be identified using the $p < .0001$ threshold. The volume of the pSTS in the first experiment in experts ($M = 337$ mm^3, $SE = 57$ mm^3) was no bigger than that in novices ($M = 311$ mm^3, $SE = 40$ mm^3; $t(33) = 0.55$, $p = .27$), and this was also the case in the second experiment (experts: $M = 373$ mm^3, $SE = 71$ mm^3; novices: $M = 442$ mm^3, $SE = 53$ mm^3; $t(23) = 0.35$, $p = .73$). Again, adding the size of the ROIs in the analysis produced essentially the same pattern of results.

RESULTS

Experiment 1: Perception of Chess Positions and Chess Objects

Behavioral Results

Although the task was relatively simple, experts were still better at detecting repetitions of chess positions ($d' = 3.02$, $SE = 0.05$) than novices ($d' = 2.84$, $SE = 0.04$; $t(33) = 2.84$, $p = .008$). The same trend was found in spotting the repetitions of chess objects (experts: $d' = 3.04$, $SE = 0.04$; novices: $d' = 2.91$, $SE = 0.06$), but the difference did not reach statistical significance ($t(33) = 1.73$, $p = .09$). There were no differences between the two groups when they had to indicate the repetitions of faces (experts: $d' = 2.91$, $SE = 0.07$; novices: $d' = 2.99$, $SE = 0.09$; $t(33) = 0.68$, $p = .50$), rooms (experts: $d' = 3.01$, $SE = 0.06$; novices: $d' = 2.97$, $SE = 0.08$; $t(33) = 0.39$, $p = .70$), and tools (experts: $d' = 2.94$, $SE = 0.08$; novices: $d' = 3.02$, $SE = 0.04$; $t(33) = 0.94$, $p = .36$).

fMRI Univariate Analysis

Not only were the experts better at spotting the repetitions of chess positions, but their FFA also responded more ($M = 1.20$, $SE = 0.10$) than the FFA in novices ($M = 0.65$, $SE = 0.11$) when the chess positions were presented ($t(33) = 3.59$, $p = .001$). On the other hand, there were no differences in the FFA activation between experts (M = 0.65, SE = 0.09) and novices (M = 0.60, SE = 0.12) when observing the chess objects ($t(33)$ = 0.33, p = .74). The chess positions elicited in general more FFA activation than chess objects ($t(34)$ = 3.47, p = .001). The differences were only confined to chess stimuli because when they were presented with faces, experts (M = 1.77, SE = 0.16) and novices (M = 2.03, SE = 0.12) did not differ in their FFA response ($t(33)$ = 1.27, p = .21). The same lack of expertise modulation in the FFA was found with the two neutral categories, rooms (experts: M = 0.75, SE = 0.11; novices: M = 0.52, SE = 0.14; $t(33)$ = 1.19, p = .24) and tools (experts: M = 0.82, SE = 0.09; novices: M = 0.77, SE = 0.11; $t(33)$ = 0.27, p = .70).

In contrast to the FFA, the other face-related areas, pSTS, did not display the same pattern of results. There were no significant differences between experts (M = 0.30, SE = 0.21) and novices (M = 0.14, SE = 0.17) in the pSTS activation when chess positions were observed ($t(33)$ = 0.61, p = .55). The same lack of skill differences was observed for chess objects (experts: M = 0.28, SE = 0.18; novices: M = 0.12, SE = 0.13; $t(33)$ = 0.70, p = .49). The difference between chess positions and chess objects was also not found in pSTS ($t(34)$ = 0.21, p = .84). There were no differences between experts (M = 0.73, SE = 0.18) and novices (M = 0.94, SE = 0.18) when they observed faces ($t(34)$ = 0.80, p = .43). The other two neutral stimulus categories also produced no skill differences in pSTS (for rooms, experts: M = 0.18, SE = 0.18; novices: M = 0.01, SE = 0.16; $t(33)$ = 0.72, p = .47; for tools, experts: M = 0.12, SE = 0.17; novices: M = 0.16, SE = 0.12; $t(33)$ = 0.22, p = .82).

fMRI MVPA

The univariate fMRI analysis showed that the FFA is modulated by expertise as well as the kind of chess stimuli, chess positions, or chess objects. As can be seen in Figure 2A, the MVPA confirms that the FFA in experts

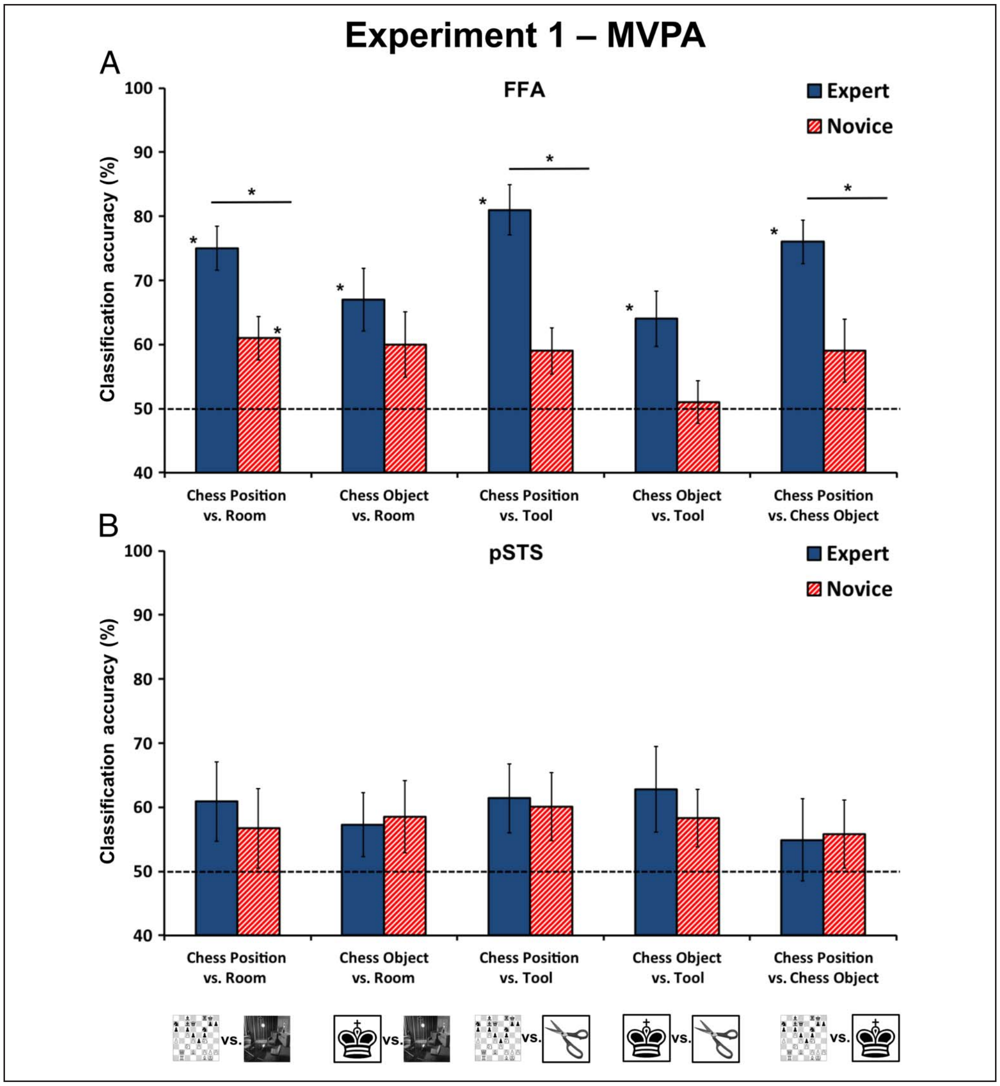

Figure 2. MVPA results in Experiment 1. (A) The success rate for the FFA in differentiating between chess stimuli (positions and objects) and other neutral stimuli (rooms and tools) in experts and novices. (B) The success rate for the pSTS in differentiating between chess stimuli and other neutral stimuli in experts and novices. The dotted line represents 50% success rate—chance level. Error bars indicate *SEM*. *p < .01 (adjusted for multiple comparisons).

can reliably differentiate between chess positions and other neutral categories: rooms ($t(15) = 7.4$, $p < .001$) and tools ($t(15) = 7.8$, $p < .001$). Experts' FFA also reliably differentiated between chess objects and the other two neutral categories: rooms ($t(15) = 3.5$, $p = .002$) and tools ($t(15) = 3.3$, $p = .002$). The FFA in novices, on the other hand, could not match the success rate of classification in experts' FFA. The FFA in novices could reliably distinguish between chess positions and rooms ($t(18) = 3.2$, $p = .003$), but in all other comparisons, the FFA could not reliably differentiate between chess and neutral categories when the significance level was adjusted for multiple comparisons: chess object versus room ($t(18) = 1.97$, $p = .03$), chess positions versus tool ($t(18) = 2.18$, $p = .021$), and chess object versus tool ($t(18) = 0.24$, $p = .039$).

Experts' FFA was significantly better than that of novices at differentiating chess positions from rooms ($t(33) = 2.89$, $p = .007$) and tools ($t(33) = 4.01$, $p < .001$). However, the differences in the FFA sensitivity between experts and novices did not reliably differentiate the chess objects from rooms ($t(33) = 0.99$, $p = .33$) and tools ($t(33) = 2.32$, $p = .026$).

One way to check the sensitivity of the FFA to expertise is to compare chess positions and chess objects directly. Experts' FFA could differentiate between chess positions and chess objects ($t(15) = 7.7$, $p < .001$), but the FFA of novices could not reliably tease apart the two chess stimuli ($t(18) = 1.88$, $p = .038$). The differences in the success rate between the FFA of experts and novices in recognizing chess positions and objects were also significant ($t(33) = 2.86$, $p = .004$).

The other face area, pSTS, displayed a different pattern of results, as seen in Figure 2B. Although there was a tendency in experts for the pSTS to be able to reliably distinguish between chess and neutral stimuli, one of the binary comparisons approaches the corrected significance level of $p < .01$ (chess position vs. room: $t(15) = 1.76$, $p = .048$; chess position vs. tool: $t(15) = 1.69$, $p = .09$; chess object vs. room: $t(15) = 2.12$, $p = .025$; chess object vs. tool: $t(15) = 1.91$, $p = .038$; chess position vs. chess object: $t(15) = 0.77$, $p = .23$). The same tendency was noticeable in novices, but again, none of the comparisons survived the set significance level (chess position vs. room: $t(18) = 1.34$, $p = .09$; chess position vs. tool: $t(18) = 1.52$, $p = .07$; chess object vs. room: $t(18) = 1.91$, $p = .035$; chess object vs. tool: $t(18) = 1.84$, $p = .041$; chess position vs. chess object: $t(18) = 1.09$, $p = .15$). There were also no differences between experts and novices when it came to the ability of their pSTS to differentiate between chess and neutral stimuli (chess position vs. room: $t(33) = 0.48$, $p = .67$; chess position vs. tool: $t(33) = 0.16$, $p = .87$; chess object vs. room: $t(33) = 0.18$, $p = .86$; chess object vs. tool: $t(33) = 0.64$, $p = .52$). Finally, the experts' FFA did not differentiate more reliably between chess position and chess object than the pSTS of novices ($t(33) = 0.10$, $p = .91$).

Cross-categorization MVPA

In the next step, I went further and asked if the differences between faces and other neutral stimuli (rooms and tools) can be used to distinguish between chess stimuli and neutral stimuli. In this cross-categorization procedure, I first trained the FFA of experts and novices to distinguish between faces, on the one hand, and rooms and tools, on the other (see Figure 3A). Then, the obtained activation pattern in the FFA was used to distinguish between chess stimuli, on the hand, and the neutral stimuli, on the other. In other words, I checked whether the faces and chess stimuli share similar underlying processes that may help the FFA to differentiate both stimuli from the neutral stimuli using the same underlying activity within the FFA.

Figure 3B shows that none of the cross-categorization procedures in the FFA were significant. Only the FFA of experts in the comparison between faces and rooms and its implementation on chess positions versus rooms approached significance level ($t(15) = 1.84$, $p = .043$). All other cross-categorizations were not significant (face vs. room to chess positions vs. room: $t(15) = 0.64$, $p = .26$ for novices; face vs. tool to chess positions vs. tool: $t(15) = 0.71$, $p = .25$ for experts and $t(18) = 0.38$, $p = .35$ for novices; face vs. room to chess object vs. room: $t(15) = 1.13$, $p = .14$ for experts and $t(18) = 0.79$, $p = .22$ for novices; face vs. tool to chess object vs. tool: $t(15) = 0.12$, $p = .45$ for experts and $t(18) = 0.04$, $p = .47$ for novices). When we compared the success of experts' and novices' FFA on the cross-categorization, there was again marginally significant differences for the comparison face versus room to chess positions versus room ($t(33) = 2.06$, $p = .048$). None of the other cross-categorization comparisons were different between experts and novices (face vs. tool to chess positions vs. tool: $t(33) = 0.26$, $p = .79$; face vs. room to chess object vs. room: $t(33) = 0.05$, $p = .96$; face vs. tool to chess object vs. tool: $t(33) = 0.12$, $p = .90$).

Figure 3C shows that the control face ROI, the pSTS, was not successful in the cross-categorization procedure. None of the procedures reached the significance levels adjusted for multiple comparisons (face vs. room to chess positions vs. room: $t(15) = 1.21$, $p = .12$ for experts and $t(15) = 1.0$, $p = .16$ for novices; face vs. tool to chess positions vs. tool: $t(15) = 1.24$, $p = .11$ for experts and $t(18) = 0.78$, $p = .22$ for novices; face vs. room to chess object vs. room: $t(15) = 1.28$, $p = .11$ for experts and $t(18) = 0.68$, $p = .25$ for novices; face vs. tool to chess object vs. tool: $t(15) = 1.54$, $p = .08$ for experts and $t(18) = 0.26$, $p = .40$ for novices), and there were no differences between pSTS of experts and novices (face vs. room to chess positions vs. room: $t(33) = 0.10$, $p = .91$; face vs. tool to chess positions vs. tool: $t(33) = 0.48$, $p = .64$; face vs. room to chess object vs. room: $t(33) = 0.37$, $p = .71$; face vs. tool to chess object vs. tool: $t(33) = 1.08$, $p = .28$).

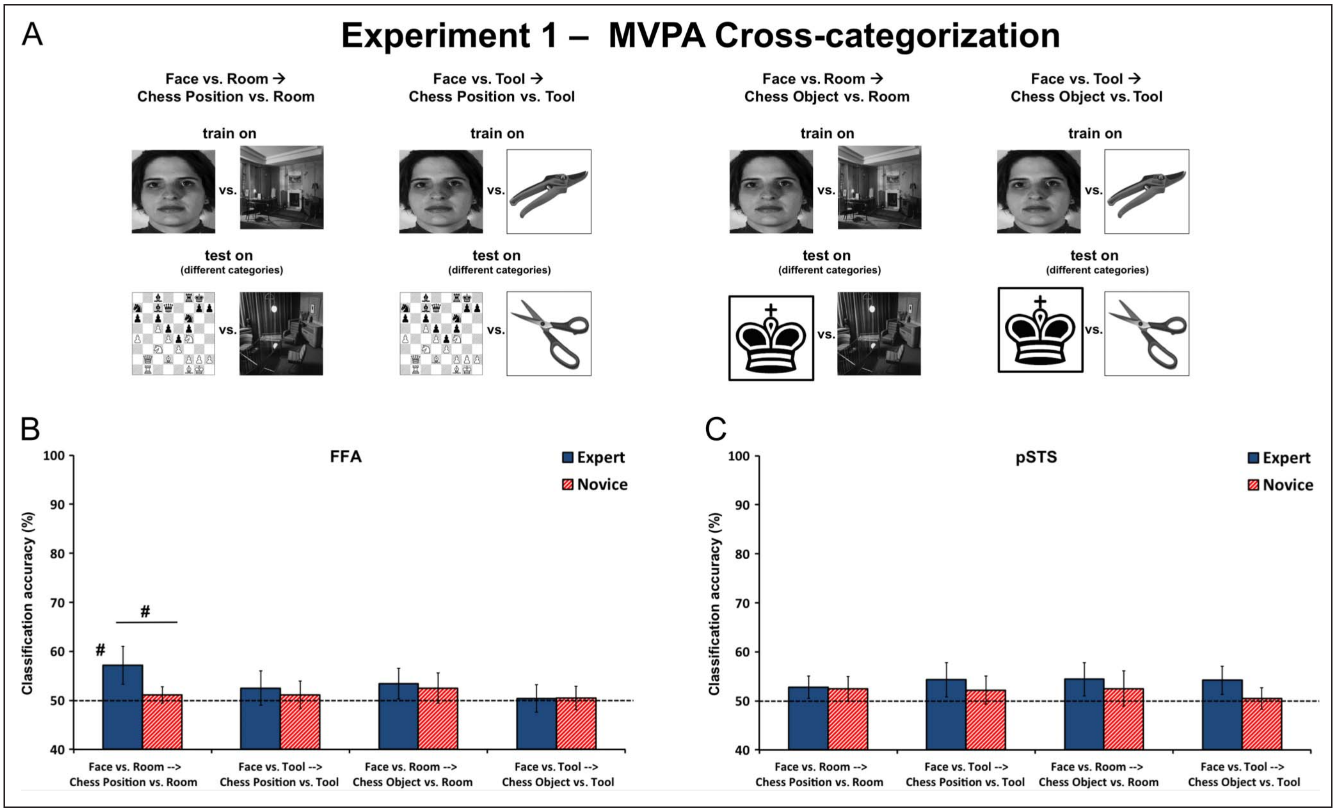

Figure 3. MVPA cross-categorization results in Experiment 1. (A) Illustration of the cross-categorization procedure. Instead of training and testing on the same categories (but different instances of the same categories), it was trained on one type of category and tested on a different type of category. I trained first the classification algorithm on the binary comparison of faces and rooms. Then, the learned patterns were tested on the binary comparison involving a new category—chess positions. The same procedure was done for the tools (instead of rooms—second column), and then the same was repeated for chess objects instead of the chess positions (third and fourth columns). (B) Classification accuracy for the cross-categorization procedure presented as percentage of correctly classified instances of the binary comparisons with rooms and tools for the FFA in experts and novices. (C) Classification accuracy for the cross-categorization procedure presented as percentage of correctly classified instances of the binary comparisons with rooms and tools for the pSTS. The dotted line represents 50% success rate—chance level. Error bars indicate *SEM*. #$p < .05$ ($*p < .012$ adjusted for multiple comparisons).

Experiment 2: Individuating Chess Objects and Their Interrelations

I have established that the FFA's response to chess stimuli, in particular chess positions, is modulated by chess expertise. However, I could not find evidence, even with the use of the sensitive MVPA, that isolated chess objects, the building blocks of chess positions, were differently represented in chess experts' FFA than in chess novices' FFA. In the second experiment, I sought to shed further light on the relationship between the FFA and expertise. I was interested in the role of the FFA in the individuation of isolated chess objects and their relations to other chess objects. The second experiment is identical to the commonly employed individuation paradigm in other domains (e.g., Xu, 2005; Rhodes et al., 2004; Gauthier et al., 1999, 2000). The experiment goes one step further and also examines recognition of domain-inherent relations between those objects. I presented two chess objects (a king plus a variable chess object) on a reduced 3 × 3 square chessboard. Participants indicated either whether the two presented chess objects were in a check relation ("check task") or whether the variable piece was a bishop or a knight ("identity task"). In the nonchess control task, the identity task was repeated with two geometrical shapes instead of chess pieces (see Figure 1B).

Behavioral Results

Experts were faster in the chess tasks than novices, even when they only had to individualize the chess object (identity, experts: $M = 0.52$ sec, $SE = 0.01$ sec; novices: $M = 0.59$ sec, $SE = 0.02$ sec; $t(23) = 2.81, p = .009$) and especially when they had to indicate if the check relations was present or not (check, experts: $M = 0.58$ sec, $SE = 0.02$ sec; novices: $M = 0.71$ sec, $SE = 0.02$ sec; $t(23) = 4.15, p < .001$). The speed advantage of experts was confined to the chess-related tasks, as there were no significant differences when chess experts and novices had to individualize geometrical shapes (control, experts: $M = 0.68$ sec, $SE = 0.03$ sec; novices: $M = 0.66$ sec, $SE = 0.03$ sec; $t(23) = 0.47, p = .64$).

fMRI Univariate Analysis

Although experts were faster in chess-related tasks, their FFA was not more activated than the FFA of novices in any of the chess tasks (identity, experts: *M* = 0.23, *SE* = 0.07; novices: *M* = 0.21, *SE* = 0.10; *t*(23) = 0.19, *p* = .85; check, experts: *M* = 0.25, *SE* = 0.06; novices: *M* = 0.23, *SE* = 0.08; *t*(23) = 0.22, *p* = .83). There were also no differences in the activation of the FFA between experts (*M* = 0.18, *SE* = 0.08) and novices (*M* = 0.20, *SE* = 0.06) in the control task (*t*(23) = 0.22, *p* = .83). It is important to note that there were no differences in the FFA activation between the three tasks (*F*(2, 48) = 1.16, *p* = .32), despite their apparent difference in difficulty as indicated by the RT. Therefore, the FFA also did not respond differently to the individuation of a single isolated chess object or an isolated relation between two chess objects.

The other face area, the pSTS, was not differently activated by any of the tasks (*F*(2, 48) = 0.34, *p* = .71), nor was it modulated by expertise in any of the three tasks (identity, experts: *M* = 0.10, *SE* = 0.15; novices: *M* = 0.28, *SE* = 0.18; *t*(23) = 0.76, *p* = .58; check, experts: *M* = 0.08, *SE* = 0.16; novices: *M* = 0.22, *SE* = 0.20; *t*(23) = .56, *p* = .58; control, experts: *M* = 0.13, *SE* = 0.15; novices: *M* = 0.07, *SE* = 0.14; *t*(23) = 0.31, *p* = .76).

fMRI MVPA

As seen in Figure 4A, the lack of reliable response to chess objects was confirmed with the more sensitive MVPA. Experts' FFA could not distinguish above chance between individuating chess objects and neutral objects (identity vs. control: *t*(11) = 1.47, *p* = .085), between relations among chess objects and individuation of neutral objects (check vs. control: *t*(11) = 0.78, *p* = .28), and between chess individuation and chess relations (check vs. identity: *t*(11) = 1.27, *p* = .11). The FFA in novices was not more successful as none of the comparisons reached the necessary statistical threshold to become significant (identity vs. control: *t*(12) = 0.85, *p* = .21; check vs. control: *t*(12) = 1.95, *p* = .037; check vs. identity: *t*(12) = 1.67, *p* = .061). As with the univariate fMRI analysis, there

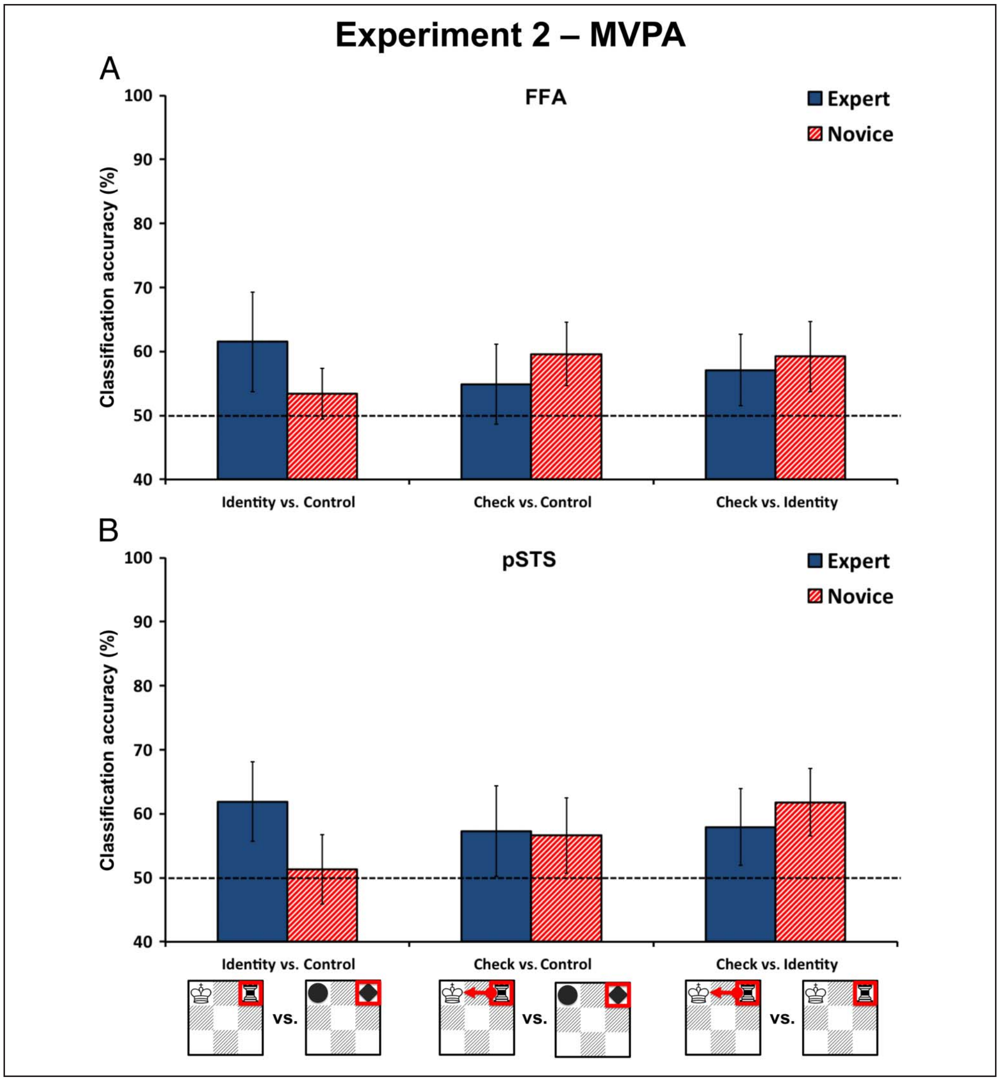

Figure 4. MVPA results in Experiment 2. (A) The success rate for the FFA in differentiating between check, identity, and control tasks in experts and novices. (B) The success rate for the pSTS in differentiating between check, identity, and control tasks in experts and novices. The dotted line represents 50% success rate—chance level. Error bars indicate *SEM*.

were no significant differences between the FFA in experts and novices (identity vs. control: $t(23) = 0.94, p = .35$; check vs. control: $t(23) = 0.59, p = .56$; check vs. identity: $t(23) = 0.27, p = .79$).

Figure 4B shows that the pSTS was not much better at differentiating chess from control stimuli. The pSTS of experts could not reliably distinguish between individuation of chess and neutral objects (identity vs. control: $t(11) = 1.90$, $p = .042$), between the identification of relations among chess objects and the individuation of neutral objects (check vs. control: $t(11) = 1.03, p = .17$), or between chess individuation and chess relations (check vs. identity: $t(11) = 1.32, p = .12$). The pSTS in novices was also not successful in differentiating the stimuli above chance (identity vs. control: $t(12) = 0.25, p = .82$; check vs. control: $t(12) = 1.11, p = .28$; check vs. identity: $t(12) = 2.24$, $p = .022$), and there were no significant differences in the pSTS success rate of differentiation between experts and novices (identity vs. control: $t(23) = 1.29, p = .21$; check vs. control: $t(23) = 0.08, p = .94$; check vs. identity: $t(23) = 0.49, p = .63$).

Needless to say, the cross-categorization procedure was also unsuccessful, which is not surprising given the lack of the reliable differentiation between the stimuli with the MVPA.

DISCUSSION

Most of the previous studies on the function of the FFA have used stimuli visually similar to faces. Here, I employed the chess stimuli to circumvent the similarity problem, but the novelty of the work lies in the use of different chess stimuli as well as the employment of more sensitive techniques of analysis (MVPA). In two experiments, I demonstrated that the FFA is indeed sensitive to expertise but in a more subtle way than previously thought. In the first experiment, chess experts' FFA could reliably differentiate between chess and other neutral stimuli, such as rooms and tools. In novices, not even a sensitive technique such as MVPA could demonstrate the sensibility in the FFA between chess and other stimulus categories. Different types of chess stimuli, however, elicited a different pattern in experts' FFA. Chess positions, complex stimuli made out of several individual objects (see Figure 1A), were easily differentiated in experts' FFA, whereas single isolated chess objects were not that well indexed in experts' FFA. The MVPA demonstrated that even experts' FFA may be sensitive above chance to isolated chess objects, but the general success rate was not reliably different from that of novices, which was generally unsuccessful in differentiating between chess objects and neutral objects (see Figure 2B).

The isolated chess objects might be familiar to chess players, but they are rarely encountered in isolation. The second experiment further examined the FFA response to isolated chess objects by asking the chess players to actively individualize, that is, name, the object in question and connect it to another object on a miniature chessboard. Even this explicit individuation instruction in combination with the sensitive MVPA did not result in reliable FFA responses to isolated chess objects in either experts or novices (see Figure 4A).

One appealing feature of chess stimuli for the investigation of the FFA function is their lack of similarity with faces. However, when one goes beyond visual similarity and considers underlying processes in face and chess perception, the two categories suddenly share many common features (Tarr & Cheng, 2003). The chessboard defines the space of chess positions, and they consist of multiple objects, which form spatial relations. Faces also have clearly defined spaces as well as individual features whose spatial relations are essential to face recognition. Chess experts grasp the essence of chess positions by perceiving the chess objects and the relations between them as groups (Reingold, Charness, Schultetus, & Stampe, 2001) and not as individual objects like novices (Gobet & Simon, 1996). People with intact face perception also grasp faces as a whole and not as a sum of individual features. Prosopagnosic people struggle with face recognition precisely because they perceive the individual features separately (Van Belle et al., 2011), not unlike the way that chess beginners perceive chess objects in chess positions (Reingold et al., 2001; Saariluoma, 1995).

Another similarity between the processes behind skilled face and chess perception is their high efficiency and automaticity. A recent study by Boggan, Bartlett, and Krawczyk (2012) tapped into the shared underlying processes by showing that chess experts experienced the same composite effect with chess positions as people do with faces. Even more intriguing is the finding of negative correlation between the starting age of chess playing and the face composite effect (Figure 4 in Boggan et al., 2012). In other words, starting early with chess results in less holistic face perception. There are many possible reasons for this negative relation, but one of them is that both face and chess perception share common mechanisms. Once these mechanisms have been captured early by chess expertise, less is left for the development of face perception in a holistic manner (but see, McGugin, Van Gulick, & Gauthier, 2016; Wang, Gauthier, & Cottrell, 2016).

The holistic processing in expertise may be a matter of degree rather than an all-or-nothing phenomenon. The FFA in novices was not sensitive to chess stimuli in almost all comparisons except the one between chess positions and rooms. It is possible that this result is a consequence of the alpha error despite the correction for multiple comparisons. On the other hand, it may indicate that the holistic process develops with exposure rather than being an all-or-nothing phenomenon. The design of this study employed the expertise approach (Bilalić et al., 2010, 2012), which enables the uncovering of even small effects because of huge differences between experts and novices (Campitelli & Speelman, 2013). A more subtle approach with participants at several developmental stages (e.g., Boggan et al., 2012; Bilalić et al., 2009; Bilalić, McLeod, & Gobet, 2008) may be used to reveal whether holistic processing does indeed increase gradually with expertise.

Considering the similarities between the chess and face perception, it may not be that surprising that the FFA has been sensitive to chess expertise. The FFA is thought to be responsible for holistic parsing of individual parts of faces (Arcurio, Gold, & James, 2012), and the previous results indicate that similar holistic processing underlies the perception of chess positions (Boggan et al., 2012). The results of the study therefore confirm the expertise hypothesis of the FFA function and are in accordance with the other recent study involving radiological images (Bilalić et al., 2016). At first sight, they also seem to rule out the possibility that the FFA is not responsible for holistic processing but rather responds to curved shapes (Ohayon, Freiwald, & Tsao, 2012; Tsao, Freiwald, Tootell, & Livingstone, 2006; Wilkinson et al., 2000; Kosslyn, Hamilton, & Bernstein, 1995). Unlike some radiological images, chess positions are hardly oval in shape. The problem with this conclusion is that the cross-categorization, a more stringent test of shared processing between faces and chess stimuli, was not quite successful (see Figure 3). Even experts' FFA was unable to reliably differentiate between chess and neutral stimuli when the learning was initially done on the faces and the same neutral stimuli. The same procedure, however, was successful with the FFA of radiologists (Bilalić et al., 2016; see Figure 2). There are many differences between chess and radiological expertise, but one of them, as mentioned above, is that radiological stimuli are oval in shape unlike chess stimuli. It is difficult to draw firm conclusions about the role of the oval shape in the FFA from the two separate studies, but it is certainly an intriguing question for future studies.

There may be different reasons why some studies failed to identify the expertise effect in the FFA (de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Moore, Cohen, & Ranganath, 2006; Yue, Tjan, & Biederman, 2006; Grill-Spector et al., 2004; Rhodes et al., 2004), such as the fact that they used test stimuli that were similar but outside experts' specialization (e.g., antique cars with modern car experts). Another problem, suggested by our results, may be the use of isolated, context-deprived stimuli (see also Bar, 2004). Namely, the FFA was not sensitive to individual chess objects (Experiment 1) even when they are explicitly individuated, and their function retrieved and put into relations with other objects (Experiment 2). This is surprising as those individual objects and their relations are the main building blocks of chess positions, the very same stimuli that consistently elicit expertise effects in the FFA. Similarly, the expertise hypothesis postulates that the FFA is important for individuation of objects. Yet, the explicit individuation task in Experiment 2 (identity task) has not produced the expected expertise modulation of the FFA. One possibility is that the performed experiment lacked the necessary power to discover the expertise effects in the FFA with isolated chess objects. After all, the studies featured a dozen participants at most in each group, and the nonsignificant results should not be confused with a complete absence of effects. It is impossible to exclude this possibility, but one should keep in mind that two experiments were performed with a relatively large number of participants for expertise studies. If anything, the expertise effect in FFA seems to be considerably smaller with isolated chess objects than with chess positions.

The other possibility is that the identity task in Experiment 2 may not be sensitive enough to the individuation processes. The differentiation between two different objects (knight and rook) may be too crude to elicit the necessary individuation mechanisms for eliciting the FFA activation. Differentiating between two visually different versions of the same object (rook presented in two distinct designs) may be closer to the individuation process one finds in faces and other categories. This intriguing prospect remains to be examined in future studies, but the lack of the expertise effects in FFA with isolated chess objects may also be taken as further evidence of the FFA's involvement in holistic processing. Chess objects may not lack distinctive features by which they are recognized, but they certainly seem to have fewer features of this kind than chess positions, whose complexity is often compared with the number of atoms in the universe (Shannon, 1950).

There has been much talk about the role of the FFA in visual expertise, and this study is obviously no exception, as it confirmed its role in chess expertise. The other face area, the pSTS, was not significantly involved in chess expertise even when the MVPA was employed. One should not forget, however, that the cross-categorization procedure, where the activation patterns of faces were used to differentiate chess positions from other stimuli, was not quite successful (see Figure 3B). The perception of faces and chess positions may therefore not share the same underlying processes but rather only some of them. The same could hold for faces and any other visual category (Wang et al., 2016). The perception of any stimuli, even faces, goes beyond a single brain region, even if it is the FFA (Duchaine & Yovel, 2015). The previous studies identified that the FFA is expertise modulated even by nonchess activity, such as counting the objects in a chess position (Bilalić, Langner, et al., 2011). However, the chess-specific task demands were indexed in other inferotemporal and medial parietal areas, such as collateral sulcus and retrosplenial cortex (Bilalić et al., 2010, 2012). This is in accordance with other expertise domains, where a number of areas form a neural network necessary for many processes that visual expertise requires (Harel, 2015; Harel, Kravitz, & Baker, 2013). The FFA may indeed be an important area for chess expertise, but its role in chess perception, and in visual expertise in general, remains to be put into context with other relevant brain areas.

Here, the game of chess was used to disentangle the current controversy about the FFA function. The two experiments confirmed the expertise hypothesis of the FFA function but also extended it in an important way. The FFA is not a face-specific brain module but rather a more general piece of brain machinery, honed through experience with particular stimuli, which parses individual parts of the stimulus into a whole. The FFA is not only responsible for individuation, but at its heart are the processes that enable fast and efficient perception of complex stimuli. The more complex the stimuli, the more likely it is that the brain will require the help of the FFA in grasping its essence. Finally, another conclusion to take away from the two experiments presented here is the suitability of chess and the expertise approach of comparing experts with novices in general (Bilalić, Kiesel, et al., 2011; Boggan & Huang, 2011), as an exploration vehicle in cognitive neuroscience.

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