How visual expertise changes representational geometry: A behavioral and neural perspective

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Abstract.

Many people develop expertise in specific domains of interest, such as chess, microbiology, radiology, and, the case in point in our study: ornithology. It is poorly understood to what extent such expertise alters brain function. Previous neuroimaging studies of expertise have typically focused upon the category level, for example, selectivity for birds versus nonbird stimuli. We present a multivariate fMRI study focusing upon the representational similarity among objects of expertise at the subordinate level. We compare the neural representational spaces of experts and novices to behavioral judgments. At the behavioral level, ornithologists (n = 20) have more fine-grained and task-dependent representations of item similarity that are more consistent among experts compared to control participants. At the neural level, the neural patterns of item similarity are more distinct and consistent in experts than in novices, which is in line with the behavioral results. Additionally, these neural patterns in experts show stronger correlations with behavior compared to novices. These findings were prominent in frontal regions, and some effects were also found in occipitotemporal regions. This study illustrates the potential of an analysis of representational geometry to understand to what extent expertise changes neural information processing.

INTRODUCTION

The effects of visual expertise, sometimes defined as *automatic processing of items as a result of domain specific learning* (Bukach et al., 2006), on the neural representations of objects of expertise have been studied for almost two decades in a large number of fMRI and EEG studies (starting from Gauthier et al., 1999, 2000). Although the exact nature of neural expertise effects and the location of these effects and their distribution are still up for debate (e.g. McKone and Kanwisher, 2005; Curby and Gauthier, 2010; Harel et al., 2013), it has become clear that visual expertise changes the way in which objects of expertise are represented in the brain. However, previous studies lack the level of detail to explain to what extent the representations of objects in experts change at the level of detail that really matters: the representation of individual objects of expertise.

Measuring the representational space of within-category similarity

Studies have focused on a wide range of domains of visual expertise, like bird expertise, chess, radiology, car expertise, expertise with musical instruments and notation, expertise in computer programming and so on (e.g. Bilalić, Grottenthaler, Nagele, & Lindig, 2014; Bilalić, Langner, Ulrich, & Grodd, 2011; Floyd, Santander, & Weimer, 2017; Gauthier et al., 2000; Haller & Radue, 2005; Harel, Gilaie-Dotan, Malach, & Bentin, 2010; Harley et al., 2009; Hoenig et al., 2011; Martens, Bulthé, van Vliet, & Op de Beeck, 2018; McGugin, Gatenby, Gore, & Gauthier, 2012; Wong & Gauthier, 2010). Many fMRI studies investigating real-world expertise have reported an increase in neural activation for the expert object category in experts compared to novices, or a positive correlation between neural activation and level of expertise (Harley et al., 2009; McGugin et al., 2012). These effects have been found in visual regions like the lateral occipital complex (LOC, e.g. Grill-Spector, Knouf, & Kanwisher, 2004; Mongelli et al., 2017; Moore, Cohen, & Ranganath, 2006; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006), the fusiform face area (FFA) and neighboring regions (e.g. Gauthier et al., 2000; Harley et al., 2009; McGugin et al., 2012; Xu, 2005), early

visual cortex (EVC, e.g. Harel, Gilaie-Dotan, Malach, & Bentin, 2010; Martens, Bulthé, van Vliet, & Op de Beeck, 2018), in areas outside the visual cortex like the auditory cortex (e.g. Hoenig et al., 2011), and in prefrontal regions (e.g. Harel et al., 2010; Krawczyk, Boggan, McClelland, & Bartlett, 2011; Moore et al., 2006). Expertise-related neural changes have also been induced by extensively training participants in recognizing and categorizing novel objects (e.g. Brants, Wagemans, & Op de Beeck, 2011; Gauthier et al., 1999; Brants, Bulthé, Daniels, Wagemans, & Op de Beeck, 2016). In addition to fMRI studies, EEG studies have demonstrated the presence of neural expertise effects in the form of an enhanced N170 response to objects of expertise, for both real-world domains of expertise (e.g. Tanaka and Curran, 2001; Gauthier and Curby, 2005) and for laboratory-trained participants (e.g. Rossion et al., 2002; Scott et al., 2006, 2008).

Although widely varying methods and research designs have been used in the search for neural expertise effects, most of these studies share one commonality: they investigated the neural activation underlying the expert object *category*. However, experts show a superior performance in identifying and classifying visually similar objects *within* a specific domain, at a more subordinate level compared to novices (Tanaka & Taylor, 1991). For example, when presented with an image of a bird, an ornithologist will preferentially identify this bird at the level of its species (e.g. a Western yellow wagtail) while a novice will simply identify this animal as a “bird”. This subordinate level expert processing has been the focus of many behavioral studies on perceptual learning and expertise (e.g. Gauthier and Tarr, 1997; Tanaka et al., 2005; Scott et al., 2006; Wong et al., 2009).

As a logical consequence, all studies investigating visual expertise and its neural basis have included experts that were very proficient at making fine-grained distinctions between visually similar objects within a specific domain, whether they were laboratory-trained or already had several years of experience. However, none of the neural studies cited above have actually investigated neural expertise effects at the subordinate level. While it is certainly valuable to investigate the neural responses that are triggered by the expert object category, important effects might be missed by this lack of specificity at the

neural level (Martens et al., 2018). Exploring the effects of expertise on the neural representations of the individual objects of expertise would better approximate expert behavior and improve the ecological validity. Discriminating representations at this fine level is a challenge though, even for advanced methods such as multi-voxel pattern analysis (MVPA), as has been illustrated by an earlier study with laboratory training (Brants et al., 2016) and for distinguishing subordinate object distinctions in general (Eger et al., 2008). In these studies, the strength of selectivity of untrained objects was relatively weak (i.e. low signal to noise), as some objects are hard to perceive for novices. Consequently, this low signal to noise ratio influences the sensitivity of the MVPA decoding, making fine discriminations hard. A few studies have resorted to the method of fMRI adaptation to resolve these problems (e.g., Folstein, Palmeri, & Gauthier, 2013; Gillebert, Op de Beeck, Panis, & Wagemans, 2009; Van Der Linden, Murre, & van Turennout, 2008), but this indirect method of inferring neural selectivity has important interpretational problems (Larsson et al., 2016) and only provides limited insights in the properties of the representational space as a result of mostly not obtaining a full similarity matrix, but only a subset of possible combinations of stimuli or dimensions.

The current study: Towards representational similarity analysis of visual expertise

In the current study, we use multi-voxel pattern analysis (MVPA) fMRI to determine whether and to what extent visual expertise changes the way in which individual objects of expertise are represented in the brain. We use ornithology (bird expertise) as the test domain. We apply MVPA to determine the distributed neural responses to individual birds in responsive regions in high-level visual cortex and prefrontal cortex, with primary visual cortex as a further control region. These neural bird representations are combined in a representational dissimilarity space, which we compare between bird experts and bird novices. Furthermore, we aim to compare this neural representational space to the mental (behavioral) representational space of the same individual objects, for both experts and novices.

METHODS

Participants

We recruited 41 subjects to participate in this study: 21 candidate bird experts, who were active birdwatchers, and 20 control participants. Half of these participants (11 ornithologists, 9 control participants) already took part in a previous fMRI study on expertise (Martens et al., 2018). One candidate bird expert was excluded due to a developmental disorder. To confirm the self-reported level of knowledge concerning birds, all new participants (10 ornithologists, 11 control participants) completed a perceptual and a semantic task on bird expertise, which were also administered in the previous study. No participants had to be excluded based on their behavioral results (see details below). The final subject sample consisted of 20 ornithologists with an average age of 28.3 ± 5.5 years (5 females, average experience of 11.1 ± 4.6 years) and 20 control participants with an average age of 28.6 ± 4.5 years (6 females, no experience with birds). The two subject groups were matched for level of education. All participants were healthy adults with normal or corrected-to-normal vision, and all provided a written informed consent for the behavioral tasks and the fMRI scan. The study was approved by the Medical Ethical Committee of KU Leuven. Twenty subjects per group was the group size specified a priori, the same number as included by Martens et al. (2018) which was higher than the numbers reported in other neuroimaging studies of expertise. An a priori power analysis was not feasible given that no previous study investigated subordinate representations in the context of expertise.

Determination of expertise level

Before the fMRI scan, all participants completed a behavioral session, which was longer for the new participants (~ 90 minutes) than for those who already took part in a previous study (~ 60 minutes). The previous study investigated domain-general and domain-specific changes in neural processing in two expertise domains. The new participants first completed a perceptual discrimination task and a semantic

task (see Martens et al., 2018). For the remaining participants, results for these tasks were taken from the previous study.

The perceptual discrimination task, which was used to assess the participants' knowledge of birds, consisted of 80 pairs of colored images of European bird species that were selected with the help of a bird expert. Half of these pairs consisted of birds that belonged to the same bird species, the other half consisted of birds belonging to different species. The visual similarity of the birds within each pair varied across pairs. Participants had to decide for each pair whether both birds did or did not belong to the same species. Ornithologists reached an average score of 84% in the discrimination task (*SD* = 9.4%, min. = 67%, max. = 96%), scoring significantly higher than control participants who performed at chance level (average score of 51%, *SD* = 6.2%, min. = 40%, max. = 64%; $t(19) = 11.26$, $p < .001$). In the semantic task, a second assessment of expertise, participants were asked to name 30 colored images of birds as precise as possible. The more specific the answers (e.g. specific bird species, sex of the bird, Latin name), the higher the score (one, two or three points) that was awarded (for more details, see: Martens et al., 2018). On this task, all ornithologists (average 68.6, *SD* = 15.7, min. = 42.2, max. = 93.8) outperformed all the control participants (average 9.2, *SD* = 3.4, min. = 1.1, max. = 16.7).

As a third task to measure expertise, after the neural data had been collected, we asked participants to name the 24 bird types they had seen during the scan session, to ensure that ornithologists were familiar with these specific bird species. With an average score of 83.5% on the naming task after the scan session (*SD* = 14.1%, min. = 50%, max. = 100%), ornithologists demonstrated that they were overall familiar with the 24 specific birds that were presented to them in the scanner, while control participants were not (average of 7%, *SD* = 5.4%, min. = 0%, max. = 20.8%; $t(19) = 21.49$, $p < .001$).

Stimuli

The 24 birds that were selected for the behavioral similarity tasks and the fMRI experiment consisted of eight triplets (see Figure 1). Within these triplets, visual appearance and species of the birds were manipulated. Each triplet consisted of two birds belonging to the same species but that were visually different (birds A and B, e.g.: a visually different male and female or a species with different summer and winter plumage) and a third bird (bird C) from a different species that was visually similar to bird B. Of these 24 birds, 13 were songbirds (5 different songbird families, 9 different species), 5 were wading birds (2 different bird families, 3 different species) and 6 were birds of prey (2 different bird families, 4 different species). The experiments included 4 exemplar images of each of the 24 birds.

insert Figure 1 here

Behavioral similarity judgments

All participants provided similarity judgments of the 24 birds using a multiple object arrangement (MOA) paradigm (Kriegeskorte & Mur, 2012). Participants were asked to arrange the different stimuli based on their similarity in a two-dimensional space on the computer screen. The distances between the stimuli were interpreted as (dis)similarities: the closer together they were placed, the more similar they were. Participants performed the MOA task twice: first they were asked to arrange the 24 birds according to their taxonomy (similarity of bird *species*), next they arranged the same birds according to their *visual* similarity, while disregarding any species information. For each task, participants had 20 minutes to repeatedly arrange the stimuli which were presented in different subsets depending on the amount of information available of each object at that time (for more details, see Kriegeskorte & Mur, 2012).

Apparatus for fMRI

We collected neural data at the Department of Radiology of the University Hospitals Leuven using a 3T Philips Ingenia CX scanner with a 32-channel head coil. Functional images were acquired via an EPI

sequence with a TR of 3 s, TE of 30 ms, 54 slices, 2.5 x 2.56 mm in plane voxel size, slice thickness of 2.5 mm, inter-slice gap of 0.2 mm, flip angle of 90° and an 84 x 82 acquisition matrix, covering the whole cerebral cortex. A high-resolution T1-weighted anatomical image was collected for each participant (182 slices, 0.98 x 0.98 x 1.2 mm resolution, TR of 9.6 ms, TE of 4.6 ms, 256 x 256 acquisition matrix). The stimuli were presented with a custom-made script using PsychToolbox 3 (Brainard, 1997) in Matlab and they were projected onto a screen which could be viewed through a mirror mounted on the head coil.

fMRI procedure and experimental design

The functional data were collected using an event-related design consisting of 24 conditions representing the 24 birds (see Stimuli). The experiment included 10 to 12 runs, each lasting 6 min and 12 s (126 volumes per run). Each of the 24 conditions was presented four times per run, these 96 trials were interspersed with 96 fixation trials ranging from 1 to 9 seconds. We rapidly presented four different colored images of the same condition (bird) per trial: one of these four images was exactly the same image as was used in the MOA tasks, the other three images were pictures taken from different viewpoints. Image repetition with different viewpoints results in more neural activation, while minimizing effects of retinotopy and low-level confounds, which otherwise could have influenced neural responses in LOC (Sayres & Grill-Spector, 2008). Each image was presented for 500 ms without inter-stimulus interval (resulting in a 2 s presentation per trial) on a uniform gray background at a uniform size of 500 x 500 pixels. We created 12 separate event-related optimized sequences using Optseq2 (Greve, 2002, available at: http://surfer.nmr.mgh.harvard.edu/optseq), these 12 designs were counterbalanced across runs and across participants. Participants were asked to perform a one-back similarity judgment task (without specifying whether they should pay attention to the species or visual appearance of the birds) by pressing a button from one to four, one meaning “not at all similar” and four meaning “very similar”. A simple one-back similarity task was chosen to guarantee optimal performances among all participants in both groups. As a result, the differences between the stimuli would be relevant and consequently lead to a good signal

to pick up these differences among all participants in both groups. The order of the buttons was counterbalanced across runs.

Preprocessing and statistical analysis

The Statistical Parametric Mapping software package (SPM12, Welcome Department of Cognitive Neurology, London) was used to preprocess and analyze all imaging data. The following preprocessing steps were applied to the functional images: slice timing correction, spatial realignment (to the mean image) to correct for head movements, co-registration of the anatomical image and the functional images, spatial normalization to the standard Montreal Neurological 152-brain average template, resampling to a voxel size of 2.5 x 2.5 x 2.5 mm and spatial smoothing using a Gaussian kernel of 5 mm FWHM. We controlled for excessive head motion during scanning by discarding all functional runs in which movement in successive images exceeded the extent of one voxel, overall one run had to be discarded. For each participant, a general linear model was fitted, including regressors for each of the 24 conditions (birds) and the six motion realignment parameters to control for signal variation due to head motion.

Regions of interest

Based upon earlier work, we expect object representations and training effects to reside in high-level visual cortex and prefrontal cortex, with more basic representations of visual features in low-level visual cortex. To investigate these predictions, we delineated three bilateral anatomically defined regions of interest (ROIs) (i.e. *large ROIs*) in each participant: high-level visual cortex (HVC; BA 36, 37 and 20, average size ± SD of 572 ± 132 voxels), frontal cortex (FC; 4453 ± 2055 voxels), and as a control low-level visual cortex (LVC; Brodmann areas (BA) 17 and 18 which included V1 and nearby cortical regions, 719 ± 205 voxels). The anatomical masks that defined these three regions were created using the WFU PickAtlas Toolbox (Wake Forrest University PickAtlas, fmri.wfubmc.edu/cms/software). We selected all voxels located within these masks that were significantly active above an uncorrected threshold of $p < .001$ for

213 the contrast [all conditions - fixation]. These ROIs and the methods to construct them are exactly the same
214 as in Martens et al. (2018).

215 For further exploratory analyses, we subdivided high-level visual cortex and frontal cortex in
216 smaller regions (i.e. *small ROIs*). To define these regions, we used the data from the group of mineralogists
217 in Martens et al. (2018) as a localizer. First, we defined category-selective regions within high-level visual
218 cortex. We restricted the possible pool of voxels to be the voxels included in the aforementioned HVC
219 ROI. We then obtained four contrasts of interests from the 17 mineralogist participants in (Martens et al.,
220 2018): bird > nonliving objects, faces > nonliving objects, objects > scrambled images, and scenes >
221 nonliving objects. Each particular contrast was computed in a simple t-test in a second-level whole-brain
222 analysis, and voxels were selected using threshold $p < .001$ (uncorrected). Given that these category-
223 selective areas can overlap, we set exclusions in the functional criteria (Bracci et al., 2017) as follows: Bird-
224 selective areas (left BSA, average size 97±17 voxels; right BSA, 213±22 voxels) were defined contrasting
225 bird versus nonliving objects and the response (beta value) was numerically higher than face- and object-
226 selective voxels. Next, face-selective areas (left FSA, 147±28 voxels; right FSA, 118±18 voxels) were
227 defined contrasting faces versus nonliving objects with BSA excluded. Following this exclusions, object-
228 selective areas (left OSA, 75±28 voxels; right OSA, 88±21 voxels) were defined contrasting objects versus
229 scrambled images with BSA and FSA excluded. Scene-selective areas (left SSA, 217±35 voxels; right SSA,
230 116±20 voxels) were defined contrasting scenes versus nonliving objects (no overlap with other ROIs). All
231 category-selective regions were defined per hemisphere separately.

232 In the prefrontal cortex, we also defined four more restricted regions of interest for explorative
233 purposes, namely the left (229±91 voxels) and right (235±111 voxels) dorsolateral prefrontal cortex
234 (DLPFC) and the left (85±78 voxels) and right (69±63 voxels) inferior frontal gyrus (IFG) were defined
235 selecting all visually active voxels [all conditions - fixation] within the anatomical masks BA9 and BA46 and
236 BA44-45, respectively.

Multi-voxel pattern analyses

We applied correlational multi-voxel pattern analyses (MVPA) to investigate the neural representational space of the 24 birds in ornithologists and control participants. For each subject and for each ROI, we created a neural dissimilarity matrix consisting of the pairwise (dis)similarities between the neural response patterns of the 24 birds. The following steps describe the creation of a dissimilarity matrix for one subject and one ROI. We extracted the parameter estimates of the responses per voxel for each condition and for each run. The response in each voxel was normalized by subtracting the average response across all conditions per run. This way, per run a multi-voxel selectivity pattern was obtained for each condition. Next, the runs were randomly divided into two independent subsets (repeated 100 times and results averaged across all 100 iterations): for each condition, the response pattern in the first subset was correlated with the response patterns of all conditions in the second subset. This resulted in an asymmetrical 24 x 24 correlation matrix, which we made symmetrical by averaging both halves and transformed into a dissimilarity matrix (1-correlation). For subsequent analyses, only the upper half of the matrix was used. To test whether reliable information about the 24 birds was present in the neural response patterns, we compared the diagonal values of the dissimilarity matrix (within-condition dissimilarities) to the off-diagonal values (between-condition dissimilarities); the within-condition dissimilarities should be significantly lower than the between-condition dissimilarities.

RESULTS

Mental representational space of objects of expertise

To be able to investigate the mental representational space for the 24 birds of both experts and novices, all participants were asked to arrange the birds first according to their species similarity and in a second task according to their visual similarity. The dissimilarity matrices are shown in Figure 2. At a first glance, it becomes clear that both ornithologists and control participants arranged the birds according to the bird

orders in both tasks: songbirds were grouped together, as were wading birds and birds of prey respectively.

insert Figure 2 here

To compare how consistent the subjects within each group solved both tasks, we calculated within-group correlations for each task. Each subject's behavioral dissimilarity matrix (upper half, excluding the diagonal) was correlated with the individual dissimilarity matrices from all other subjects belonging to the *same* group. These correlations were averaged, resulting in one within-group correlation per subject per task (Figure 3A). For both the species task and the visual task, the average within-group correlation for ornithologists was significantly higher than the average within-group correlation for novices, indicating that the experts solved both tasks more consistently (species task: $t(38) = 11.04$, $p < .001$; visual task: $t(38) = 2.97$, $p = .008$).

insert Figure 3 here

Next we calculated the between-group correlations (each subject's dissimilarity matrix correlated with the individual dissimilarity matrices from all subjects belonging to the *other* group) and compared these to the within-group correlations. If the structure of the mental representational spaces of the two subject groups would differ, we would expect the between-group correlation to be lower than a reference value which lies in between the within-group correlations of the relevant task. This reference in case of a null hypothesis (no difference in mental representational space) is calculated as the square root of the product of the two within-subject correlations (e.g., Op de Beeck, Deutsch, Vanduffel, Kanwisher, & DiCarlo, 2008). This approach (Op de Beeck et al., 2008) has actually become a standard in a slightly different application, namely to calculate the noise ceiling (signal to noise or SNR) in fMRI data (Bracci & Op de Beeck, 2016; see Nili et al., 2014 for a thorough explanation). Similar to this SNR application, different participants are considered as different measurements of the same similarity structure. The

correlations between subjects of the same group provide a ceiling value for correlations that can be obtained when correlating with subjects from another group (our current application) or with data from a different modality such as behavior (the SNR application). For the visual task, this benchmark was .44. The empirically measured between-group correlation (Pearson's r = .42) did not differ significantly from this reference value ($t(19) = 1.04$, $p = .31$), indicating that experts and control participants solved the visual similarity arrangement task in a similar manner. However, for the species task, the measured between-group correlation (Pearson's r = .43) was significantly lower than the reference value of .48 ($t(19) = 5.26$, $p < .001$), signaling a qualitative difference between the bird arrangements performed by the two subject groups. Visual inspection of the dissimilarity matrices of both tasks (see Figure 2) suggests that both groups arranged the birds in terms of the bird orders. Within the orders there is a specific substructure in experts that is not present in controls and also not in the other task. Note however that even for the between-group comparisons we find positive correlations, slightly higher than the within-group correlations for novices. This illustrates that the overall structure of the representational space is not affected strongly by the task.

The design of the study allows us to probe one specific qualitative difference between the groups in their mental representations. As mentioned in the Methods section, the 24 stimuli were chosen in such a way that bird species could not easily be derived from the visual features of the birds alone. The stimuli were divided into triplets in which two birds (A and B) belonged to the same species but were visually different and two birds (B and C) belonged to a different species but were visually similar (see Figure 1). We calculated for each subject the average distance between birds A and B and the average distance between birds B and C, for both MOA tasks (see Figure 3B). In the species task, ornithologists successfully made the distinction between birds belonging to the same species and birds bearing a visual similarity: they placed birds A and B closer together than birds B and C ($t(19) = 10.04$, $p < .001$). In the visual task, there was no difference in distance between birds A and B on the one hand and birds B and C on the other

($t(19) = 0.05$, $p = .96$), suggesting that ornithologists were using both species and visual information while judging the visual similarity of the birds. Control participants placed the visually similar birds closer together in the visual task ($t(19) = 2.11$, $p = .048$) and the same tendency was present in the species task, although the difference did not reach significance ($t(19) = 2.09$, $p = .051$). This indicates that the control participants were misled by the visual resemblance of the birds belonging to a different species. In each task, ornithologists placed birds A and B closer together than control participants did ($t(39) = 6.85$, $p < .001$). Control participants on the other hand, judged the visually resembling birds to be more similar than ornithologists ($t(39) = 2.55$, $p = .015$). Summarized, the experts compared to novices, have richer and more fine-grained representations of item similarities and show more inter-subject consistency in these representations.

Neural representations of objects of expertise: Increased distinctiveness, higher between-subject consistency, and stronger correlations with behavior

To investigate the influence of expertise on the neural representations of objects of expertise in low-level visual cortex, high-level visual cortex and the frontal lobe, we presented the same 24 bird images to a group of bird experts ($n = 20$) and a group of control participants ($n = 20$) while collecting neural data. We defined three *large ROIs* that are intended to capture the visual information processing that unfolds through the ventral visual stream from primary visual cortex (LVC) to more anterior lateral and medial occipitotemporal cortex (HVC) and from there to frontal cortex (FC), using the same ROI definition as before in Farah Martens et al. (2018).

insert Figure 4 here

We depicted the neural dissimilarity matrices in each large ROI and for both subject groups (see Figure 4). Interestingly, visual inspection of the matrices suggests that for both subject groups,

information about the bird orders seemed to strengthen from the lower-level to the higher-level regions. In LVC, the neural representational spaces of both experts and novices did not reveal any striking structure, while in HVC and particularly in FC, a quadrant-like structure starts to emerge. This structure is more clearly visible in the matrices of the expert group. Below we characterize the effects in these matrices in more statistical terms. First of all, we tested whether reliable information about the 24 birds was present in the neural response patterns within each ROI. Since these conditions all belonged to the same category and therefore were visually similar, it could be the case that multi-voxel pattern analysis was not sensitive enough to distinguish the neural representations of the different birds from each other. For each participant and for each ROI, we compared the within-condition dissimilarities (diagonal cells of the dissimilarity matrices) to the between-condition dissimilarities (off-diagonal values) (see Figure 5). For both the ornithologists and the control participants, in all three ROIs the average within-condition dissimilarities were significantly smaller than the average between-condition dissimilarities (see Table 1), indicating that the multi-voxel patterns conveyed information about the presented birds.

insert Figure 5 here

Table 1. *Overview of the paired t-test statistics for each large ROI, in each subject group on the difference between within- and between-condition dissimilarities.*

		M* ± *SD **(within)**	***M* ± *SD*** **(between)**	***t***	***p***	***df***
LVC	**Experts**	0.60 ± 0.10	1.02 ± 0.00	17.4	< .001	19
	Controls	0.61 ± 0.13	1.01 ± 0.00	13.1	< .001	19
HVC	**Experts**	0.85 ± 0.08	1.01 ± 0.00	8.10	< .001	19
	Controls	0.88 ± 0.06	1.01 ± 0.00	9.00	< .001	19
FC	**Experts**	0.89 ± 0.06	1.00 ± 0.00	8.00	< .001	19

Controls	0.93 ± 0.05	1.00 ± 0.00	6.30	< .100	19

As a quantitative indication for the distinctiveness of the response patterns, we calculated for each subject and each ROI the difference between the within-condition dissimilarities and the between-condition dissimilarities. In LVC and HVC, there was no difference between ornithologists and control participants in the distinctiveness of the multi-voxel response patterns (between-condition – within-condition, LVC: $t(38) = 0.44$, $p = .66$; HVC: $t(38) = 1.15$, $p = .26$). In FC, in contrast, the neural representations of the different birds were more distinct in the experts compared to the novices ($t(38) = 2.17$, $p = .036$). This might be a first cause of the clearer matrix structure for experts in Figure 4, in particular through a stronger diagonal that would also allow a wider range of values in the off-diagonal cells.

Next, we investigated the representational similarity in the off-diagonal cells. Similarly to earlier analyses on the behavioral matrices, we asked ourselves how consistent the neural representational spaces of ornithologists and control participants were within and between groups. For each ROI, we again calculated the within-group and between-group correlations between the neural dissimilarity matrices for each participant. Results are shown in Figure 6. In LVC, there was no difference in consistency between the two subject groups ($t(38) = 0.31$, $p = .76$). However, in HVC and in FC, there was a significant difference between the within-group correlations of ornithologists and control participants (HVC: $t(38) = 4.92$, $p < .001$; FC: $t(38) = 7.88$, $p < .001$). The neural representational space for the 24 birds in ornithologists was more consistent compared to the representational space in control participants for these higher-level ROIs. This result is in line with the behavioral results, which showed that the experts solved the object arrangement tasks more consistently compared to novices. This might be a second cause of the clearer matrix structure for experts in Figure 4.

insert Figure 6 here

Finally, we investigated whether the neural patterns in experts would not only be more distinctive and more consistent, but also be qualitatively different. As for the behavioral matrices, we again compared the average correlation between groups to the reference correlation that would be expected based on the within-group correlations in that specific ROI (see Mental representational space of objects of expertise and Figure 6). The between-group correlations did not differ from the expected reference value in any of the ROIs (LVC: $t(19) = 0.18$, $p = .86$; HVC: $t(19) = 0.96$, $p = .35$; frontal lobe: $t(19) = 1.33$, $p = .20$). This indicates that the structure of the neural representational space of the 24 birds was not influenced very strongly by expertise: the mutual relationships between the birds were similar for novices and experts. This finding suggests that the structure of the neural representational space is not drastically different between the two groups. This situation is similar to the behavioral result for the visual task. Likewise, the neural data did not show a difference between experts and novices with regard to sensitivity to same and different species images within triplets in any of the ROIs (AB vs BC images, all group comparisons $p > .426$). However, we doubt that the neural data have the sensitivity to investigate these specific subsets of the data given that the standard errors are very large when focusing analyses upon a small subset of pairwise comparisons. Consistent with this reasoning, we find that the mean dissimilarity across all off-diagonal elements is much less variable across participants (SD varies from 0.009 to 0.023 between subject groups and ROIs) compared to the mean dissimilarity in the AB (SD between 0.11 and 0.19) and BC (SD between 0.12 and 0.27) comparison. This increase of SD with an order of magnitude strongly affects our ability to uncover group differences in AB or BC relative to group differences in overall dissimilarity, as the same absolute difference in dissimilarity would yield an effect size that is an order of magnitude smaller.

Next, we investigated how the neural representational space compares to the behavioral similarities. For each subject, we correlated the individual behavioral dissimilarity matrix for each task

with the neural dissimilarities for the three ROIs (see Table 2). No group differences were found in LVC (species task: $t(38) = 0.68$, $p = .50$; visual task: $t(38) = 0.17$, $p = .87$). In HVC, there was a tendency towards stronger correspondences between the behavioral and neural data in the expert group (species task: $t(38) = 2.40$, $p = .021$; visual task: $t(38) = 1.70$, $p = .098$. This effect was statistically more robust in FC (species task: $t(38) = 2.55$, $p = .015$; visual task: $t(38) = 2.41$, $p = .021$). The group differences in HVC and FC were also clearly present when the average behavioral matrix was used per group (two-tailed p-values ranging from .003 to .041). The increased correlations in the expert group seem to relate to what the behavioral matrices of the two tasks have in common, because the same analysis with partial correlations (i.e. between the group neural RDMs in LVC, HVC and the FL on the one hand and the behavioral RDMs of the species and visual task on the other hand) did not result in equally robust group differences (most extreme $p = .04$, for FC with the visual task). In conclusion, correlations between behavioral and neural similarity were higher in the experts in high-level visual and frontal cortex.

Table 2. Overview of the test statistics for each large ROI, in each behavioral task, between each subject group on the correlation between the neural representational space and the behavioral similarities. Significant group differences are underlined.

		M ± SD (Controls)	***M ± SD (Experts)***	***t***	***p***	***df***
LVC	**Species**	0.08 ± 0.05	0.06 ± 0.09	0.68	.5	38
	Visual	0.06 ± 0.07	0.06 ± 0.06	0.17	.87	38
HVC	**Species**	0.08 + 0.09	0.15 + 0.1	2.4	.021	38
	Visual	0.08 ± 0.07	0.13 ± 0.1	1.7	.098	38
FC	**Species**	0.08 + 0.11	0.2 + 0.06	2.55	.015	38
	Visual	0.09 + 0.11	0.19 + 0.15	2.41	.021	38

Explorative analyses in smaller regions of interest

We performed further exploratory analyses on smaller sub-regions within HVC and FC (i.e. small ROIs). We consider these analyses to be post hoc and exploratory, because our original plan was to only include the three large ROIs included in the main manuscript. Smaller ROIs typically show much more noisy multi-voxel patterns, and we doubted that our study would have sufficient sensitivity at this finer spatial level given that we search for selectivity for subordinate differences between stimuli. Nevertheless, such analyses can provide relevant information about the anatomical distribution of the strongest effects, and resonates with earlier literature in which a lot of attention was given to specific regions of interest such as the fusiform face area.

Interestingly, at the finer level of smaller ROIs, many sub-regions tended to show the same effect as the larger region did, albeit not always significant. First, we report the findings in the frontal ROIs. The effect sizes of both the increased distinctiveness (diagonal – off-diagonal) and the higher inter-subject consistency (all $p < .01$ of between-group comparisons) in experts seems similar in all four frontal ROIs and also compared to the effects in the large FC ROI. For distinctiveness, the data at this smaller scale were not sensitive enough to show convincing group differences. Although the uncorrected p-value was below .05 in right DLPFC ($t(38) = 2.24$, $p = .031$), this was no longer significant when correcting for multiple ROIs. There were no significant main or interaction effects in a repeated-measures ANOVA with the factors 'hemisphere' and 'location', but this could be due to a lack of sensitivity at the level of smaller ROIs. For within-group correlations, each smaller frontal ROI showed a significantly larger correlation for the ornithology experts compared to controls (all $p < .001$; see Figure 7A), revealing that the strong effect in the large frontal FC ROI is distributed across multiple sub-regions.

insert Figure 7 here

In high-level visual cortex, the large HVC ROI showed larger within-group correlations for ornithologists. We investigated the distribution of this effect within high-level visual cortex. Here the group differences seem variable between smaller ROIs (see Figure 7B). When we correct for the number of sub-ROIs (8), the only significant effects were seen in right bird-selective voxels ($t(38) = 5.90$, $p_{uncorr} < .001$) and in right face-selective voxels ($t(38) = 3.58$, $p_{uncorr} < .005$). It is tempting to see this finding as a sign that effects in visual cortex are lateralized to the right hemisphere and restricted to voxels that process more animate stimuli. We checked this statistically through an ANOVA with two within-subject factors 'hemisphere' and 'preferred category', and 'group' as between-subject factor. This ANOVA showed a main effect of hemisphere ($F(1,38) = 48.54$, $p < .001$), indicating that bird representations in high-level visual cortex are more consistent across subjects in the right hemisphere, irrespective of group. In addition, there was an interaction between hemisphere and group ($F(1,38) = 25.84$, $p < .001$), on top of a main effect of group ($F(1,38) = 10$, $p = .003$), confirming that expertise effects were stronger in the right hemisphere. Finally, there was also an interaction between 'preferred category' and group ($F(3,114) = 6.56$, $p < .001$), showing that strength of expertise effects differ between these sub-ROIs. Note however that there were also trends (significant at uncorrected level) in a left ROI (left face-selective: $t(38) = 2.71$, $p_{uncorr} = .01$), and a nonanimate-preferring ROI (right SSA: $t(38) = 2.40$, $p_{uncorr} = .02$), suggesting that neither factor is absolute.

DISCUSSION

In the present study, we investigated the influence of visual expertise in ornithology on the mental and neural representations of individual objects of expertise. In behavior as well as fMRI we found evidence for a rich representational similarity structure. Both behavioral and neural results indicated a quantitative enhancement of the representations of objects of expertise in experts compared to novices. The mental as well as the neural representational spaces, in the higher-level regions, were more consistent among

experts. Furthermore, in the frontal lobe, the experts' neural response patterns for the individual objects of expertise were more distinctive. Correlations between behavioral and neural similarity were higher in the experts in high-level visual and frontal cortex.

This study investigates neural expertise effects at the more detailed, subordinate level. So far, research on the neural basis of expertise has mostly focused upon the neural activity underlying the expert object category instead of the individual objects of expertise (Bilalić, Langner, Ulrich, & Grodd, 2011; Bilalić, Grottenthaler, Nagele, & Lindig, 2016; Floyd et al., 2017; Gauthier et al., 2000; Gauthier & Tarr, 2002; Harel et al., 2010; Harley et al., 2009; Martens, Bulthé, van Vliet, & Op de Beeck, 2018; Mongelli et al., 2017). In an earlier expertise study (Martens et al., 2018), we shed light on the interaction between the specific domain of expertise and the localization and the extent of the underlying neural changes at the whole-brain level. Using large-scale univariate and multivariate analyses, we systematically compared the neural responses to expert object categories in two groups of visual experts, ornithologists and mineralogists, and a group of control participants. Results indicated the presence of distributed expertise-related neural changes for both domains of expertise, with more widespread effects for ornithology compared to mineralogy. Furthermore, these neural expertise effects consisted of a combination of domain-specific neural changes in high-level visual cortex, and domain-independent expertise effects in the frontal lobe.

The reason why many studies have not looked at within-object categories is that the neural representations of visually similar exemplars within a specific category are very hard to differentiate. While selective neural responses to visually similar objects have already been detected using multi-voxel analyses (e.g. Alfred et al., 2018; Caspari et al., 2014; Connolly et al., 2012; Eger et al., 2008), the current study demonstrates that it is possible to distinguish individual objects belonging to the same animate category and comparing those between experts and novices. Some related, however different research on the within category of conceptual representations, is the work by Cetron and colleagues (2019, 2020)

who demonstrated the presence of concept knowledge information (e.g. forces on structures) in anterior VOTC in engineering students compared to novices. Given this background, our findings are a very important step towards a further investigation of how expertise changes the representation of visual objects of expertise.

In this study we demonstrated a significant enhancement of behavioral and neural representations in experts, using ornithologists as the case in point. At the behavioral level, experts showed more inter-subject consistency in their similarity judgments compared to novices. Furthermore, the similarity structure in experts was more adaptable to the task at hand, showing interesting differences between a visual and a more semantic task that were not observed in the novices. Previous studies in various domains have already shown that expertise changes representations as assessed through behavior, including studies that focused upon the geometry of mental representations (e.g. Ballester, Patris, Symoneaux, & Valentin, 2008; Collins & Behrmann, 2020; Gillan, Breedin, & Cooke, 1992; Kivlighan Jr, D. M. & Quigley, 1991; Schvaneveldt et al., 1985; Soufflet, Calonnier, & Dacremont, 2004).

We investigated the neural correlates of such behavioral changes by analyzing the representational geometry at the subordinate level for the domain of birds. Representations at the neural level were different in experts compared to controls in several ways. These effects were most clearly demonstrated in frontal cortex and sometimes also present in high-level visual cortex. First, neural patterns of different bird conditions were more distinct from each other, as derived from a more pronounced diagonal in the dissimilarity matrices. The more this diagonal is present, the more it matters whether a neural response pattern is compared to a neural pattern from the same condition or from a different condition (Ritchie et al., 2017). Second, the neural representation was more consistent among experts than among novices, as derived from higher correlations between matrices from different experts than between matrices from different novices. To our knowledge, this is the first time that such an effect is demonstrated at the neural level. In general, this finding resonates with the situation that the process

of becoming an expert involves a lot of training that is shared among experts. Specifically in the domain of ornithology, experts would typically have learned about the same taxonomic differences and have engaged in active learning of bird species. As a third finding, we found that the neural representations in frontal cortex were more correlated with the behavioral similarity spaces in experts than in novices, demonstrating the behavioral relevance of the investigated neural patterns and changes therein.

Each of these effects suggest that the neural representations of objects of expertise have become stronger and more robust. Note that the three effects are not redundant. For example, to get an increased consistency, we need more similarity between individuals. In contrast, the increased distinctiveness has to be due to the strength of neural representations *within* individuals. Yet, it is possible that these three effects would be consequences of one underlying mechanism that results in an overall increase in the robustness, reliability, or signal to noise ratio of the representational similarity structure measured in experts. If the signal to noise ratio of neural patterns within an individual increases, then we do not only expect a higher within-subject distinctiveness, but also a possibility for higher consistency between individuals and a higher correlation with behavior. In this regard it is also important to consider that each bird condition was represented in the experiment by multiple images presented on each trial. One hypothesis is that the increased distinctiveness that we measured, reflects a representation that is more invariant to these differences at the image level. Given that our experimental design was not set up to test image level responses, further experiments will be needed to determine what the exact cause is of the more robust representations in experts.

There were also aspects in which neural representations of experts and novices did not differ in any brain region. Between-group correlations of neural representations between experts and novices were about as high as could be expected given the within-group correlations. In addition, at the neural level we did not find the very specific semantic effect of whether or not two visually dissimilar birds would belong to the same species. The absence of such differences could be due to several aspects of our design

and methods. First, while in the scanner, participants were not specifically instructed to judge the birds' similarity based on their species, instead they were free to perform the task in a way that they deemed to be most fitting. Results of the behavioral tasks showed that a structural difference between the representational spaces of the two subject groups only emerged when subjects were explicitly asked to take species information into account. We decided to use a less constrained task of which we were sure that novices could also perform it without difficulties. However, it is possible that changes in the neural representational space due to expertise would be amplified by instructing the subjects to perform an expertise-related species task while in the scanner. Further studies could tackle this issue by having the subjects perform two different tasks while in the scanner: one expertise-related task and one unrelated task with the same objects of expertise (e.g. Harel, Gilaie-Dotan, Malach, & Bentin, 2010). Secondly, the method of MVPA might simply not be sensitive enough to pick up subtle changes in the mutual relations between the neural representations of the objects of expertise at the subordinate level. In particular, the specific effects of semantics only affect a few cells in the similarity matrices, not the general structure of the similarity space. It could be that more pronounced expertise-related changes to the neural representational space are present but that we simply cannot detect them using the experimental design and data quality that we currently have.

In sum, we have demonstrated that visual expertise changes neural information processing and is associated with an increased distinctiveness and between-subject consistency of behaviorally relevant neural representations, in particular in prefrontal cortex and to some extent also in high-level visual cortex.

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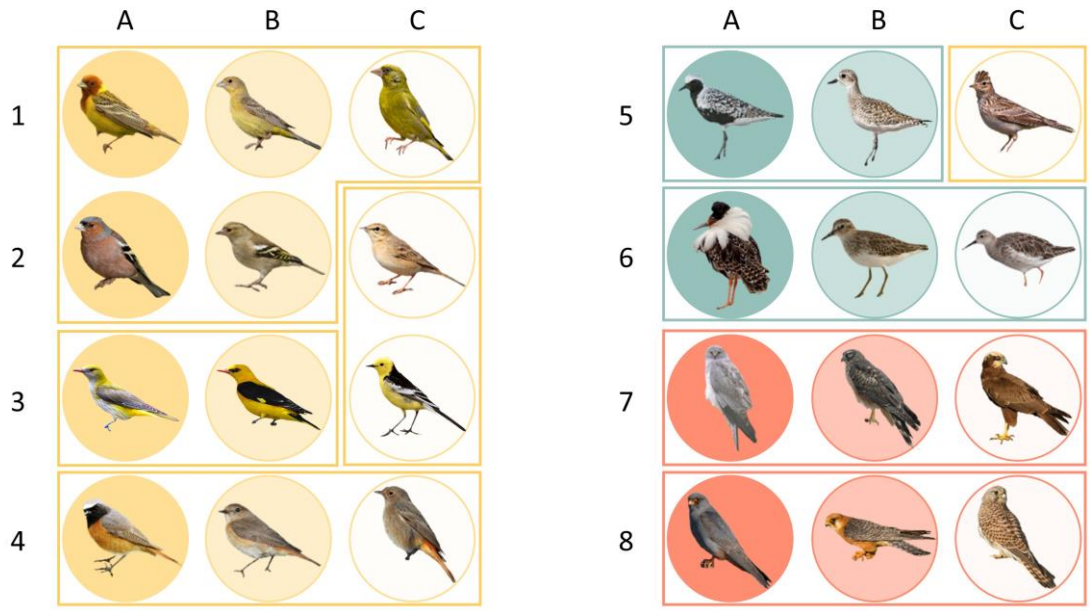


Figure 1. The 24 birds that were selected consist of eight triplets. In each triplet, birds A and B belong to the same species but are visually different, while birds B and C belong to different bird species but are visually similar. The bird species are grouped into bird families, which are indicated by rectangular frames. Furthermore, the bird families belong to three large bird orders: songbirds (yellow), wading birds (blue) and birds of prey (red).

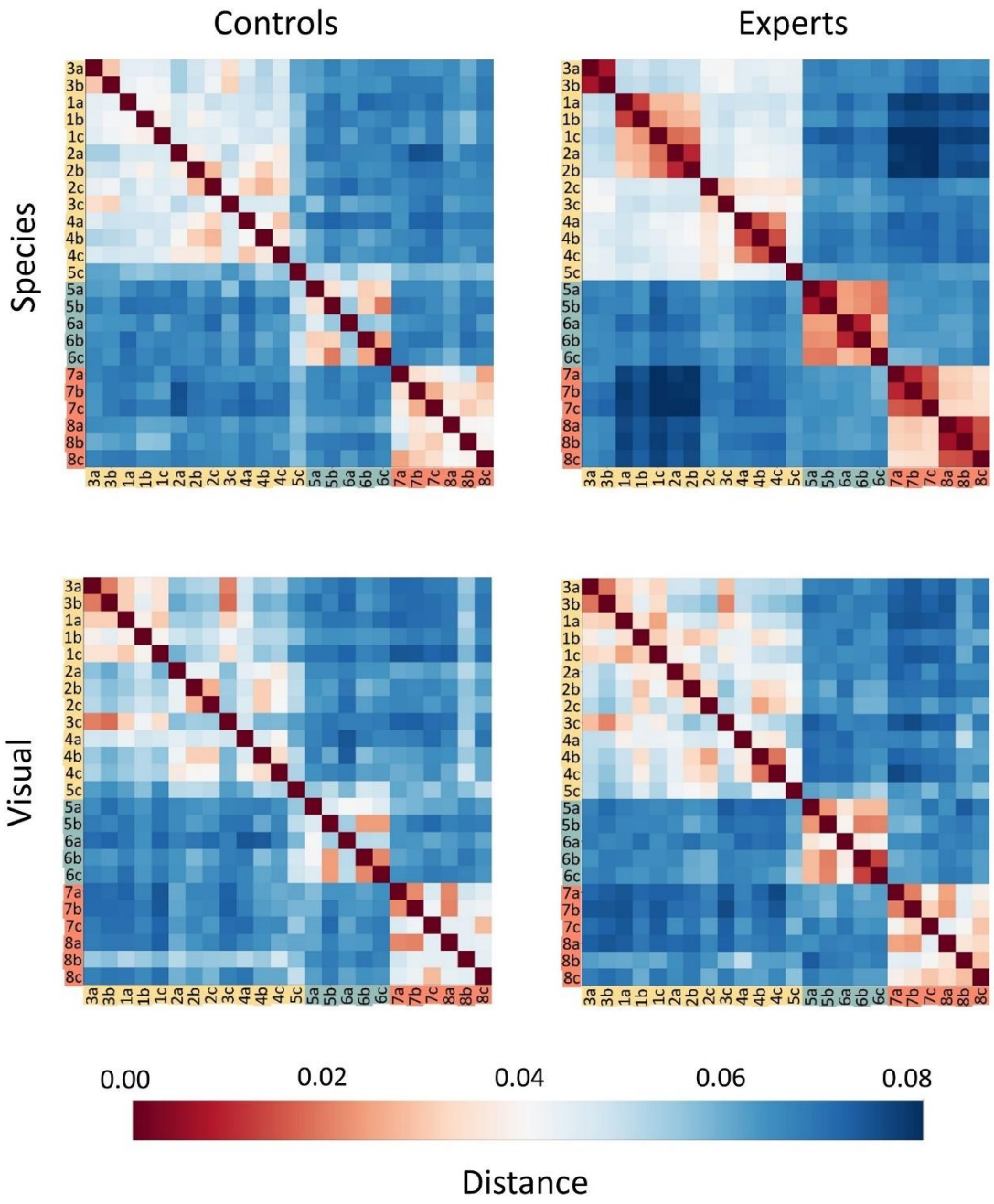


Figure 2. Matrices representing the average pairwise dissimilarities or distances between the 24 birds based on the behavioral MOA arrangements made by ornithologists and control participants in the species task and the visual task. Smaller dissimilarities are visualized with reddish shades and larger dissimilarities with bluer shades. All diagonal values are set to zero. The matrices are sorted in such a

way that they reflect the taxonomy of the birds. Songbirds are indicated by yellow labels, wading birds by blue labels and birds of prey by red labels. The bird codes match the codes used in Figure 1.

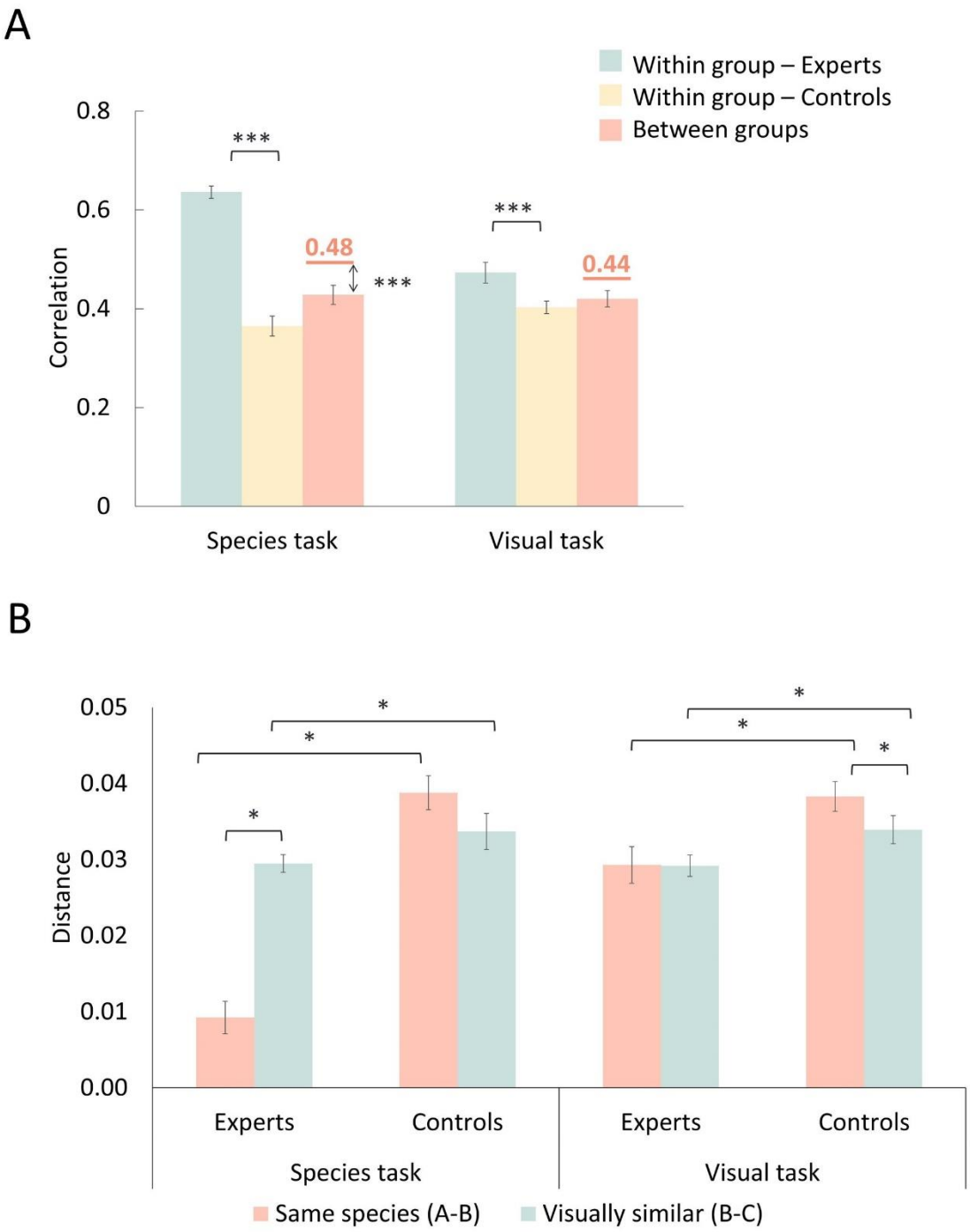


Figure 3. **A.** Bar graph depicting the average within- and between-group correlations of the arrangements made by ornithologists and controls in the species task and the visual task. Error bars display the standard error of the mean (SEM). Significant group differences are indicated by asterisks:

*** $p < .001$. The horizontal lines on the between-group correlations represent the reference value of expected between-correlations based upon within-group correlations and the assumption that there are no differences in representational structure between groups. **B.** Overview of the average distance between birds A and B (i.e. same species) and the average distance between birds B and C (i.e. visually similar) for the MOA visual and species task in experts and controls. Error bars display the standard error of the mean (SEM). Significant group differences are indicated by asterisks: * $p < .05$.

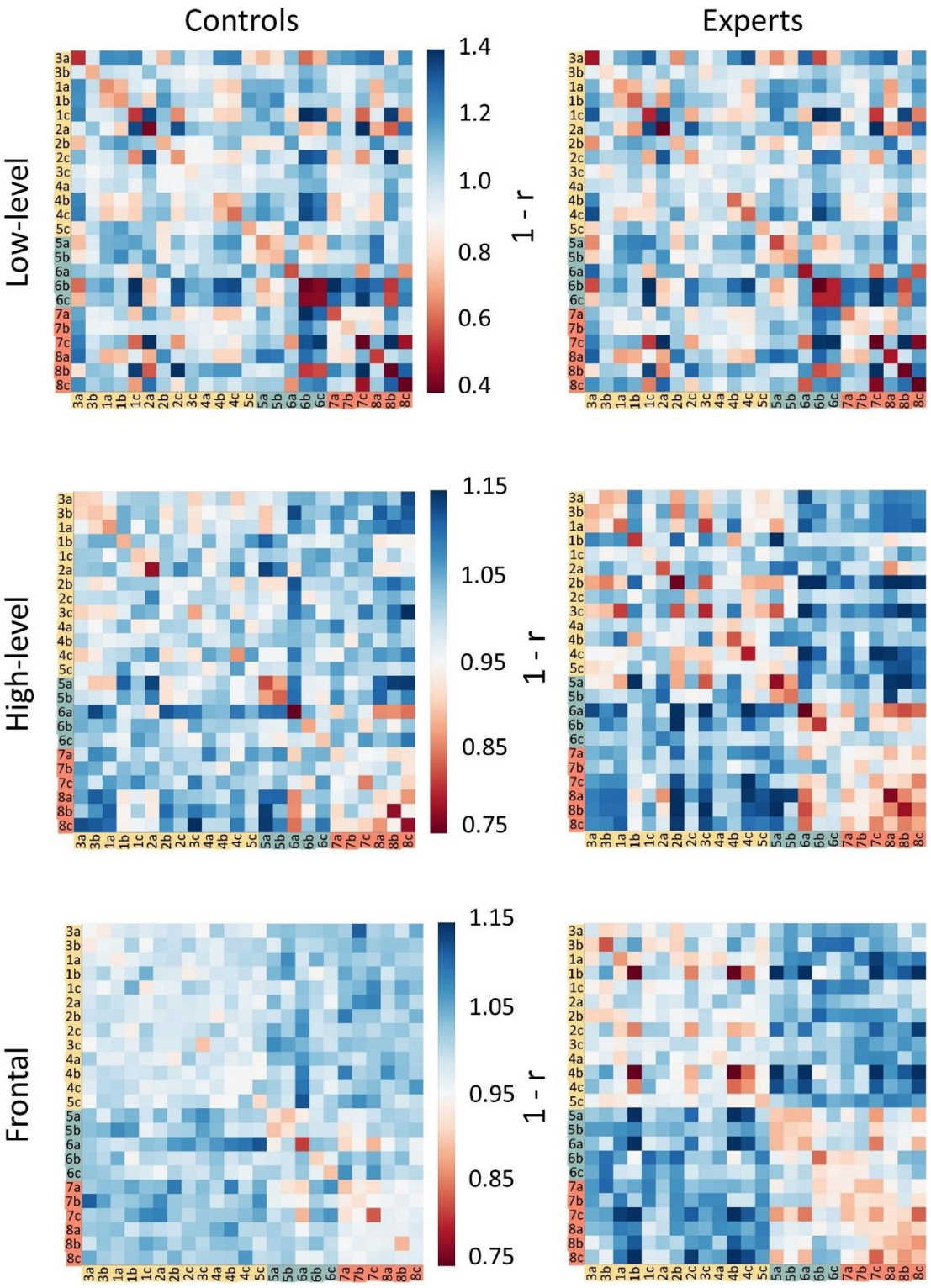

Controls
Experts
Low-level
High-level
Frontal
1 - r
1.4
1.2
1.0
0.8
0.6
0.4
1.15
1.05
0.95
0.85
0.75
3a 3b 1a 1b 1c 2a 2b 2c 3c 4a 4b 4c 5c 5a 5b 6a 6b 6c 7a 7b 7c 8a 8b 8c

Figure 4. Matrices representing the average pairwise dissimilarities (1-correlation) between the neural response patterns underlying the 24 birds for expert and control participants in the low-level visual cortex (LVC), the high-level visual cortex (HVC) and the frontal lobe (FL). Smaller dissimilarities are visualized with reddish shades and larger dissimilarities with bluer shades. The matrices are sorted in such a way that they reflect the taxonomy of the birds. Songbirds are indicated by yellow labels, wading birds by blue labels and birds of prey by red labels. The bird codes match the codes used in Figure 1.

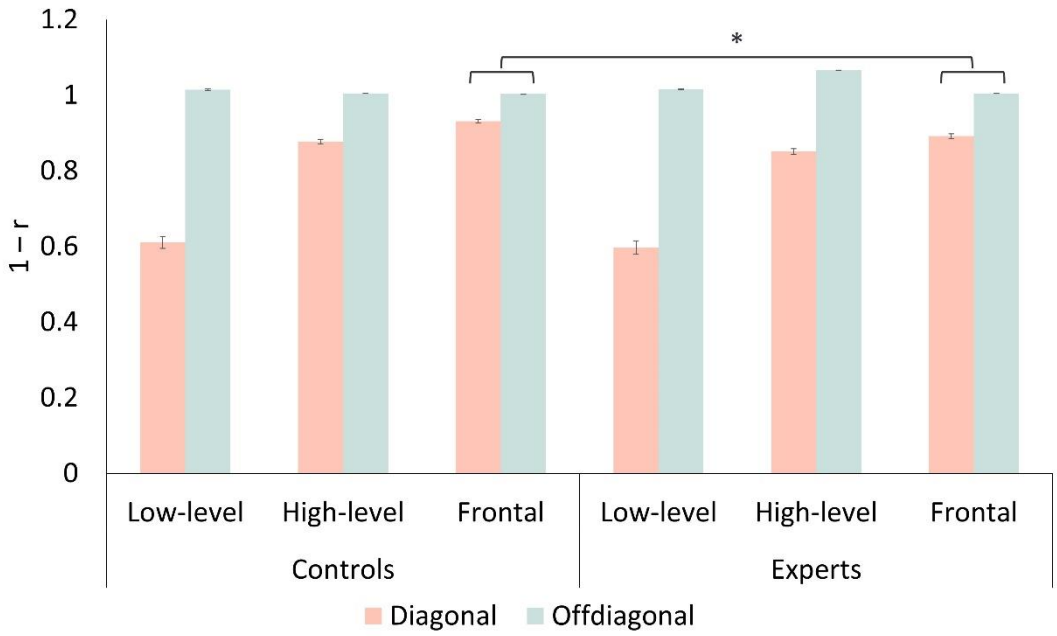


Figure 5. Overview of the diagonal and off-diagonal values of the RDMs in Low-level, High-level and Frontal ROI, for Controls and Experts. Error bars represent the standard error, significant group differences are indicated by asterisks: * $p < .05$.

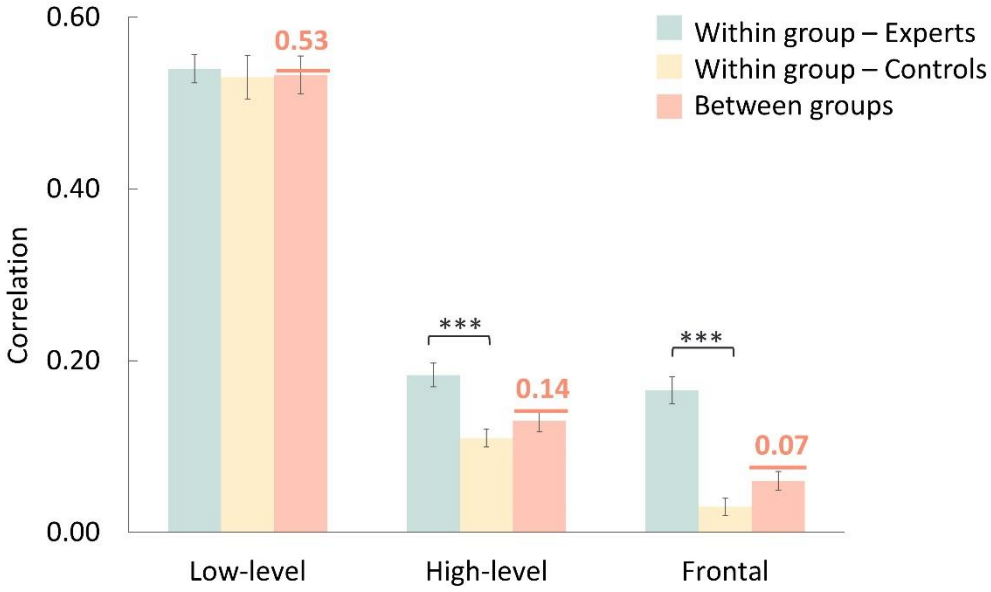
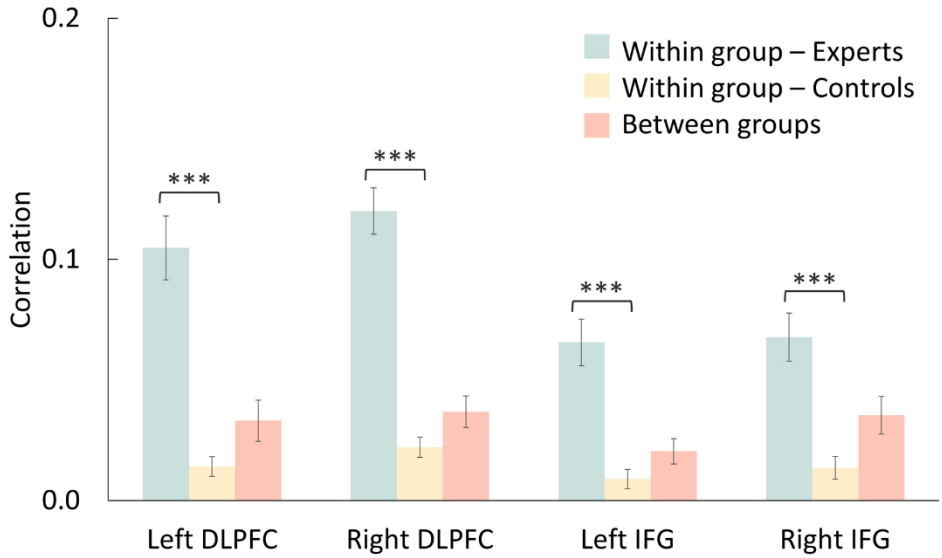


Figure 6. Bar graph depicting the average within- and between-group correlations of the neural representational spaces of Experts and Controls in the low-level visual cortex, high-level visual cortex and the frontal lobe. Error bars display the standard error of the mean (SEM). The reference value for the between groups correlations is displayed by the horizontal line. Significant group differences are indicated by asterisks: *** $p < .001$.

A


0.2
0.1
0.0
Correlation
Within group – Experts
Within group – Controls
Between groups
***
***
***
***
Left DLPFC
Right DLPFC
Left IFG
Right IFG

B

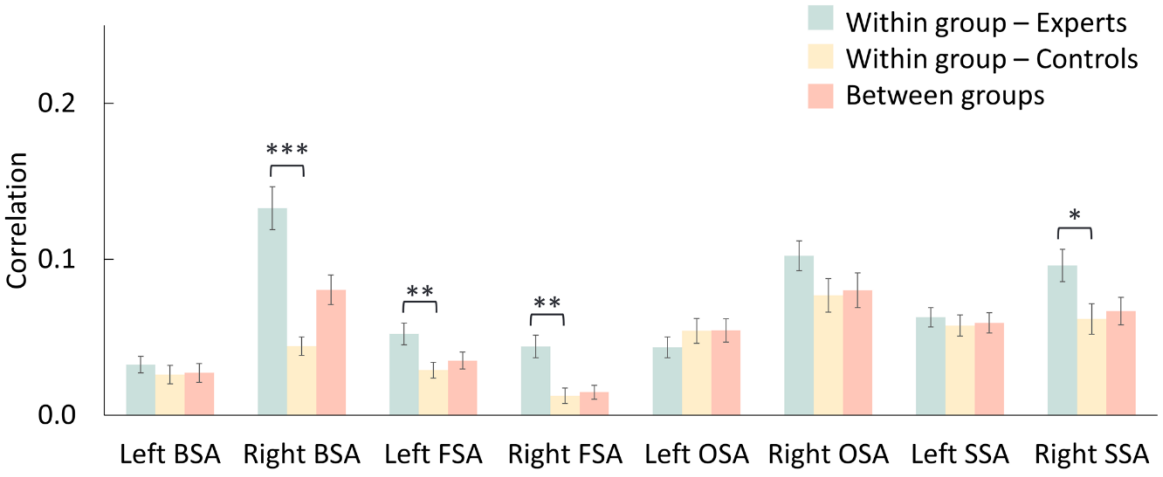

0.2
0.1
0.0
Correlation
Within group – Experts
Within group – Controls
Between groups
***
**
**
*
Left BSA
Right BSA
Left FSA
Right FSA
Left OSA
Right OSA
Left SSA
Right SSA

Figure 7. **A.** Bar graph depicting the average within- and between-group correlations of the neural representational spaces of Experts and Controls in the left and right dorsolateral prefrontal cortex, and inferior frontal gyrus. Error bars display the standard error and significant group differences are indicated by asterisks: *** $p < .001$ **B.** Bar graph depicting the average within- and between-group correlations of the neural representational spaces of Experts and Controls in the left and right bird-selective areas (BSA), face-selective areas (FSA), object-selective areas (OSA), and scene-selective areas (SSA). Error bars display the standard error. Significant group differences are indicated by asterisks: *** $p_{uncorr} < .001$, ** $p_{uncorr} < .01$, * $p_{uncorr} < .05$.