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Inside the expert’s brain

The neural basis of visual expertise

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Summary

Experience and learning shape human behavior and alter brain functioning. To investigate the effects of learning on visual object representations in the brain, real-world visual experts are studied.

Many different domains of visual expertise (e.g. bird expertise, car expertise, radiology etc.) have been linked to changes in neural processing, and these neural effects of expertise have been found in a wide variety of brain regions. In the first fMRI study, we aimed to 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.

A large body of research exists on both behavioral and neural effects of visual expertise, however, these two separate streams in the literature show large discrepancies. While many behavioral studies have emphasized the importance of subordinate-level processing in expertise, not a single study has investigated the neural activation underlying *individual* objects of expertise in a real-world domain. We aimed to fill this gap in the literature by investigating both mental and neural representations of individual objects of expertise in experts and compare them to those of novices to detect expertise-related changes. In a second experiment, we investigated the mental representations of individual objects of expertise and their perceptual similarity. Results showed a quantitative enhancement of the mental representational space of objects of expertise in experts compared to novices. Furthermore, expertise induced qualitative changes in the form of more fine-grained, subordinate-level distinctions in experts' mental representational spaces. These expertise effects were influenced by top-down factors.

In the final experiment of this dissertation, we explored whether and how expertise changes the way in which individual objects of expertise are represented in the brain. We applied multi-voxel pattern analyses to investigate the neural representational spaces of objects of expertise for both experts and novices. Results indicated quantitatively enhanced neural representations of objects of expertise in experts compared to novices, in higher-level brain regions. The overall structure of the neural representational space was not altered by expertise. Finally, the mental and neural representational spaces of both experts and novices were compared. The studies described in this dissertation advanced our understanding of the neural basis of visual expertise.

Samenvatting

Het menselijk gedrag en het functioneren van onze hersenen worden beïnvloed wanneer we leren en ervaring opdoen. Om de effecten van leren op visuele objectrepresentaties in de hersenen te onderzoeken, worden visuele experts bestudeerd.

Veel verschillende domeinen van visuele expertise (zoals vogelexpertise, auto-expertise, radiologie enz.) zijn in verband gebracht met veranderingen in neurale activatie en deze neurale effecten van expertise zijn gevonden in een breed scala van hersengebieden. In de eerste fMRI-studie trachtten we licht te werpen op de interactie tussen het specifieke domein van expertise en de locatie en de omvang van de onderliggende neurale veranderingen in de volledige hersenschors. Met behulp van grootschalige univariate en multivariate analyses vergeleken we systematisch de neurale responsen voor expertise-gerelateerde objectcategorieën in twee groepen van visuele experts, ornithologen en mineralogen, en een groep controle-participanten. De resultaten wezen op de aanwezigheid van gedistribueerde neurale veranderingen voor de beide domeinen van expertise, met meer wijdverspreide effecten voor ornithologie in vergelijking met mineralogie. Bovendien bestonden deze neurale expertise-effecten uit een combinatie van domein-specifieke neurale veranderingen in de hogere-orde visuele cortex, en domein-onafhankelijke expertise-effecten in de frontale lob.

Er is reeds veel onderzoek uitgevoerd naar zowel de gedrags- als de neurale effecten van visuele expertise, maar deze twee afzonderlijke stromen in de literatuur vertonen grote discrepanties. Veel gedragsstudies naar visuele expertise hebben het belang benadrukt van informatieverwerking op een onderschikkend niveau door experts (discriminatie van objecten op een meer gedetailleerd niveau in vergelijking met niet-experts). Toch heeft geen enkele studie de neurale activatie onderzocht die ten grondslag ligt aan *individuele* objecten van expertise, in plaats van de expertise-gerelateerde object*categorie*, in een echt expertise-domein. Wij willen dit hiaat in de literatuur opvullen door zowel mentale als neurale representaties van individuele objecten van expertise bij experts te onderzoeken en deze te vergelijken met die van niet-experts om expertise-gerelateerde veranderingen te detecteren. In een tweede experiment onderzochten we de mentale representaties van individuele objecten van expertise en hun perceptuele gelijkenissen. De resultaten wezen op een kwantitatieve versterking van de mentale representatieruimte van individuele expertise-objecten bij experts in vergelijking met niet-experts. Bovendien leidde expertise tot kwalitatieve veranderingen in de vorm van meer gedetailleerde distincties (op onderschikkend niveau) tussen de individuele objecten in de mentale representatieruimte van experts. Deze effecten van expertise werden beïnvloed door top-down factoren.

In het laatste experiment van dit proefschrift hebben we onderzocht of en hoe expertise de manier beïnvloedt waarop individuele objecten van expertise worden gerepresenteerd in de hersenen. We analyseerden multi-voxel patronen om de neurale representatieruimte van objecten van expertise voor zowel experts als niet-experts te onderzoeken. Resultaten duidden op kwantitatief versterkte neurale representaties van expertise-objecten in experts in vergelijking met niet-experts, en dit in hogere-orde hersenregio’s. De algemene structuur van de neurale representatieruimte bleef ongewijzigd. Ten slotte werden de mentale en neurale representatieruimtes van zowel experts als niet-experts vergeleken. De studies die beschreven staan in dit proefschrift vergroten onze kennis van de neurale basis van visuele expertise.

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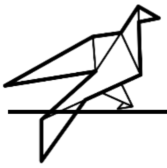
1

General Introduction



1.1 VISUAL OBJECT RECOGNITION

1.1.1 The visual system

When you ask a child which part of our body we use to see, they will undoubtedly respond “the eyes”. However, the eyes are just the beginning of a complex process in which visual information about the outside world is transferred into the brain. Light that falls onto the retina is converted into neural signals which are sent towards the occipital cortex and onto higher-level visual regions in the brain where the visual information is reconstructed and interpreted. The cortical processing of visual information starts in the primary visual cortex or V1 in which neurons detect edges and orientations (e.g. edges that are oriented horizontally or vertically). The neurons in V1 provide the input for two distinct visual streams: the dorsal stream or the “where / how” pathway and the ventral stream or the “what” pathway (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982; see Fig. 1.1). The dorsal stream ends in the posterior parietal cortex and is responsible for visually guided action by encoding the location of an object (“where”), directing eye movements and guiding the reaching for and the grabbing of the object (“how”). The ventral stream ends in the inferior temporal cortex (IT) and ensures form recognition and identification of the object (“what”). The ventral stream consists of a series of brain regions which are organized in a hierarchical way, containing both feedforward (bottom-up) and feedback (top-down) connections. The neurons in V1 feed information to the neighboring regions V2 and V3 which have increasingly broader receptive fields and further analyze the information from V1. Further along the “what” pathway is visual area V4, the main color center of the brain (Bartels & Zeki, 2000). Finally, visual information accumulates in the inferior temporal or ventral temporal cortex and the lateral occipital complex (LOC), which house complex representations of the shape and identity of the perceived objects. These brain regions are responsible for object recognition.

1.1.2 Object recognition

The importance of object recognition in our daily lives cannot be stressed enough. Imagine having to actively think about the meaning of every object we see, or even experiencing a small delay between seeing and understanding what we see. Normal functioning would be made impossible. We constantly interpret everything that appears in our visual field and we do so with astonishing speed. Humans are able to accurately categorize a scene which has been presented for just 100 ms, or in other words: we are able to identify 10 scenes per second (Greene & Oliva, 2009). Even though the appearance of an object can vary greatly depending on the viewing conditions like point of view, lighting, distance to the object and so on, we are still able to exactly identify what we are looking at, and in record time.

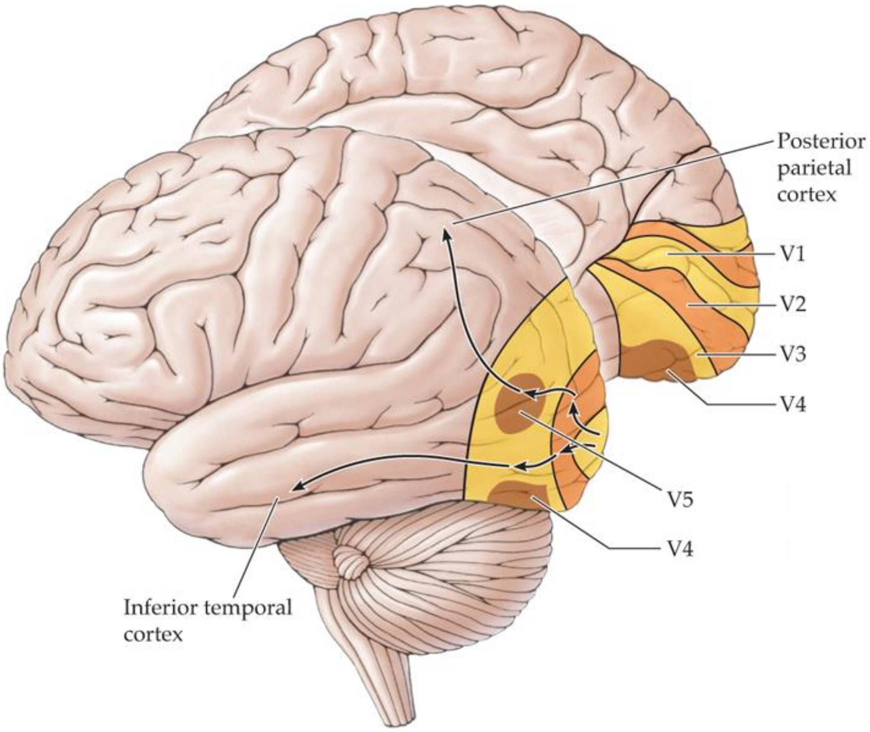


Figure 1.1. The visual system. *The dorsal visual pathway, which starts in primary visual cortex (V1) and ends in the posterior parietal cortex, serves visually guided action. The ventral visual pathway, which starts in V1 as well and ends in inferior temporal cortex (IT), encodes the shape and identity of perceived objects. Figure adapted from Martin (2012).*

The inferior temporal cortex and LOC are object-selective, meaning that they are activated more strongly when viewing objects compared to visual noise or scrambled objects (Malach et al., 1995). These brain regions process representations of a wide range of object categories, both large and small, animate and inanimate, natural and human-made and independent of the format of the object (e.g. photograph or line drawing; Ishai, Ungerleider, Martin, & Haxby, 2000). How and where in the object-selective cortex are these different categories of objects represented? Several smaller brain regions within occipitotemporal cortex (OTC) are category-specific: they respond very strongly to their preferred object category, but less so to any other type of object (see Fig. 1.2). For example, the fusiform face area (FFA) in ventral temporal cortex and the occipital face area (OFA) are highly selective for faces (Kanwisher, McDermott, & Chun, 1997). Face-selective regions have been found in human fMRI studies as well as in monkeys (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003). Furthermore, the extrastriate body area (EBA) specifically processes bodies and body parts (Downing, Jiang, Shuman, & Kanwisher, 2001), the parahippocampal place area (PPA) processes scenes, places, and visual landmarks such as houses (Epstein & Kanwisher, 1998) and the visual word form area (VWFA) processes letter strings (Cohen et al., 2000).

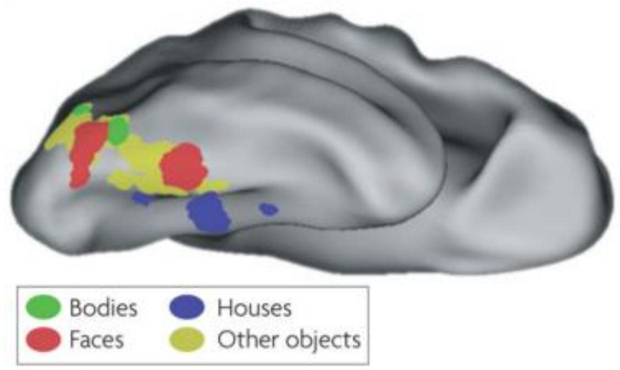


Figure 1.2. Object-selective regions. *Ventral pathway regions in the right hemisphere of one individual that were significantly activated in the following contrasts: bodies > faces + houses (green), faces > bodies + houses (red) and houses > faces + bodies (blue). The yellow areas represent regions that were significantly active for the contrast objects > scrambled in a group of people. Figure adapted from (Op de Beeck, Haushofer, & Kanwisher, 2008).*

Does this mean that the object-selective cortex is entirely made up out of distinct and highly specialized regions or modules whose sole function it is to represent one specific category of objects? Up until now, these kind of specialized regions have only been found for the object categories mentioned above. Downing, Chan, Peelen, Dodds and Kanwisher (2006) searched for selective regions for a wide range of other object categories like birds, chairs, flowers, musical instruments, insects, cars and so on, but they did not find any new specialized regions within the occipitotemporal cortex. Possibly, these category-specific regions do exist but have not yet been found due to insufficient methods or a too low scan resolution, in which case high resolution scanning could offer a solution (Schwarzlose, Baker, & Kanwisher, 2005). However, it seems more likely that for example a specialized "chair region" does not exist. A division into separate modules with a high preference for every existing object category would not be the most efficient way to organize the object-selective cortex. Then how are other objects represented? Instead of a localized increase in activity like for faces, other object categories are represented by a distributed pattern of activity across a broader region of cortex like LOC (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). These distributed patterns of selectivity for the different object categories appear to form a large-scale map, consisting of a gradient of selectivity across the object-selective cortex (Op de Beeck, Haushofer, & Kanwisher, 2008). The underlying dimensions of this large-scale map, and whether or not the category-specific regions like FFA are a part of it, are subject to discussion. Several dimensions have been proposed to be the dominant principle of organization. One possibility is eccentricity (Levy, Hasson, Avidan, Hendler, & Malach, 2001). This concept is related to the retinotopic organization (organization based on the visual field) that can be found very strongly in early visual areas like V1 and that extends in a weaker manner into lateral occipital and occipitotemporal cortex. This theory suggests that object categories which rely on detailed inspection and are mostly seen in the center of the visual field (e.g. faces) are represented in brain regions processing central information, while other object categories (e.g. buildings) are processed in brain regions associated with peripheral information (Levy et al., 2001). A second principle of organization that has been proposed is the type of processing that is elicited by the stimulus or object category. More specifically, what might determine the neural representation of an object category is whether it is processed in a holistic or in a part-based manner. Holistic processing is the tendency to process an object as a unified whole instead of processing all parts of the object separately, the mutual relations between the different parts and the total configuration are crucial to the recognition of the object (McGugin, Gatenby, Gore, & Gauthier, 2012; Richler & Gauthier, 2014). This type of processing has been mainly found for faces (Tanaka & Farah, 1993; Tanaka & Sengco, 1997; although some argue against the view that faces are processed holistically; see Burton, Schweinberger, Jenkins, & Kaufmann, 2015). Thus it is proposed that face-selective regions like FFA are actually regions in which holistic processing is implemented (Gauthier & Tarr, 2002; Tarr & Gauthier, 2000). Another potential underlying dimension of the organization of object-selective cortex could be the perceived shape of objects. Research has shown that unfamiliar objects with similar perceived shapes elicit similar neural response patterns (Op de Beeck, Torfs, & Wagemans, 2008). However, evidence has also been found for objects with very dissimilar perceived shapes that are processed in closely related brain regions. For example, even though the overall shape of hands is very different from other body parts like legs and torsos, a hand-preferring region has been located in the left lateral occipital sulcus which partially overlaps with the left body-selective EBA (Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010).

Although relevant evidence has been found for each of the above mentioned dimensions, they can only partially explain the way in which object-selective cortex is functionally organized (Op de Beeck et al., 2008). The most dominant criterion that determines the selectivity of the high-level visual cortex seems to be (semantic) object category. This corresponds to our mental representational space of objects or in other words: our perceived similarity between different object categories. Most people will intuitively organize different object categories based on their meaning instead of their form (e.g. all plant categories, whether they are flowers or trees, will be grouped together). The visual cortex represents different object categories in a continuous semantic space. Research has shown that this semantic map possibly includes several dimensions such as mobile vs. immobile categories, social vs. non-social categories and animate vs. inanimate categories (Huth, Nishimoto, Vu, & Gallant, 2012). The distinction between animate and inanimate categories is quite prominent in occipitotemporal cortex (Downing et al., 2006; Kriegeskorte et al., 2008). Living or animate objects differentially activate regions in the lateral fusiform gyrus, while inanimate objects are processed more medially (medial fusiform gyrus). Logically, the animate-inanimate gradient stretches between the FFA on one side and PPA on the other side (Mahon & Caramazza, 2009). Finally, it is important to note that the potential dimensions driving the functional organization of object-selective cortex mentioned above are not necessarily mutually exclusive. Each of these dimensions could contribute to a greater or lesser extent to the large-scale selectivity map that is the object-selective cortex. For example, Bracci and Op de Beeck (2016) illustrated that in ventral and lateral OTC, information about both shape and semantic category are represented independently.

The question remains how the organization of the object-selective cortex arises. Is the underlying large-scale map of object representations innate, is the gradient of selectivity a product of visual experience, or is it a combination of both?

1.2 LEARNING AND EXPERTISE

1.2.1 Perceptual and visual object learning

Experience and learning enable us to adapt to our ever-changing environment. We overcome challenges by acquiring new or modifying existing knowledge and skills. Perceptual learning consists of learning to recognize entirely new stimuli or increase our sensitivity to variations in familiar stimuli. It exists in all sensory modalities, for example: one can learn to hear the difference between musical tones, improve the ability to distinguish two points that are touching the skin or learn to distinguish different grape varieties when tasting wine. In this case, we focus on visual perceptual learning. Studies on visual perceptual learning have focused on a wide range of very low-level stimuli (like learning to discriminate between subtle changes in line orientations) to very high-level stimuli (e.g. learning to categorize artificially created objects) (Fine & Jacobs, 2002).

There are different theories concerning the mechanisms of perceptual learning and categorization. According to these theories, we learn to categorize new stimuli by comparing its visual representation to some form of representation of the category that is stored in memory and judging its similarity to the category. Exemplar-based theories of perceptual learning state that categories are represented in the form of individual exemplars of the category with which we have had experience (Nosofsky, 1987, 2011). The prototype theory asserts that categories are stored in memory in the form of an abstract summary or prototype, which can be seen as the ‘average’ of all exemplars that have been experienced (Mervis & Rosch, 1981; Posner & Keele, 1968). Both theories emphasize the importance of the concept of similarity in the field of perceptual learning: only by resemblance to a prototype or to exemplars can a new stimulus be assigned to a category.

Several properties are attributed to perceptual learning. Often, effects of perceptual learning are not only specific to the stimulus category (e.g. Searston & Tangen, 2017), but also to the stimulus configuration used during training, like the location of visual stimuli in an orientation discrimination task. In other instances, learning effects are, to some extent, generalized across stimuli and tasks (Fahle, 2005; Gegenfurtner & Seppänen, 2013). Furthermore, top-down attention can modulate effects of perceptual learning; greater and faster improvements are achieved for attended versus unattended stimuli (Byers & Serences, 2012). However, perceptual learning does not only occur with explicit task instructions focused upon the trained stimuli, it can even occur in the absence of directed attention towards or even perception of the 'trained' stimulus feature (Seitz & Dinse, 2007).

Perceptual learning is inherent to our perceptual system. Training using basic visual tasks, like orientation discrimination of line segments or discrimination of spatial frequencies of gratings, results in long-term improvements in sensitivity for the trained stimulus category. This indicates that even in the adult brain neural plasticity remains in the visual cortex (Gilbert, Li, & Piech, 2009). Research on the neural effects of visual object learning has indeed shown that visual experience influences the way in which objects are represented in the brain (e.g. Folstein, Palmeri, & Gauthier, 2013). The neural effects of visual object training have typically been studied by measuring and comparing the neural response to a category of novel objects both before and after intensive training, or by comparing trained to untrained objects (Brants, Wagemans, & Op de Beeck, 2011; Gauthier & Tarr, 1997; Wong, Palmeri, Rogers, Gore, & Gauthier, 2009). This type of experiments has shown that training with a specific category of objects induces changes in the neural activation underlying the representation of that category, indicating that the large-scale map of object representations in object-selective cortex is at least partly formed by experience.

The exact way in which learning affects object representations in the brain is still largely unknown. Human fMRI studies have reported an increase as well as a decrease in the magnitude of the neural response to a trained object category (e.g. Gauthier & Tarr, 1997; Kourtzi, Betts, Sarkheil, & Welchman, 2005; van der Linden, Murre, & van Turennout, 2008). Furthermore, studies applying multi-voxel pattern analyses (MVPA; see section '*Experimental techniques*' in this chapter) have shown that training changes the multi-voxel patterns of selectivity that represent the trained object category (Brants, Bulthé, Daniels, Wagemans, & Op de Beeck, 2016; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006). Some studies have found these training-related neural changes to be restricted to small subregions of the visual cortex (Gauthier & Logothetis, 2000; Logothetis, Pauls, & Poggio, 1995). However, other studies have demonstrated that visual object learning introduces rather distributed neural effects, with the magnitude of the effect varying across subregions of the visual cortex (Brants, Bulthé, Daniels, Wagemans, & Op de Beeck, 2016; Op de Beeck, Baker, DiCarlo, &

Kanwisher, 2006; Op de Beeck & Baker, 2010). Another way in which learning can affect neural object representations is by encoding the object dimensions that are relevant for the categorization of the objects. When learning to categorize objects, the neural representations in visual cortex are stretched along the category-relevant dimensions, meaning that the neural representations of objects that vary along a category-relevant dimension become more distinct (Folstein, Gauthier, & Palmeri, 2012; Folstein et al., 2013; Folstein, Palmeri, Van Gulick, & Gauthier, 2015; Sigala & Logothetis, 2002).

1.2.2 Visual expertise

A good approach to studying the effects of learning or experience in any given domain is by studying real-world experts, since expertise can be seen as an extreme form of learning. Experts are individuals who are able to produce superior performances on a regular basis within a specific domain. Their achievements within this domain surpass those of novices in the same domain, as well as their own achievements in other domains. People have been interested by expertise for a long time. Originally, expertise was seen as an innate ability that cannot be trained or practiced. Chess masters were assumed to be people with a great intellectual capacity to extensively search for alternative chess moves (Ericsson & Lehmann, 1996). Later, the role of experience and deliberate practice in expertise was emphasized (Ericsson & Lehmann, 1996; Ericsson, Krampe, & Tesch-Römer, 1993). Now it is generally estimated that 10 years of deliberate practice are necessary to become an expert. Over the years, a wide range of experts from different domains have been studied, like chess masters (Bilalić, Langner, Ulrich, & Grodd, 2011), professional musicians (Schlaug, 2001), radiologists (Bilalić, Grottenthaler, Nagele, & Lindig, 2014) and even the Brazilian footballer Neymar (Naito & Hirose, 2014).

However, in this dissertation the emphasis is placed on visual expertise, which is defined as a consistent superior performance compared to novices in recognizing, categorizing and identifying objects within a specific domain (Ericsson & Lehmann, 1996; Harel, Kravitz, & Baker, 2013; Shen, Mack, & Palmeri, 2014). Visual experts are very proficient in discriminating between visually similar objects belonging to a homogeneous object category (see Fig. 1.3 for an example). Behavioral studies on visual expertise have indicated that experts have the tendency to identify and classify objects of expertise at a more subordinate level compared to novices (Tanaka & Taylor, 1991). While a novice might refer to a bird simply as being a bird (the basic level of categorization), a bird expert will preferentially categorize this bird using the subordinate level of categorization, in this case the species of the bird (e.g. "robin"). What is more, a bird expert would be equally fast to recognize this bird at the basic level as he would be to identify it more specifically. Several learning studies have indicated that training participants to identify or categorize objects at the subordinate level greatly enhances the participants' ability to discriminate these objects, showing a much greater improvement than participants that are trained at the basic level (e.g. Scott, Tanaka, Sheinberg, & Curran, 2006; Tanaka, Curran, & Sheinberg, 2005; Wong et al., 2009).

Figure 1.3. Example of two visually similar objects. *These two birds are visually very similar, even though they belong to different species (left: little ringed plover, right: common ringed plover). Bird experts are very good at discriminating and categorizing visually similar birds.*

Visual expertise has been used for almost two decades in a large number of fMRI and EEG studies to investigate the effects of learning on the neural representations of object categories in the human brain. To give an idea of the extent of the domain of visual expertise in neuroscience, here are examples of different types of expertise that have been investigated: car expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000; McGugin et al., 2012; Xu, 2005), bird expertise (Gauthier et al., 2000; Xu, 2005), chess expertise (Bilalić, Langner, et al., 2011), radiology (Bilalić et al., 2014; Haller & Radue, 2005; Harley et al., 2009), expertise with musical instruments and notation (Hoenig et al., 2011; Wong & Gauthier, 2010), expertise in computer programming (Floyd, Santander, & Weimer, 2017) and so on. This wide range of studies has generated very divergent results for which a consensus on the proper interpretation has yet to be reached. This is illustrated by the contrasting conclusions that have been made in available literature reviews (e.g. Curby & Gauthier, 2010; Harel et al., 2013; McKone & Kanwisher, 2005). The question remains which brain regions are most influenced by effects of intensive learning and which voxels remain unaltered, or in other words: which factors determine the distribution and localization of expertise effects?

The expertise hypothesis

One of the first studies in which the neural correlates underlying a real-world domain of visual expertise were investigated was the influential study by Gauthier, Skudlarski, Gore, and Anderson (2000). Gauthier and colleagues recruited 11 car experts and 8 bird experts and presented them with images of cars, birds, faces and familiar objects inside the scanner. They measured the neural response of the two expert groups to their respective expert object categories in face-selective regions. The results indicated an increase of activation in response to objects of expertise in right FFA and OFA. Furthermore, they found that the neural activation in the right FFA was related to the experts' score on a behavioral test of expertise. This study provided evidence for the perceptual process view of expertise and the expertise hypothesis. The perceptual process view considers expertise to be stimulus-driven and automatic. Experts' performances are highly efficient and seem to be effortless. Furthermore, the hypothesis predicts that expertise-related neural changes are restricted to local populations of neurons (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier & Tarr, 1997). Following this reasoning, long-term visual experience with a specific object category would lead to a region in OTC that is highly selective for this category (more so than for other categories). These kind of category-specific regions of course exist for faces (FFA and OFA), bodies (EBA) and scenes (PPA). The face-selective region FFA plays a central role in the expertise hypothesis, a more specific version of the perceptual process view. According to this hypothesis, FFA is the brain region in which 'expert processing' takes place (Gauthier et al., 2000; Gauthier et al., 1999; Sigala & Logothetis, 2002), independent of the visual object category in which the expert has been trained ('domain-general'). We have all been learning to discriminate faces from each other since the day we were born, and even though faces are very homogeneous (same parts, same overall structure), we are all highly proficient in doing so. This has lead the proponents of this theory to conclude that FFA's selectivity for faces has arisen due to the fact that we are all experts in processing faces, and not because faces form a special object category. The ‘expert processing’ that is implemented in FFA is believed to be the tendency to process objects in a holistic manner (see section 1.1.2 ‘*Object recognition*’ in this chapter). Holistic processing is an important feature of face perception (Gauthier & Tarr, 2002; Tarr & Gauthier, 2000). Furthermore, it has been associated with other homogeneous object classes with which humans have a lot of experience (Boggan, Bartlett, & Krawczyk, 2012; Gauthier et al., 2014). Thus, the expertise hypothesis predicts that expertise-related neural changes for homogeneous object classes are mainly situated in FFA.

Apart from the above mentioned study by Gauthier and colleagues (2000), several other fMRI studies in which experts were compared to novices have indeed demonstrated an increased activation in the FFA in response to objects of expertise. These studies included real-world experts with multiple years of experience with chess (Bilalić, Langner, et al., 2011), cars (McGugin, Gatenby, et al., 2012; Xu, 2005), radiology (Bilalić et al., 2014; Harley et al., 2009) and even Pokémon cards (James & James, 2013). Experience-related neural changes in FFA were also demonstrated in participants who were extensively trained to recognize novel objects (e.g. ‘Greebles’; Gauthier et al., 1999).

Despite these results, the expertise hypothesis has been subject to controversy. First of all, several other fMRI studies have failed to find an expertise effect in face-selective regions, including studies with real-world experts (Bartlett, Boggan, & Krawczyk, 2013; Grill-Spector, Knouf, & Kanwisher, 2004; Krawczyk, Boggan, McClelland, & Bartlett, 2011; Rhodes, Byatt, Michie, & Puce, 2004) and laboratory-trained participants (Brants et al., 2011; Op de Beeck et al., 2006; Wong et al., 2009). Furthermore, it has been suggested that at least in a subset of studies the increased response for objects of expertise found in FFA might be due to the nature of the presented stimuli (birds, cars, Greebles, Pokémon characters) and the degree to which they resemble faces (Kanwisher & Yovel, 2006; Op de Beeck et al., 2006; Xu, 2005). In addition, some behavioral studies argue against holistic processing for objects of expertise (Hsiao & Cottrell, 2009; Robbins & McKone, 2007; Weiss, Mardo, & Avidan, 2016). But one of the most important criticisms that has been expressed, is that the above mentioned studies focused on a limited number of regions of interest (ROIs) and did not systematically compare the response to expertise objects in face-selective regions to other regions in or beyond the visual cortex, hereby potentially missing crucial effects (Harel, 2015; Harel et al., 2013; Op de Beeck & Baker, 2010).

The interactive view of expertise

According to the interactive view of expertise, visual expertise does not solely induce bottom-up perceptual (stimulus-driven) changes, but is also impacted by top-down factors like conceptual knowledge, attention and decision-making (Harel, 2015; Harel et al., 2013). For example, Harel, Gilaie-Dotan, Malach and Bentin (2010) performed an experiment in which the task relevance of the objects of expertise was manipulated. Car experts and novices were presented with images of cars and airplanes and were instructed to detect repetition of car images while ignoring both repeated and unrepeated airplane images ('attend cars' task) and vice versa ('attend airplanes' task). They found widespread expertise-related neural changes in and beyond the visual cortex, however, this expertise-related activation drastically diminished when cars were task irrelevant. McGugin et al. (2015) manipulated task relevance as well, they found that reducing attention to objects of expertise diminished expertise effects but did not make them disappear completely. The importance of attentional engagement in expertise was also demonstrated in a behavioral study in which experts showed a clear preference for pictures of objects related to their field of expertise (Hershler & Hochstein, 2009).

This interplay between bottom-up and top-down processes implies that a wider range of brain regions are involved in visual expertise. According to the interactive view, the neural correlates underlying visual expertise are not limited to a specific, local region in the brain but instead are expressed by rather moderate changes in neural activation that are distributed across a larger patch of cortex (Brants et al., 2016; Harel, 2015, 2016; Kourtzi et al., 2005; Op de Beeck & Baker, 2010). The presence of expertise-related neural activation has been demonstrated in visual cortex beyond the FFA, for example in early visual cortex (Harel et al., 2010), in LOC (Harel et al., 2010; Jiang et al., 2007; Op de Beeck et al., 2006) and other parts of the (occipito)temporal cortex (Bilalić, Langner, Erb, & Grodd, 2010; Bilalić, Turella, Campitelli, Erb, & Grodd, 2012; Krawczyk et al., 2011; Moore, Cohen, & Ranganath, 2006; Wong, Palmeri, Rogers, et al., 2009), in the parahippocampal gyrus (PHG; Harel et al., 2010) and in the fusiform gyrus (FG; Harel et al., 2010; Rhodes et al., 2004). Even brain regions outside the visual cortex have emerged in the search for expertise effects, including prefrontal regions (Bartlett et al., 2013; Harel et al., 2010; Jiang et al., 2007; Krawczyk et al., 2011; Moore et al., 2006) and parietal regions (Bartlett et al., 2013; Bilalić, Kiesel, Pohl, Erb, & Grodd, 2011; Bilalić et al., 2012; Harel et al., 2010; Moore et al., 2006).

Experts' performances are not automatic but instead consist of a complex interplay of perceptual stimulus characteristics, preferential attention for the expert object category and retrieving and updating conceptual knowledge about the category. What we know about the stimuli and what we expect based on previous experiences determines where we focus our attention and how we process the stimuli (Bilalić, 2017). It is proposed that the fronto-parietal network, in which neural expertise effects have been found, underlies the top-down attentional control that comes into play in expertise (Bartlett et al., 2013; Corbetta & Shulman, 2002; Harel, 2015).

Informativeness

It seems clear that the localization of expertise effects in and beyond the visual cortex varies widely between studies. However, the reason why certain neural subregions are affected by a particular domain of expertise and a particular task while others are not, is still unclear. It has been suggested that the extent to which neurons and brain regions are involved in a particular type of expertise depends on their informativeness for the field of expertise and the task at hand (Op de Beeck & Baker, 2010). Developing expertise with a particular object category will likely induce neural changes in those brain regions that already had a preexisting selectivity for that category (Brants et al., 2016). This means that expertise effects in visual cortex are domain-specific. A study in which juvenile monkeys were trained to discriminate between three new categories of stimuli, induced the emergence of distinct, specialized brain regions for each separate stimulus set. The locations of these regions were similar across monkeys but different across stimulus sets, suggesting that experience had modulated a preexisting map of neural object representations (Srihasam, Vincent, & Livingstone, 2014).

This concept of informativeness has its origin in the field of visual neuroscience. Research has shown that orientation training in monkeys with stimuli that are presented in a fixed position of the visual field induces improvements in neural sensitivity for the trained orientation in trained neurons in V1 (with a corresponding receptive field), while no changes in neural tuning are found for untrained neurons (Schoups, Vogels, Qian, & Orban, 2001). Similarly, orientation training also induced changes in the tuning curve of the most informative neurons for the trained orientation in V4 in monkeys (Raiguel, Vogels, Mysore, & Orban, 2006). The idea of informativeness is also related to the neuronal recycling hypothesis (Dehaene & Cohen, 2007) which explains the cortical localization of new cultural functions such as reading by suggesting that such evolutionary novel functions ‘recycle’ existing brain circuitry. The brain regions which are most likely to be recycled are the regions which are devoted to the most similar existing functions. Dehaene and Cohen (2007) provide convincing arguments for the ‘recycling’ of evolutionarily older brain regions for two new cultural functions: reading and arithmetic. However, the ‘recyling’ of informative brain regions in the context of perceptual expertise needs further investigation.

1.3 EXPERIMENTAL TECHNIQUES

1.3.1 functional Magnetic Resonance Imaging

The neural data that are presented in this dissertation were acquired using functional Magnetic Resonance Imaging (fMRI). FMRI is a non-invasive technique which allows us to measure and visualize neural activity by detecting changes in the brain’s blood flow. When the metabolic activity of neurons increases, the blood supply to that region increases as well to meet the demand of oxygen. Active neurons consume oxygen and convert oxyhemoglobin (oxygenized red blood cells) into deoxyhemoglobin (deoxygenized red blood cells). An fMRI scan measures the concentration of deoxyhemoglobin in the blood, which is termed the BOLD-signal (blood-oxygen-level dependent contrast; Ogawa, Lee, Kay, & Tank, 1990). This way, activated brain regions are identified. The spatial resolution of fMRI is high (1-3 mm), but the temporal resolution is lower: there is a delay of a few seconds between the actual increase in neuronal signaling and the arrival of oxygenated blood in the engaged brain area.

Participants are placed into the MRI scanner and are asked to perform a specific task. This way, brain regions that are active and relevant for that task are identified. Note that the brain serves a multitude of different functions, brain regions that are active while a participant is performing a task are not necessarily specific for that task (e.g. while identifying faces, brain regions that subserve vision in general but that are not specific to face processing are active as well). Therefore, neural activity must always be compared to a carefully chosen baseline neural response, in order to identify those brain regions in which the neural activity for the experimental condition is greater (or smaller) relative to the baseline condition. For example, to identify face-selective regions, the neural activation elicited by viewing faces should be contrasted against the activation elicited when viewing man-made objects or scrambled images.

Preprocessing

Collected fMRI data first need to undergo a series of preprocessing steps before the actual statistical analyses can be carried out. The data in this dissertation underwent the following steps.

In the studies presented in this dissertation, the entire brain was scanned in 3 seconds. Because the brain is scanned in slices, functional scans need to be corrected for slice timing differences (the first slice is scanned approximately 3 seconds earlier than the last slice). Second, it is inevitable that participants move their heads slightly (1-2 mm in every direction) during a scan session that can last up to 90 minutes. Therefore, functional scans are realigned to each other to correct for the participants' head movements and are later co-registered with the anatomical image to ensure a perfect overlap between the functional and anatomical data. Scans during which participants have made relatively large, sudden movements (e.g. translations of more than 1 voxel size) are deleted from the data set.

Each person's brain is unique in the sense that there are small interindividual differences in the anatomy of the brain (e.g. on average a man's brain is slightly larger than a woman's brain). To be able to compare neural activation across participants, the functional and anatomical images of each participant need to be normalized so that they form a uniform space. In this case, images were normalized to the Montreal Neurological 152-brain image, which is a template created by averaging the anatomical scans of 152 individuals. Finally, the functional scans are spatially smoothed to increase the signal-to-noise ratio; neural activation is smeared out across voxels (volumetric pixels) to make sure that actual neural 'signals' are not lost in random noise.

1.3.2 Univariate analyses

After the neural data have been preprocessed, a general linear model (GLM) is fitted to the data to estimate the linear relationship between the different experimental conditions of the task and the recorded neural activation in each voxel, resulting in a beta value for each voxel and each experimental condition.

Traditionally, univariate analyses of fMRI data are used to identify brain regions that are significantly more activated when performing a specific task. For each voxel, a contrast is calculated by subtracting the beta value of a baseline condition (e.g. fixating a dot on an otherwise blank screen) from the beta value of the experimental condition, resulting in a contrast map. To investigate which brain regions are more involved in one experimental condition compared to the other, the contrast maps of both conditions are statistically compared. It is possible to study the neural activation that is elicited by the different experimental conditions at the whole-brain level by visualizing significantly active voxels across the entire cortex. Another possibility is to apply ROI-based analyses. In this case, the univariate neural activation is investigated in a limited set of pre-selected brain regions. These brain regions or ROIs can be delineated in each participant based on an anatomical template (aROIs) or based on independent functional localizer scans to identify ROIs (fROIs) with a high selectivity for a specific condition or category (e.g. face-selective regions). Subsequently, the beta values of the individual voxels included in this ROI are averaged and statistically compared, resulting in one measure of activation per ROI. In chapter 2 of this dissertation, both whole-brain and ROI-based univariate analyses were applied.

1.3.3 Multi-voxel pattern analyses

Traditional univariate analyses are not able to measure neural activation at a sub-regional level. Multivariate analyses on the other hand look at the spatial pattern of activation that is formed by multiple voxels simultaneously. This technique, called multi-voxel pattern analysis or MVPA (Haynes & Rees, 2006; Norman, Polyn, Detre, & Haxby, 2006), allows us to explore widespread, distributed patterns of activity for different conditions. Even if individual voxels are not significantly selective for a specific condition, the combined response pattern may very well carry information about that condition or about a specific stimulus. MVPA is sensitive to changes in activation patterns, even when the mean activation in a region remains constant. The goal of MVPA is to determine whether multi-voxel patterns associated with different conditions (or with the same condition but in different subject groups) are discriminable from each other. In this dissertation, multi-voxel patterns of activity were analyzed in three different ways.

Correlational MVPA

One way to investigate multi-voxel patterns of activation is by performing correlational analyses (Figure 1.4). This method is used to judge the similarity between the multi-voxel patterns that represent all the different experimental conditions in a specific ROI. The first step in this analysis consists of randomly dividing the acquired neural data of each participant into two equally sized subsets. The neural activation patterns of all the experimental conditions in the first subset are correlated with the patterns of all the conditions in the second subset. This procedure of dividing the data and computing the correlations is repeated 100 times and averages are calculated across these repetitions. As a result, a similarity matrix is created in which each cell contains the mutual correlation between two specific conditions. Similarity matrices can also be transformed in dissimilarity matrices by calculating 1 minus the correlation for each cell. The (dis)similarity matrices of different participants belonging to the same group are then averaged. The (dis)similarity matrices can be used to judge which experimental conditions have very similar neural representations and which conditions elicit very differing neural activation patterns. In chapters 2 and 4 of this dissertation, correlational multi-voxel pattern analyses were applied.

MVPA decoding: subject classification

The classical approach to MVPA decoding is used to answer the question whether multi-voxel patterns underlying different experimental conditions are statistically distinct from each other. This analysis is again applied within a pre-selected (functional or anatomical) ROI. A model is trained to learn to distinguish two experimental conditions (e.g. condition ‘cars’ and condition ‘dogs’) based on their neural activation patterns. Next, the trained model is tested with new data from the two conditions that the model has never ‘seen’ before. For each new activation pattern, the trained model classifies the pattern into one of the two experimental conditions (e.g.: the model predicts whether the activation pattern was linked to the 'face' or the 'car' condition). The overall classification accuracy of the model is calculated as the proportion of times the model correctly classified the activation patterns into one of the two conditions. If the classification accuracy is above chance level (50% in the case of two conditions), then the activation patterns underlying the different experimental conditions in the selected ROI are distinguishable from each other.

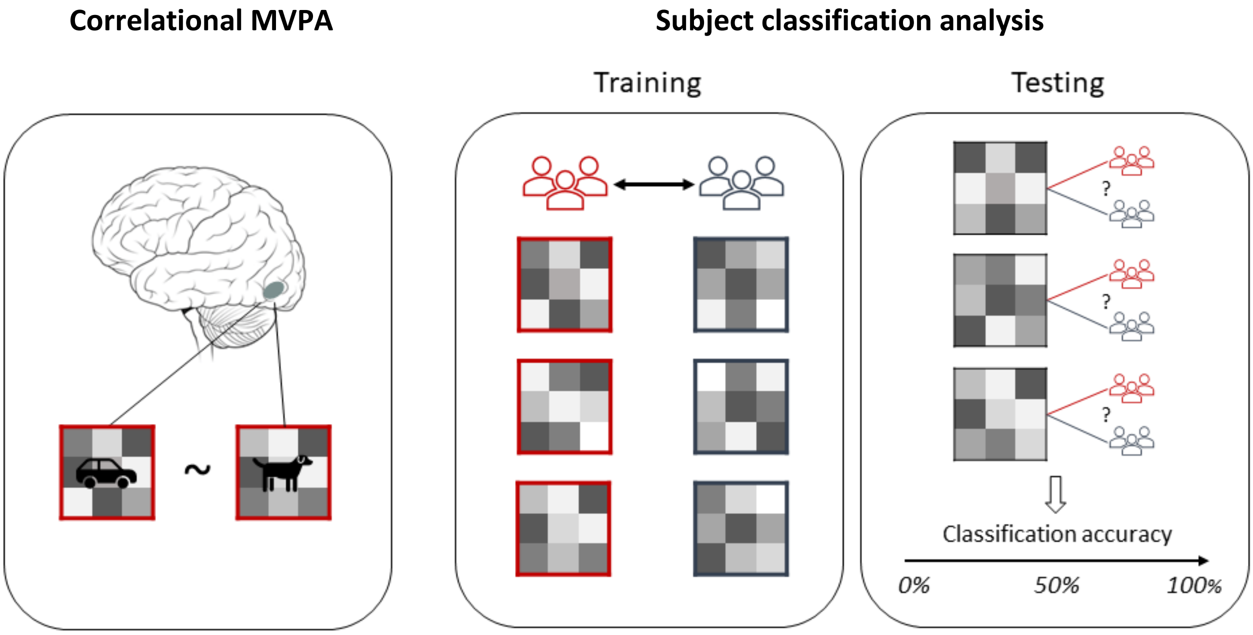


Figure 1.4. Schematic overview of correlational MVPA and the subject classification analysis.

In this dissertation, the principle of MVPA decoding was used in a different way; we applied subject classification analyses to determine whether multi-voxel patterns for the same experimental condition but in *different subject groups* were distinguishable from each other (Figure 1.4). In this case, the data set consists of the multi-voxel patterns that are elicited by a selected experimental condition in a specific ROI, of all the participants from the two subject groups. First, for each of the two subject groups, one participant is randomly selected and left out of the data set. Next, a linear classifier (model) is trained on the patterns of all the subjects (training sample) except for the left-out pair (test sample), to learn to distinguish the neural response patterns (for the selected experimental condition) of the two subject groups. After training, the left-out pair (new data) is used to test the trained model: the response pattern of each of the two subjects is classified as belonging to one subject group or the other. This procedure is repeated until each participant is left out of the training sample once. A classification accuracy is calculated as the proportion of times in which test participants were correctly classified as belonging to subject group 1 or 2. The higher the classification accuracy, the better the classifier was able to make a distinction between the neural representations of the experimental condition of the two subject groups.

MVPA decoding: subject generalization

Furthermore, we used MVPA decoding in the form of a subject generalization analysis (Figure 1.5). In a subject generalization analysis, data from three subject groups are analyzed. On the one hand, the neural activation patterns for experimental condition A of subject groups 1 (1A) and 2 (2A) are compared. On the other hand, the neural responses for experimental condition B of subject groups 1 (1B) and 3 (3B) are compared. Any potential differences between 1A and 2A are then related to differences between 1B and 3B, to investigate whether they are similar or not. This way, any shared mechanisms between the neural responses of subject group 2 to condition A (2A) and the neural responses of subject group 3 to condition B (3B) are uncovered. In this dissertation, we used the subject generalization analysis to compare the neural activation patterns of two different groups of experts (groups 2 and 3) for their respective expertise conditions (conditions A and B) by comparing the response patterns of each expert group to the activation patterns of a group of control participants (group 1; responses to conditions A and B).

Again, a classifier is trained to make a distinction between the neural representations of subject groups 1 and 2 (for condition A: 1A and 2A), however, in the testing phase the classifier is presented with neural data from subject groups 1 and 3 (for condition B: 1B and 3B). The generalization accuracy is calculated as the proportion of times in which a test participant from group 1 (1B) is classified as belonging to group 1 (1A), and a test participant from group 3 (3B) is classified as belonging to group 2 (2A). A high generalization accuracy indicates the presence of very similar mechanisms that distinguish the activation patterns for 1A and 2A on the one hand and the activation patterns for 1B and 3B on the other hand. In the case of the expert groups, this would mean that effects of expertise in expert group 1 (compared to control participants) are very similar to effects of expertise in expert group 2 (compared to control participants). The subject classification and the subject generalization analyses were both applied in chapter 2.

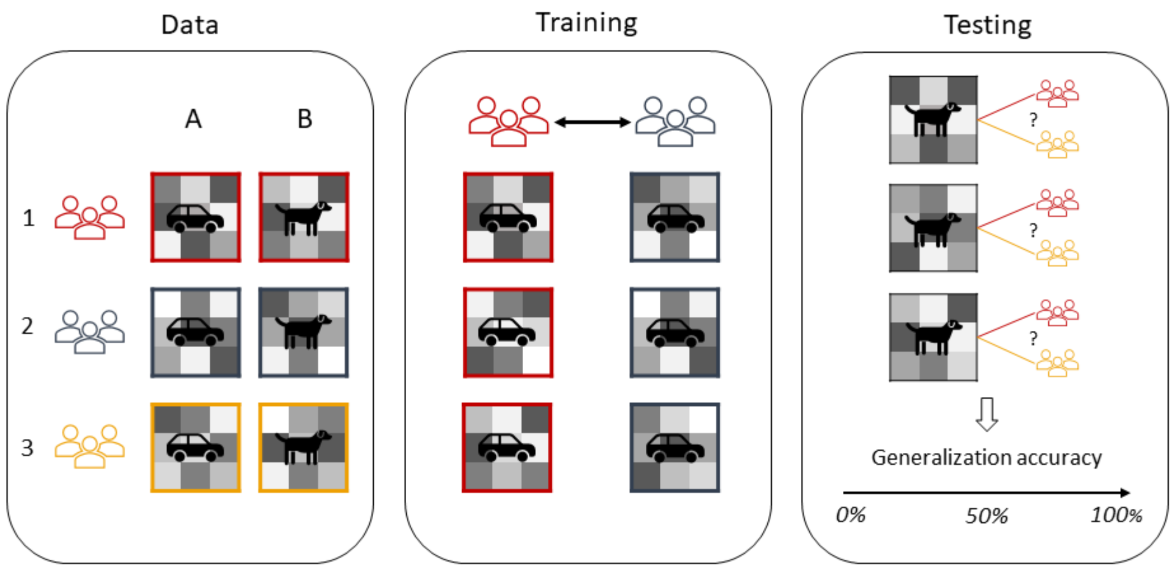


Figure 1.5. Schematic overview of the subject generalization analysis.

1.4 OBJECTIVES

Despite the large body of research investigating the neural correlates of visual expertise, many questions remain unanswered.

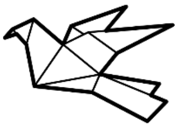
A first gap in our understanding of the neural correlates underlying visual expertise concerns the wide variety of brain regions in which expertise effects have been found. In the second chapter of this dissertation, we aim to shed light on the interaction between the specific domain of expertise and the localization and the extent of the underlying neural changes. We conducted a large-scale fMRI study in which we systematically compared two domains of visual expertise, ornithology and mineralogy. We applied both univariate and multivariate analyses to compare the neural responses to the respective expert object categories (birds and minerals) between the two expert groups and a third group of control participants. Importantly, while some studies have already compared different domains of visual expertise, this is the first to investigate expertise-related neural changes of two groups of experts at the whole-brain level. By focusing upon a limited set of ROIs, potential expertise effects might be missed. Other studies adopted a broader perspective and performed at least some whole-brain univariate or multivariate analyses, but they were limited to only one domain of expertise. We investigated whether visual expertise induces domain-specific neural changes, possibly showing a bias to those regions which are most activated by the object domain ('informative regions'). Alternatively, more general correlates of visual expertise that are similar across different domains could play a role, either at the level of specific regions of interest or at a more distributed level.

A major shortcoming in the literature on visual expertise concerns the discrepancy between behavioral and neural (whether it be EEG or fMRI) studies. While many behavioral studies have emphasized the importance of subordinate-level processing in expertise (i.e. categorizing or discriminating objects at a fine-grained, detailed level), not a single study has investigated the neural activation underlying *individual* objects of expertise.

In a second experiment (chapter 3) we investigated the mental representations of individual objects of expertise in bird experts and compared them to the mental representations of novices. Both bird experts and novices provided behavioral similarity judgments of a carefully chosen stimulus set of birds in a multiple object arrangement task. Similarity between individual objects or exemplars is an important aspect of perceptual learning: we learn to categorize new objects by comparing its visual representation to a prototype or to exemplars that are stored in memory. Mental representational spaces or similarity spaces displayed the similarity between the mental representations of individual objects for both subject groups. This approach has never before been applied in the field of visual expertise. We investigated the influence of expertise on the subordinate-level similarity in the expert object category. Furthermore, we examined the influence of top-down effects by adding a task manipulation: participants were asked to perform either an expertise-related or a non-related task.

Even though all neural studies investigating real-world perceptual expertise have included experts that were very proficient at making fine-grained distinctions between visually similar objects within a specific domain, they all investigated the neural activation underlying the expert object *category*. In chapter 4 of this dissertation a study is presented in which we investigated neural expertise effects at the subordinate level by exploring whether and how bird expertise changes the way in which individual objects of expertise (birds) are represented in the brain. We applied MVPA to distinguish the distributed neural responses to individual birds in the object-selective cortex. These neural representations were combined in a representational space and subsequently compared between bird experts and novices.

Moreover, to ensure comparability we used the same stimulus set of objects of expertise in chapters 3 and 4. We aim to compare the mental (behavioral) representational spaces of both experts and novices (chapter 3) to their neural representational spaces of the same individual objects of expertise.



2

Domain-general and domain-specific neural changes underlying visual expertise

Visual expertise induces changes in neural processing for many different domains of expertise. However, it is unclear how expertise effects for different domains of expertise are related. In the present fMRI study, we combine large-scale univariate and multi-voxel analyses to contrast the expertise-related neural changes associated with two different domains of expertise, bird expertise (ornithology) and mineral expertise (mineralogy). Results indicated distributed expertise-related neural changes, with effects for both domains of expertise in high-level visual cortex and effects for bird expertise even extending to low-level visual regions and the frontal lobe. Importantly, a multivariate generalization analysis showed that effects in high-level visual cortex were specific to the domain of expertise. In contrast, the neural changes in the frontal lobe relating to expertise showed significant generalization, signaling the presence of domain-independent expertise effects. In conclusion, expertise is related to a combination of domain-specific and domain-general changes in neural processing.

2.1 INTRODUCTION

Experience and learning shape human behavior and influence the functional architecture of the brain. A widely studied exemplar of learning is visual expertise, defined as a superior performance in identifying and categorizing visually similar objects within a specific domain (Harel et al., 2013; Shen et al., 2014). Visual expertise has been associated with changes in the underlying neural activation for the expert object category, with evidence from many real-world domains of expertise as well as experimentally induced forms of expertise and learning in humans and primates (Folstein et al., 2013; Gauthier et al., 1999; Kourtzi et al., 2005; Li, Ostwald, Giese, & Kourtzi, 2007; Op de Beeck et al., 2006; Sigala & Logothetis, 2002; Sigman et al., 2005; Wong et al., 2009).

Despite the large body of available studies on this topic, a consensus has yet to be reached on the proper interpretation of their findings, as is demonstrated by the strongly differing conclusions in available literature reviews (e.g. McKone and Kanwisher 2005; Curby and Gauthier 2010; Harel et al. 2013). A recurring point of disagreement is the potentially important role played by specific brain areas, particularly the fusiform face-selective cortex (fusiform face area, FFA). Not surprisingly, many empirical studies have focused on this specific issue. Several fMRI studies in which experts were compared to novices have indeed demonstrated a relation between expertise and activation in the FFA in response to objects of expertise. These neural changes have been found in chess experts, car experts, plane experts, ornithologists and radiologists (Bilalić et al., 2014; Bilalić, Langner, et al., 2011; Gauthier et al., 2000; Harley et al., 2009; McGugin, Gatenby, et al., 2012; Xu, 2005) as well as in participants who were extensively trained to recognize novel objects (e.g. “Greebles”, Gauthier et al., 1999; Behrmann et al., 2005). An EEG study also demonstrated a competition for neural resources between faces and objects of expertise in face-selective areas in OTC (Bruno Rossion, Collins, Goffaux, & Curran, 2007). However, several other studies have failed to find an expertise effect in face-selective regions, including studies with real-world experts (Grill-Spector et al., 2004; Krawczyk et al., 2011; Rhodes et al., 2004) and laboratory-trained participants (Op de Beeck et al., 2006), even when using the original Greeble stimuli (Brants et al., 2011).

The presence of expertise-related activity has also been demonstrated in occipitotemporal cortex (OTC) beyond the FFA (Brants et al., 2011; Grill-Spector et al., 2004; Harel et al., 2010; Jiang et al., 2007; Krawczyk et al., 2011b; Mongelli et al., 2017; Moore et al., 2006; Op de Beeck et al., 2006; Rhodes et al., 2004; Wong et al., 2009). Even areas outside the visual cortex have emerged in the search for expertise effects, including prefrontal and parietal regions (Harel et al., 2010; Krawczyk et al., 2011; Moore et al., 2006) and auditory association cortex for professional musicians (Hoenig et al., 2011).

All reviews agree that various forms of expertise exist and that expertise-related neural changes *might* depend upon stimulus characteristics and domain-specific task requirements (compare, for example, Richler and Gauthier (2014) and Harel et al. (2013)). In at least a subset of the studies for example, the increased response observed in the FFA may be due to the nature of the presented stimuli and the degree to which they resemble faces (Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Xu, 2005). However, there is surprisingly little direct evidence to support such claims. It remains unclear why the localization of expertise effects in visual cortex varies widely between studies, sometimes affecting the FFA and sometimes affecting other regions.

We aim to investigate the interaction between the specific domain of expertise and the localization and the extent of the underlying neural changes. To do this, we need to compare different domains of visual expertise and focus on the related patterns of activity in the entire visual cortex and even the brain at large. While some studies have already compared different domains of visual expertise (e.g. car experts vs bird experts: Gauthier et al., 2000; Xu, 2005 and car experts vs plane experts: McGugin et al., 2012a), they only focused upon a limited set of ROIs and might therefore have missed potential expertise effects. Others adopted a broader perspective and performed at least some whole-brain univariate or multivariate analyses but were limited to only one domain of expertise (Bilalić et al., 2014; Harel et al., 2010; Mongelli et al., 2017). As a consequence, we lack insight into the degree of similarity (or disparity) between neural changes induced by different domains of visual expertise.

In the present fMRI study we combine large-scale univariate analyses, multi-voxel brain decoding and region-of-interest analyses to compare the changes in neural processing associated with two forms of expertise, bird expertise (ornithology) and mineral expertise (mineralogy). We have deliberately included one animate and one inanimate domain, because this seems to be the major distinction underlying the large-scale organization of neural object representations (e.g. Kriegeskorte et al. 2008; Mahon and Caramazza 2009; Bracci and Op de Beeck 2016). While mineralogy might seem an odd choice at first, minerals form a homogenous object category that is more representative of a nonliving category than for example the more commonly studied category of cars (Gauthier et al., 2000; Xu, 2005). Since cars are moving objects and the front views of cars resemble faces (Xu, 2005), they have often been depicted as living objects (e.g. the Pixar animation film series “Cars”). Comparing two very different domains of visual expertise offers us the opportunity to investigate whether expertise induces domain-specific neural changes, possibly showing a bias to affect those regions which are most activated by the object domain (“informative” regions; Op de Beeck and Baker 2010; Brants et al. 2016). Alternatively, more general correlates of visual expertise that are similar across different domains could play a role, either at the level of specific regions of interest (Gauthier et al., 2000) or at a more distributed level (Harel et al., 2013). Importantly, to test these hypotheses we have to investigate patterns of activity not only at the level of individual areas, but more broadly across large cortical regions.

2.2 MATERIAL AND METHODS

2.2.1 Participants

The study included 68 participants. Twenty-one candidate experts in ornithology, 27 candidate experts in mineralogy and 20 control participants took part in the behavioral session of this study. All participants completed perceptual and semantic measures for both domains of expertise (see details below). Based on the behavioral results, 10 candidate experts in mineralogy were excluded from further participation and analyses. One expert in ornithology was excluded for MRI safety reasons. The final sample of subjects consisted of 20 ornithologists (aged 26.4 ± 5 years, 5 females, average 8.6 years of experience (sd 4.6 years), apart from three outliers all within 3 and 10 years), 17 mineralogists (aged 25.3 ± 5 years, 7 females, average 6.4 years of experience (sd 3.7 years), apart from three outliers all within 3 and 8 years) and 20 control participants (aged 24.3 ± 3 years, 7 females, no experience with either birds or minerals). These sample sizes were larger than the number of participants included in the few other studies comparing two groups of experts (Gauthier et al., 2000; Xu, 2005). The subject groups were mostly matched for number of men/women. Previous research has indicated that men show an advantage for recognition of nonliving objects, while women tend to be better at recognizing living objects (McGugin, Richler, Herzmann, Speegle, & Gauthier, 2012). While it would be interesting to investigate sex differences in these domains of expertise, our subject groups consisted of too few female experts to make the comparison. All ornithologists were active birdwatchers that had taken up this hobby out of interest. The group of mineralogists consisted in part of students with an academic degree in geology and in part of participants that actively collected and identified minerals. All participants were healthy adults with normal or corrected-to-normal vision and the three groups were matched for level of education. The study was approved by the Medical Ethical Committee of KU Leuven and all participants provided a written informed consent.

2.2.2 Behavioral session and determination of expertise level

All subjects participated in a behavioral session of approximately one hour, in which they carried out several computer and paper-and-pencil tasks. First, participants were asked to fill out a questionnaire in which their self-reported knowledge of birds and minerals was measured, as well as their general interest in classifying and determining objects. This questionnaire was a Dutch translation of the questionnaire used by Gauthier et al. (2014), in which the category-specific questions were attuned to birds and minerals. Second, all participants completed two perceptual discrimination tasks, one for each domain of expertise, to determine their level of expertise. Each discrimination task consisted of 80 pairs of colored images of either European bird species or of more or less well-known minerals, which were selected with the assistance of experts in both domains. The participants had to decide for each pair of images whether both images were of the same species in the case of birds or whether they shared the same chemical composition (polymorphs) in the case of minerals. Note that for both types of expertise, the discrimination task was not strictly (though largely) a perceptual task. Both visual (birds: shape and color of claws, beak, feathers, etc.; minerals: crystal structure) and non-visual (birds: birdsong, habitat; minerals: hardness) aspects play a role in the classification of birds and minerals. Furthermore, experts need domain-specific knowledge to know how to interpret the visual information (e.g., the fact that for some species of birds the male and female exemplars are very different). The pairs in both tasks (half 'same', half 'different') varied in difficulty. The images were presented sequentially: the first image appeared for 1 second, the second image remained on the screen until a same/different response was made by pressing one of two keys on the keyboard. The design of this discrimination task was inspired by tasks used in earlier fMRI studies of expertise (Gauthier et al., 2000; Gilaie-Dotan, Harel, Bentin, Kanai, & Rees, 2012; Harel et al., 2010; McGugin, Gatenby, Gore, & Gauthier, 2012).

An additional semantic task was used to measure how well participants were able to name different objects of expertise, again for both domains of expertise. Participants were asked to name a list of 30 colored images as precise as possible, without being limited by a time constraint. Each answer was awarded one, two or three points, based on the specificity of the answer. For example, naming the correct bird species (and even giving the correct Latin name) would earn more points than naming the more general bird family. Participants with a knowledge of birds were considered bird experts if they reached an accuracy level of 65% on the bird discrimination task, which was the case for all candidate bird experts. Three participants who claimed to have no specific knowledge of birds reached the 65% boundary as well, however, they were not considered to be experts based on their low score on the semantic task for birds (maximal score of 15% correct, far below the average score of 65% for the included bird experts). For the selection of mineralogists the same logic was applied. However, the mineral discrimination task proved to be more difficult, therefore a threshold of 60% was applied. One candidate mineral expert did not reach the 60% threshold (score: 57.5%), but since his semantic score was very good (situated at the 76th percentile of semantic scores for all included mineral experts), he was still included in the study as a mineralogist. Ten other candidate mineralogy experts were excluded for further testing (no fMRI scan) because they did not reach the 60% discrimination threshold and did not compensate with a convincing score on the semantic task (scores situated below the 29th percentile of semantic scores for all included mineral experts). The thresholds for the discrimination tasks were chosen to make the distinction between experts and non-experts as clearly as possible, while taking into account the different characteristics of the performance on the two tasks. The selected thresholds for both tasks were significantly different from the chance level of 50%. Following the binomial distribution, the probability of answering exactly or more than 48 out of 80 trials (60%) correctly is p = 0.046, the probability of having exactly or more than 52 correct trials (65%) is p = 0.0048, under the null hypothesis of a distribution centered at 50%.

After the imaging data had been collected, we tested the participants' memory for the bird and mineral exemplars that had been presented to them during the scans (see fMRI procedure and experimental design). In this delayed recognition task, for both categories the 20 original images were interspersed with 20 distracters and participants were asked to indicate which of these images they had or had not seen during the experiment.

Finally, we assessed the participants' recognition ability in a third, neutral domain to assess whether the experts' performance on the relevant discrimination task (e.g. bird task for ornithologists) was related to a more domain-general skill of fine object recognition. Although participants' performance on the discrimination task of the "opposite" domain (e.g. mineral task for ornithologists) already served as a baseline measure (since it concerns an object category of which participants have no specific knowledge), we also administered the Cambridge Face Memory Test (CFMT, Duchaine and Nakayama, 2006) to all participants.

2.2.3 Apparatus

Imaging data were collected using a 3T Philips Ingenia CX scanner with a 32-channel head coil at the Department of Radiology of the University Hospitals Leuven. 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. We collected a high-resolution T1-weighted anatomical image for each participant (182 slices, 0.98 x 0.98 x 1.2 mm resolution, TR = 9.6 ms, TE = 4.6 ms, 256 x 256 acquisition matrix). The stimuli were presented using PsychToolbox 3 (Brainard, 1997) in Matlab and projected onto a screen which could be viewed through a mirror mounted on the head coil.

2.2.4 fMRI procedure and experimental design

Imaging data were collected in a block-design experiment consisting of 10 runs, each lasting 255 seconds. Within each run, 7 categories of stimuli were presented: birds, minerals, faces, scenes, living objects (animals), nonliving objects and scrambled images (Figure 2.1). Each category contained 20 gray-scale images. The images were presented on a uniform gray background at a uniform size of 300 x 300 pixels in a random left or right orientation and with a small position jitter (maximum 50 pixels in horizontal and vertical direction) around the fixation point. The order in which the categories were presented was balanced over runs and participants and the stimulus order within each category block was randomized. Each block contained 20 stimulus trials, of which three trials were an immediate repetition of the previously presented image but with a random position and orientation. Participants were asked to press a button to signal these successive image repetitions regardless of position and orientation changes. Responses were collected via a response box.

2.2.5 Analyses

fMRI preprocessing and statistical analysis

All imaging data were preprocessed using the Statistical Parametric Mapping software package (SPM12, Welcome Department of Cognitive Neurology, London). Functional images were corrected for slice timing differences as well as head movements by realignment to the mean image. The images were smoothed using a Gaussian kernel of 8 mm full-width at half maximum (FWHM) for univariate second level analyses, and a Gaussian kernel of 5 mm FWHM for the univariate ROI-analyses and for all multi-voxel analyses (subject classification, generalization and representational similarity analyses). Both anatomical and functional images were normalized to the standard Montreal Neurological 152-brain average template and the voxels were resampled to a voxel size of 2.5 x 2.5 x 2.5 mm. Due to some technical difficulties and excessive head motion, a number of functional runs had to be excluded from further analyses. We controlled for excessive head motion during scanning by discarding all runs in which participants moved more than half a voxel size (1.25 mm) on two consecutive images. For 41 participants (14 ornithologists, 11 mineralogists and 16 controls), we were able to include all 10 functional runs. For 10 participants (4 ornithologists, 4 mineralogists and 2 controls) 9 runs were included, for 4 participants (2 ornithologists and 2 controls) we included 8 runs and for the remaining 2 participants (mineralogists) we included 7 runs. For each participant a general linear model (GLM) was fitted to estimate the linear relationship between the experimental conditions and the recorded neural activation in each voxel. The fixation condition was not explicitly modeled. Motion realignment parameters were added as regressors to control for signal variation due to head motion. Further analyses were performed using t-tests between coefficients of different experimental conditions.

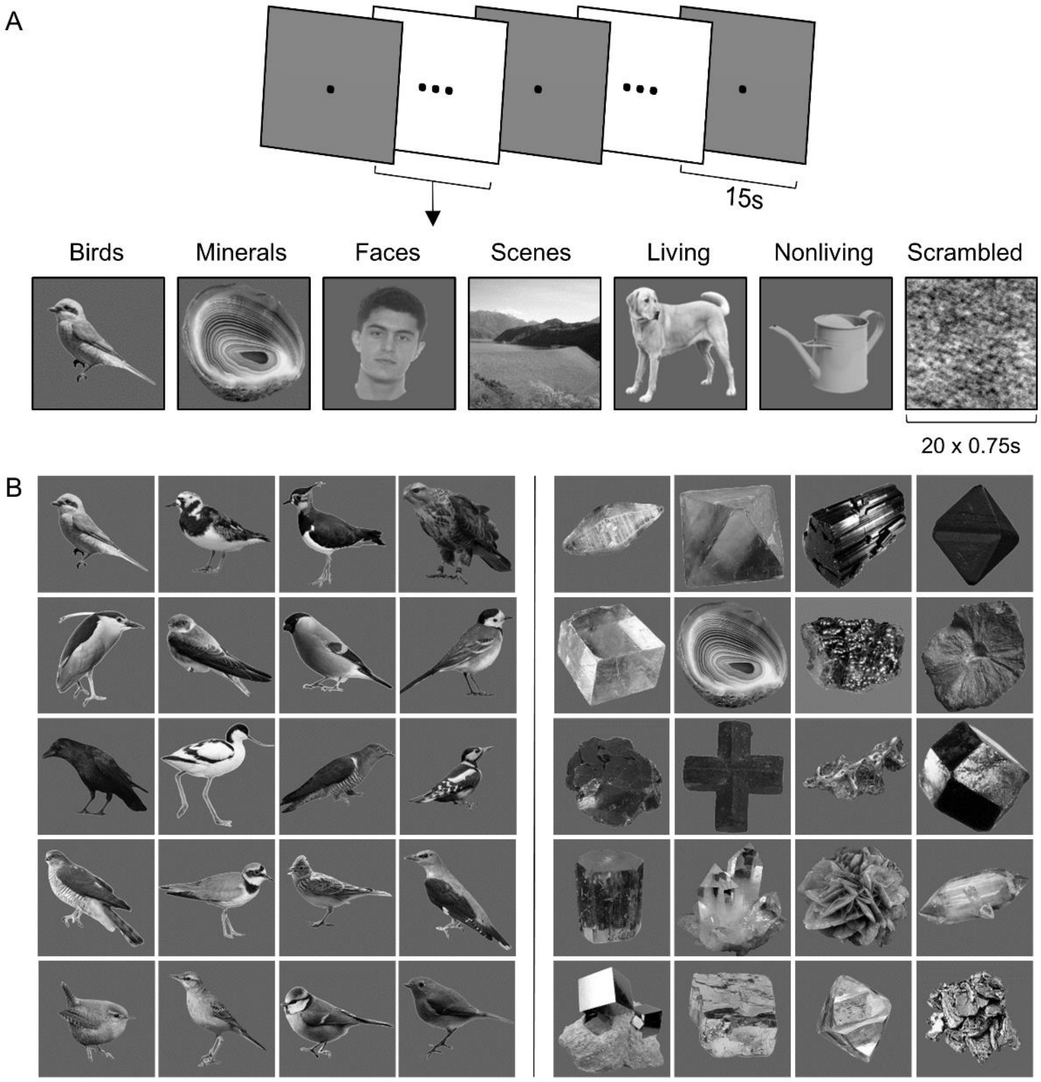


Figure 2.1. Schematic overview of the design of one experimental run and expertise stimuli. *Overview of the design of one experimental run (A), images of 7 categories were presented in a block-design (20 grayscale images per block). At the start, in the middle and at the end of each run a fixation block of 15s was presented. (B) The 20 bird stimuli and 20 mineral stimuli that were used during the experiment.*

Regions of interest

Given that object recognition has been shown to be sustained by a neural system encompassing low- and high-level regions in ventral visual cortex as well as frontal regions (e.g. Fenske et al. (2006)), we delineated three large but mutually exclusive anatomically defined regions of interest (aROIs). First, we selected all voxels that were significantly active above the threshold of $p < 0.001$ (uncorrected) in the contrast [all conditions - fixation]. Anatomical masks, created by using the WFU PickAtlas Toolbox (Wake Forrest University PickAtlas, fmri.wfubmc.edu/cms/software), were used to define the following bilateral aROIs (Figure 2.2): a low-level visual aROI (Brodmann areas 17 and 18, which included V1 and nearby cortical regions, defined in all 57 subjects), a high-level visual aROI (Brodmann areas 36, 37 and 20, defined in all 57 subjects) and the complete frontal lobe (including motor cortex, defined in all 57 subjects). Given that these masks provide a thin cortical thickness which is not realistic given the smoothed nature of our fMRI data for the between-group comparisons, the anatomical masks were expanded by two voxels in all directions to make sure that most relevant active voxels were included. The resulting minor overlap between the low-level visual aROI and the high-level visual aROI was removed from both resulting masks. Seven additional functional ROIs (fROI) were delineated manually in each individual participant, independent from the experimental data. These fROIs, that were defined using different functional contrasts, all included spatially contiguous voxels that exceeded the uncorrected statistical threshold of $p < 0.0001$. Significantly active voxels were displayed on coronal slices and manually selected. Only clusters consisting of a minimum of 20 voxels were selected. When less than 20 active voxels were found, a more liberal uncorrected threshold of $p < 0.005$ was applied. Here again, the minimum cluster size was taken into account, and the fROI was not defined if cluster size was smaller than 20 voxels. The fusiform face area (left FFA: 54 subjects; right FFA: 56 subjects) and the occipital face area (OFA) were defined by the contrast [faces - nonliving] in combination with anatomical criteria. Due to the fact that OFA could only be selected in a limited number of participants (38 left and 44 right), this region was left out of any further analyses. For the selection of the parahippocampal place area (PPA; left PPA: 57 subjects; right PPA: 57 subjects), voxels around the parahippocampal gyrus that showed responsiveness for the contrast [scenes - nonliving] were delineated. We defined two parts of lateral occipital complex (LOC) using the [nonliving – scrambled] contrast: a more posterior part in lateral occipitotemporal cortex (pLOC; left pLOC: 57 subjects; right pLOC: 57 subjects) and a more anterior part in ventral occipitotemporal cortex (aLOC; left aLOC: 57 subjects; right aLOC: 57 subjects). Both regions were selected in a mutually exclusive way. Finally, a region selective for living objects (left Living: 57 subjects; right Living: 56 subjects) and a region selective for nonliving objects (left Nonliving: 56 subjects; right Nonliving: 56 subjects) were delineated using the contrasts [living - nonliving] and [nonliving - living] respectively. Analyses in both the anatomical and the functional ROIs were performed across hemispheres (see e.g. Harel et al., 2010). The average sizes and MNI coordinates of all the ROIs mentioned above are presented in supplementary material (section 2.5.1, Table 2.2).

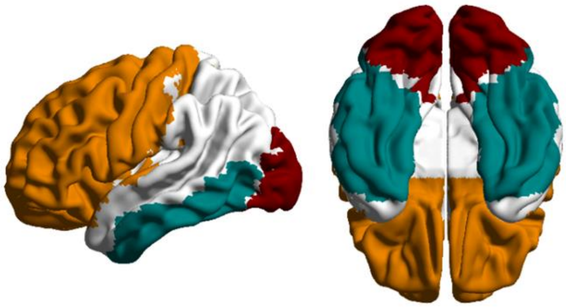


Figure 2.2. Lateral and ventral view of the three anatomically defined aROIs. *The low-level visual aROI is indicated in dark red, the high-level visual aROI in dark green and the frontal lobe in orange. The masks were visualized using BrainNet Viewer ((Xia et al., 2013) http://www.nitrc.org/projects/bnv/) and custom Matlab code.*

Univariate fMRI analysis

We performed conventional univariate fMRI analyses to determine the presence of heightened neural activation in experts compared to novices in response to objects of expertise. We calculated the mean response per voxel elicited by the different experimental conditions and compared these mean activations (beta values) between subject groups. This way, we performed whole-brain second-level analyses as well as group comparisons within specific ROIs. The effect of expertise for birds was defined by the contrast [birds – base] in which the “base” condition was a combination of the living and nonliving condition. The contrast [minerals - base] was used to define the expertise effect for minerals. For all univariate analyses, we first applied a stringent threshold of $p < 0.05$ corrected for family-wise error. However, when no effects survived, we lowered the threshold to $p < 0.0001$ (uncorrected, minimum cluster size of 10 voxels, see Lieberman and Cunningham (2009)) for all bird expertise analyses and an uncorrected threshold of $p < 0.001$ (minimum cluster size of 10 voxels) for the mineral expertise analyses. Note that these univariate maps are not meant to demonstrate significance for individual voxels, but instead to visualize where the voxels with the clearest univariate differences and thus with potential relevance for the classifiers tend to be.

Multivariate fMRI analyses: subject classification

With this analysis, we tried to answer the following question: can we make a distinction between subject groups based on their neural response patterns for a specific condition? These subject classification analyses were applied in each ROI to discriminate ornithologists from control participants and mineralogists from control participants (see Fig. 2.3A). The response per voxel per subject was defined by the univariate contrast of one of the expertise conditions versus base, e.g. [birds – base]. The contrast values were standardized by subtracting the mean value across all voxels in the subject-specific response pattern and dividing this result by the standard deviation across voxels. A linear support vector machine (SVM) was applied using the libsvm Matlab toolbox (Chang & Lin, 2011) with similar parameters as Bulthé and colleagues did (Bulthé, De Smedt, & Op de Beeck, n.d.). To train and test the SVM model, we used a leave-pair-out cross-validation (LPOCV) technique, as was used by Ung et al. (2014). For each of the two subject groups, a participant was randomly selected and left out of the training sample. Next, the classifier was trained on all subjects except for the left-out pair, which was subsequently used to test the trained model. Since all subjects viewed the same images for all the object categories, the training and testing of the classifier happened on identical images. This procedure was repeated until each participant was left out once. In the case of unequal group sizes, the procedure was repeated until each participant of the smallest group was left out once. The decoding accuracy was calculated as the proportion of times in which test participants were correctly classified as belonging to one of the two subject groups. To control for slight differences in decoding accuracies due to the random selection (pairing) of test data, the LPOCV technique was iterated 1000 times and the decoding accuracies were averaged across all iterations. The higher this resulting decoding accuracy, the better the classifier was able to make a distinction between the two groups. In order to determine the significance threshold for the decoding accuracies, we applied Monte Carlo permutation tests (Mourão-Miranda, Bokde, Born, Hampel, & Stetter, 2005). The above described LPOCV technique was again repeated 1000 times, only this time the class labels of the training sample were randomly shuffled before the model was trained, leading to a distribution of decoding accuracies based on random information. A 95% confidence interval around the mean of this distribution was calculated to determine the significance threshold for each comparison. As a sanity check, we checked that the significance thresholds obtained through permutations were very similar and not more liberal compared to the threshold expected from a simple (parametric) binomial test. According to such a binomial test, results above 62.5% would be significant with a total of 40 participants, as in classifications involving ornithologists and controls. For mineralogists and controls (N=37), the parametric threshold would be 62.2%.

Furthermore, for each individual participant a mean decoding accuracy was calculated by dividing the number of times this participant was classified as an expert by the number of times the data of this participant were used as test data. This was done for the two comparisons mentioned above: we calculated the proportion of times ornithologists and control participants were classified as an ornithologist and the proportion of times mineralogists and control participants were classified as a mineralogist. These “proportions decoded as expert” were then related to the different behavioral measures of expertise (results in Table 2.1).

Multivariate fMRI analyses: generalization

To check whether potential differences in neural representations between control participants and bird experts were similar to the differences in representations between control participants and the group of mineral experts (and vice versa), we tested generalization of subject classification (Figure 2.3B). In particular, we tested whether the classifier that was trained to make a distinction between the control group and one expert group based on the objects of expertise of that expert group (e.g., birds for ornithologists), was also able to make a distinction between the control group and the other expert group using their objects of expertise (e.g., minerals for mineralogists). Within each ROI, generalization was tested in both directions: training the classifier on the distinction ornithologists vs. control participants and testing on mineralogists vs. control participants, and vice versa. The overall “generalization accuracy” was calculated by averaging the decoding accuracies for both directions. To determine the significance threshold, we applied for each direction of generalization the same random permutation method as described above. This resulted in two distributions of decoding accuracies based on random information. By randomly selecting half of the decoding accuracies from each distribution and combining these selected values, we created a new distribution that was used to determine the significance threshold for the generalization accuracy. Again, the obtained thresholds were similar to the thresholds which would be observed using a parametric binomial test with the number of participants involved (N=57). Hence we used a parametric method to calculate the 95% confidence interval around the proportion of subject generalization in order to compare it to the maximal generalization (see next paragraph).

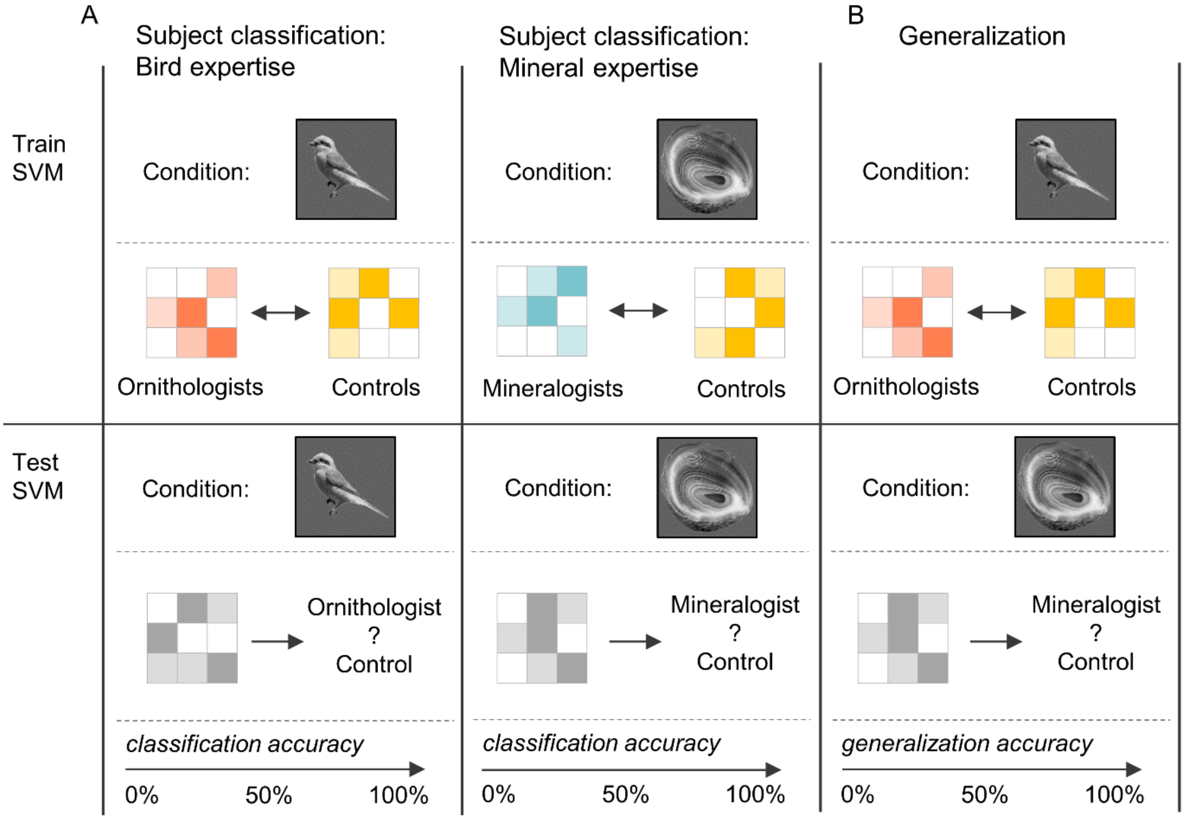


Figure 2.3. Schematic overview of the subject classification analyses and the generalization analysis. *(A) Overview of the subject classification analyses for bird expertise and mineral expertise. A classifier was trained to make a distinction between the expert group and the control group based on their neural responses for the expert object condition (birds or minerals). Subsequent testing resulted in a classification accuracy. (B) Overview of the generalization analysis. A classifier was trained on the expertise effect for one domain of expertise (e.g. bird expertise: the distinction between ornithologists and control participants for the category of birds) and tested on the other domain of expertise (e.g. mineral expertise: the distinction between mineralogists and control participants for the category of minerals). The generalization analysis was performed in two directions.*

Maximal generalization: simulations

We have already shown previously through simulations how the amount of generalization is limited by the classification accuracy in the two datasets between which the generalization is tested (Brants et al., 2016). If the two datasets differ in classification accuracy, then the generalization accuracy will be somewhere in between. We implemented these simulations with the classification accuracies obtained in the current dataset in order to quantify the maximally expected generalization accuracy given the empirically measured classification accuracies. A detailed explanation of this simulation approach is given in Brants et al. (2016).

Multi-voxel representational similarity analyses

Within the high-level visual aROI, multi-voxel patterns of activation for all the seven different conditions were correlated in a pairwise manner as a measure of their similarity or distinctness. As a first step, the data set for each participant was randomly divided into two equally sized subsets of runs (one half of the data amounted to 4 or 5 runs in which each condition was presented twice). Beta values for each voxel of the high-level visual aROI were standardized by subtracting the mean value across all conditions. For each participant, the activation patterns of all conditions in the first subset of runs were correlated with the second subset. This procedure of dividing the data and computing the correlations was repeated 100 times, resulting for each participant in a matrix of correlations averaged across those repetitions. The individual similarity matrices were averaged across participants within each group. The resulting group similarity matrices, in which each cell contained the correlation between two specific conditions, were visualized using multidimensional scaling (MDS), which arranged the experimental conditions in a two-dimensional space according to similarity in activation patterns. Highly correlated conditions are shown closer together whereas less correlated conditions are located further apart in the MDS plots. This method allowed us to investigate potential differences between experts and novices in the representational similarity between the categories of stimuli.

2.3 RESULTS

2.3.1 Behavioral indices of expertise

The final sample included 57 participants from three groups: ornithologists (N=20), mineralogists (N=17), and control participants (N=20). A variety of behavioral indices showcased the domain-specific expertise of participants. Figure 2.4 displays the proportion correct scored by the three subject groups on the discrimination and semantic tasks for birds and minerals, these scores were used to select the experts. For the discrimination tasks, we calculated d' (d-prime) for each participant based on the number of Hits (subject correctly responds that birds / minerals are the same) and False Alarms (subject responds that birds / minerals are the same while in reality they are different; $d' = z(H) - z(FA)$). These d' values were used in the following analyses. On the bird discrimination task, the ornithologists scored significantly higher than the mineralogists ($t(35) = 8.39$, $p < 0.0001$) and the control participants ($t(38) = 9.71$, $p < 0.0001$). The mineralogists outperformed the ornithologists ($t(35) = 7.50$, $p < 0.0001$) and the control participants ($t(35) = 7.84$, $p < 0.0001$) on the mineral discrimination task.

The mineralogists' performance on the mineral discrimination task was significantly lower than the ornithologists' score on the bird discrimination task ($t(35) = 5.67$, $p < 0.0001$). However, it should be noted that the two discrimination tasks were not calibrated and are therefore not really comparable. It might very well be that the mineral discrimination task was more difficult. This can be illustrated by a linear regression analysis showing that an ornithologist with 7 years of experience would reach a d' of 2.23, while an equally experienced mineralogist would only get a d' of 0.91 on the mineral discrimination task. Note that the control participants showed no difference in performance between the bird discrimination task and the mineral discrimination task ($t(19) = 1.35$, $p = 0.19$), for both tasks they performed around chance level.

The semantic tasks showed the same pattern of results. On the semantic task for birds, the ornithologists' score was higher than the mineralogists' ($t(19.95) = 13.23$, $p < 0.0001$), which was in its turn higher than the score of the control participants ($t(35) = 2.50$, $p = 0.015$). On the semantic task for minerals, the mineralogists outperformed the ornithologists (t(23.87) = 9.79, p < 0.0001) and the control participants (t(18.33) = 11.26, p < 0.0001).

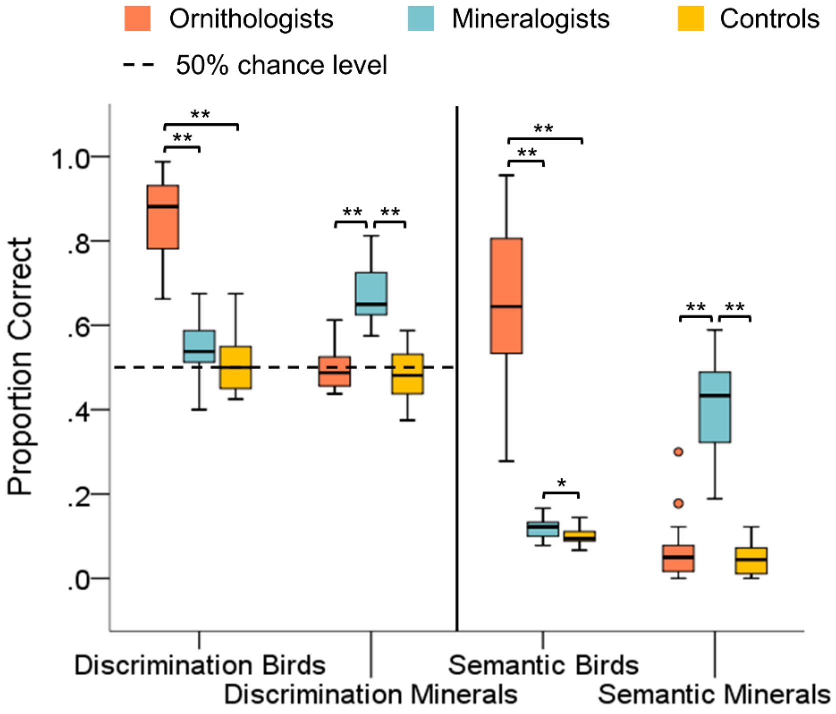


Figure 2.4. Results for the behavioral expertise tasks. *Results for the discrimination and semantic tasks for ornithologists (N=20), mineralogists (N=17) and control participants (N=20). Boxplots display the median proportion correct and interquartile range, whiskers indicate the minimum and maximum values and dots represent outliers (> 1.5 x interquartile range). Unpaired t tests were used to determine significance, which is indicated by * (p < 0.05) or by ** (p < 0.0001). For the discrimination tasks (left panel), chance level performance was at 50%. The expert group always outperformed the other two groups on those tasks related to their field of expertise. These scores were used to select the experts.*

Finally, ornithologists with more years of experience tended to score better on the bird expertise tasks compared to less experienced ornithologists. Self-reported years of experience with birds was significantly correlated with performance on the semantic task for birds (Pearson's r = 0.46, p = 0.02) and the relation to the performance on the discrimination task also tended to be positive, although not significant (Pearson's r = 0.42, p = 0.06). For mineralogists, there was no significant correlation between years of experience and the scores on the mineral tasks (semantic task: Pearson's r = 0.31, p = 0.11; discrimination task: Pearson's r = 0.40, p = 0.11). We did not find a correlation between the age of the experts and their scores on the discrimination or semantic tasks for their expert object category (Orn.: discrimination task: Pearson's r = 0.01, p = 0.95; semantic task: Pearson's r = 0.21, p = 0.38; Min.: discrimination task: Pearson's r = -0.05, p = 0.86; semantic task: Pearson's r = 0.41, p = 0.10).

As was mentioned in the methods section, the discrimination tasks and the semantic tasks were used to select the experts. Therefore, the group differences on these tasks are to be expected and circular. However, other behavioral measures showed clear differences between the three subject groups as well. On the expertise questionnaire, apart from their number of years of experience, participants also indicated on a scale of 1 to 9 how often they read text about birds/minerals and how often they looked at images of birds/minerals. The responses clearly showed a difference between the three subject groups, with the experts spending more time with their specific domain of expertise and the control participants not really spending time on either domain (text birds: Orn.: 8.0, Min.: 2.2, Con.: 1.7; images birds: Orn.: 8.0, Min.: 3.6, Con.: 2.0; text minerals: Orn.: 1.7, Min.: 7.2, Con.: 1.4; images minerals: Orn.: 1.6, Min.: 6.9, Con.: 1.6).

Furthermore, on the one-back task participants performed while in the scanner, both expert groups achieved higher scores when the task involved images belonging to their domain of expertise compared to images belonging to the other expert domain. For each participant and for each condition we calculated d' (d' for condition Birds: Orn.: 2.88, Min.: 1.89, Con.: 2.21; d' for condition Minerals: Orn.: 2.75, Min.: 2.55, Con.: 2.38). A two-way repeated measures ANOVA with subject group as a between-subjects factor and condition (7 levels) as a within-subjects factor revealed a significant interaction (F(12,324) = 2.98, p = 0.001) between subject group and stimulus condition, accompanied by a significant main effect of stimulus condition (F(6,324) = 41.77, p < 0.0001) but no main effect of subject group (F(2,54) = 2.03, p = 0.142). The interaction between stimulus condition and subject group was also significant when restricted to birds and minerals (F(2,54) = 10.76, p < 0.0001). To estimate the increase in discriminability both expert groups showed for their expert condition compared to the remaining conditions, we calculated d'(expert condition) – d'(remaining conditions). The increase in discriminability did not differ between the two expert groups (t(35) = 1.49, p = 0.15).

The findings were similar for the delayed recognition task in which participants indicated which bird and mineral images they had or had not seen during the scans. Again, for each participant and for each condition d’ was calculated. A two-way repeated measures ANOVA for unbalanced groups with subject group as a between-subjects factor and condition (birds or minerals) as a within-subjects factor showed that both expert groups were better able to recognize presented and not-presented images from their specific domain of expertise (significant interaction: $F(2,54) = 52.59$, $p < 0.0001$; d’ for condition Birds: Orn.: 3.14, Min.: 1.16, Con.: 1.09; d’ for condition Minerals: Orn.: 2.40, Min.: 2.61, Con.: 2.15). The increase in discriminability (d’(expert condition) – d’(nonexpert condition)) for the delayed recognition task was significantly different between the two expert groups ($t(35) = 3.10$, $p = 0.004$), mineralogists showed an advantage over ornithologists.

Finally, we tested whether there was any relationship between the participants’ performance on the expertise-related tasks and the third neutral domain of face perception as measured by the CFMT. The three subject groups did not differ in their face recognition ability ($F(2,54) = 0.37$, $p = 0.69$; Orn.: 75% correct, sd = 12.9%, Min.: 74% correct, sd = 10.8%, Con.: 77% correct, sd = 14.5%). For neither of the two expert groups a significant correlation could be found between the experts’ performance on the CFMT and their performances on the expertise tasks for their domain of expertise (Orn.: discrimination task: Pearson’s $r = -0.23$, $p = 0.33$; semantic task: Pearson’s $r = -0.17$, $p = 0.47$; Min.: discrimination task: Pearson’s $r = 0.26$, $p = 0.31$; semantic task: Pearson’s $r = 0.32$, $p = 0.21$).

2.3.2 Expertise-related multi-voxel patterns of selectivity

The fMRI scans probed the patterns of activity related to stimuli from the two domains of expertise, birds and minerals, as well as five other reference conditions: faces, scenes, living objects, nonliving objects and scrambled images (see Fig. 2.1).

We searched for expertise-related changes in the multi-voxel patterns by means of subject classification methods, following the scheme in Figure 2.3A. If the neural response patterns to a particular stimulus condition would be altered by expertise, then we should be able to reliably classify subjects as belonging to a particular subject group based upon these patterns. Three large aROIs were anatomically defined: a low-level visual aROI, a high-level ventral visual aROI, and the frontal lobe. The classification of subjects was tested for two selectivity patterns: the selectivity for birds and selectivity for minerals. Two group comparisons were made: (1) ornithologists vs. control participants and (2) mineralogists vs. control participants.

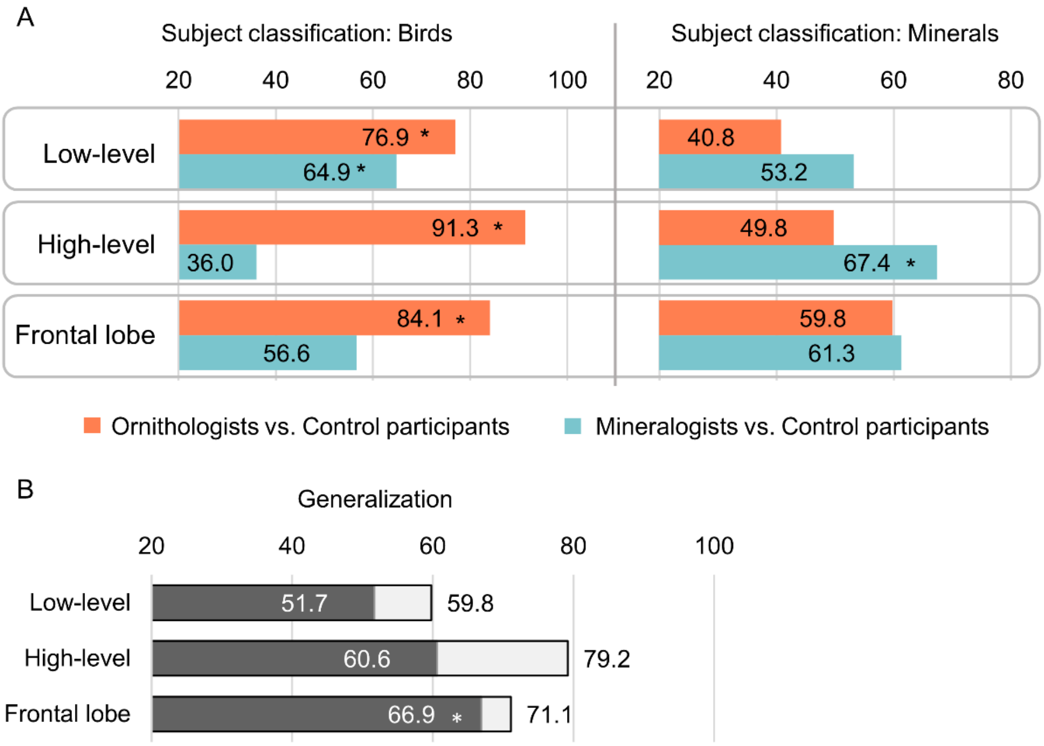


Figure 2.5. Subject classification and generalization results. *(A) Results for the subject classification analyses in percentages. Monte Carlo permutation tests were used to determine the significance threshold for each classification accuracy (see section 2.2.5), significance is indicated by a *. The left panel shows the classification of participant groups based on their neural response patterns for birds. The classifier was able to make a distinction between ornithologists and control participants in all three aROIs. The right panel shows the classification for the category of minerals, with a significant distinction between mineralogists and control participants in the high-level visual aROI. (B) Results for the generalization analysis. Generalization accuracies are depicted by the dark grey bars, the light grey bars show the maximal generalization that could be expected given the classification performances for the two expertise effects in each specific aROI (see section 2.2.5). Significance is indicated by an asterisk.*

As shown in Figure 2.5A, the multi-voxel pattern classification was able to make a distinction between ornithologists and control participants based on the selectivity for birds in each aROI. Classification accuracies in the different aROIs ranged from 76.9% ($p < 0.0001$) to 91.3% ($p < 0.0001$). A very different result was found for mineral expertise (Figure 2.5B). The distinction between mineralogists and control participants could only be made based on neural response patterns in high-level visual cortex (67.4%, p = 0.024). No significant classification was found in the low-level visual aROI (53.2%, p = 0.301) nor in the frontal lobe (61.3%, p = 0.117).

Although high-level visual cortex showed significant effects for each expertise domain, there was an obvious difference in effect size between domains (subject classification accuracies: 91.3% for bird expertise, 67.4% for mineral expertise). We hypothesized that this difference in effect size might be explained by a difference in the level of expertise between ornithologists and mineralogists. To address this issue, we performed the same analysis on a subset of the expert groups that were matched for their level of expertise. Because the discrimination and semantic tasks were not comparable between the two domains of expertise (see above), we calculated a new measure of experience using the participants' answers on the expertise questionnaire. For each expert, we calculated an average score indicating how often they read text about and looked at images of their objects of expertise (see above) and multiplied this with the number of years of experience they had. On average, the group of ornithologists had more "active experience" than the group of mineralogists (Orn.: 68.2, Min.: 43.9; t(35) = 2.35, p = 0.025). To match the two expert groups on this measure of experience, we temporarily excluded the 7 ornithologists with the most experience and the 4 mineralogists with the least experience, resulting in two groups with 13 experts each that did not differ on their level of experience (Orn.: 47.9, Min.: 50; t(24) = 0.22, p = 0.83). The subject classification accuracies in the high-level visual aROI for the matched groups were very similar to the ones that were obtained for the complete expert groups. The 13 least experienced ornithologists could be distinguished from the control participants equally well as when the most experienced ornithologists were included (90.1% vs. 91.3%). The same was true for the group of mineralogists when only the 13 most experienced participants were included (67.2% vs. 67.4%). These results showed that the difference in decoding accuracies in high-level visual cortex between the two domains of expertise was not influenced by the difference in level of experience between the two groups. (Remark: the analyses mentioned below were performed on the complete expert groups.)

As far as significant classification was possible for objects of expertise, that is, in all aROIs for ornithology and in high-level visual cortex for mineralogy, this classification was in each case higher than the classification obtained when the other group of experts was classified based upon neural activity patterns associated with the same objects (Figure 2.5). Ornithologists could not be distinguished from controls based upon the minerals condition. Likewise, mineralogists and controls could not be differentiated based on the birds condition in high-level visual cortex. Curiously, this same differentiation was possible in low-level visual cortex (64.9%, $p = 0.032$), albeit to a lesser extent than for ornithologists.

Overall, these findings fit with the general prediction that developing expertise alters the processing of objects in the domain of expertise. The findings are further confirmed by correlational analyses. We analyzed the “proportion decoded as expert” of each participant, to gain a better understanding of which participants were most often classified as being either an ornithologist (vs. a control participant, based on their neural response patterns for birds) or a mineralogist (vs. a control participant, based on their neural response patterns for minerals). We correlated the proportion of times participants (ornithologists and control participants) were classified as being an ornithologist (“proportion decoded as expert”), with their behavioral scores on the bird discrimination task (d’) and the semantic task for birds. The same correlations were calculated for participants classified as being a mineralogist (mineralogists and control participants), using the scores on the mineral expertise tasks. Results can be found in Table 2.1. Furthermore, in Figure 2.10 in the supplementary material (section 2.5.3), scatterplots display the relation between the participants’ scores on the discrimination tasks and the semantic tasks on the one hand and the “proportion decoded as expert” in the high-level visual aROI on the other hand.

For the comparison between ornithologists and control participants, in all three aROIs there was a significant positive correlation between the proportion of times participants were classified as ornithologist and the scores on the discrimination task and semantic task for birds. The higher a participant’s scores on the bird expertise tasks, the more likely this participants was to be taken for an ornithologist by a model that was trained to make the distinction between ornithologists and control participants based on their neural representations for birds. In the high level visual aROI, we also found a significant positive correlation between the proportion of times participants were classified as being a mineralogist and the scores on the mineral discrimination task. The correlation with the scores on the semantic task for minerals tended to be positive as well.

		Low-level visual		High-level visual		Frontal lobe	
Classification	**Behavioral task**	r	p	r	p	r	p
Ornithologists and controls: classified as ornithologists	Discrimination birds	0.544	0.0003	0.787	< 0.0001	0.628	< 0.0001
	Semantic birds	0.579	< 0.0001	0.812	< 0.0001	0.677	< 0.0001
Mineralogists and controls: classified as mineralogists	Discrimination minerals	-0.057	0.738	0.442	0.006	0.258	0.123
	Semantic minerals	-0.080	0.680	0.267	0.055	0.162	0.170

Table 2.1. Correlations between the "proportion decoded as expert" and performances on two behavioral tasks. *The "proportion decoded as expert" represents the proportion of times a subject was either classified as being an ornithologist (ornithologists and control participants, N = 40) or as a mineralogist (mineralogists and control participants, N = 37). The four aROI x classification situations in which the subject classification was significant, are indicated by a bold frame.*

2.3.3 Domain-specific and domain-general signatures of expertise

The rationale of our design with multiple types of expertise was to investigate whether effects of expertise are similar across different domains. Is bird processing in ornithologists changed in a similar way as mineral processing in mineralogists? To answer this question, we tested whether subject classification could be generalized across domains of expertise. More specifically, we tested whether a classifier that was trained to make a distinction between ornithologists and control participants based on their response patterns for birds, generalizes to the distinction between *mineralogists* and control participants based on their response patterns for *minerals*, and vice versa (see Fig. 2.3B). This generalization was tested in both directions in all three anatomical ROIs and an average accuracy was calculated for each aROI. The lower the generalization accuracy compared to the classification accuracies, the more evidence for domain specificity of expertise effects. The higher the generalization accuracy, the more evidence for domain-general representations.

Aside from the generalization performance, we calculated the maximal generalization that could be expected (see Materials and Methods & Brants et al., 2016). This maximal generalization, which is in between the classification performances shown in Figure 2.5, is important as a benchmark. First, if it is low, which is a consequence of low decoding performance, then the generalization analysis has insufficient sensitivity to differentiate between domain-specific and domain-general representations. More specifically, we have insufficient sensitivity when the maximum generalization is lower than our threshold of significance (61.8% - 64.7%). This was the case for the low-level visual aROI. Thus, in this region the signatures of expertise in the two domains were not strong enough to interpret the outcome of the generalization analysis.

In the high-level visual aROI, the theoretical maximal generalization was 79.2%, well above the threshold of significance. However, in the empirical data there was no significant generalization, with the generalization accuracy at 60.6%. Given that the 95%-confidence interval around a proportion of 0.606 with N=57 is [0.479 0.733], this subject generalization was significantly lower than the maximum generalization of 79.2%. Thus, at least part of the expertise effects on the neural representations of birds and minerals in high-level visual cortex were domain-specific. The way in which neural processing of expert objects in high-level visual cortex was changed by expertise depended upon the domain of expertise.

In the frontal lobe we found a different result. Generalization accuracy was significant at 66.9%, close to the predicted maximal generalization performance of 71.1%. This significant generalization signaled a substantial “overlap” between the two expertise effects in these regions. The result in the frontal lobe was remarkable, since we could not find a significant subject classification for mineralogists compared to control participants in this region. The fact that the generalization in this aROI did work, suggested that, although the decoding accuracy in the frontal lobe failed to reach significance for one of the two datasets, there must still be some meaningful information present that points to a distinction between mineralogists and control participants (similar findings in earlier studies: Oosterhof et al. 2012; Brants et al. 2016).

Taken together, the generalization of subject classification classifiers across domains of expertise indicated that expertise-related neural changes tend to reflect domain-specific effects in high-level visual cortex, whereas more general domain-independent effects of expertise were found in the frontal lobe.

2.3.4 Univariate effects of expertise

In the previous analyses, multi-voxel pattern analysis (MVPA) results showed the presence of expertise effects for both bird expertise and mineral expertise. Because MVPA does not give a direct indication of which voxels or sub-regions drive classification, the next logical step is to examine the more fine-grained locations of these expertise effects. The simplest approach is to perform a univariate test of the voxel-wise contrast value which was used in the classification. Starting with bird expertise, we compared the brain activation for the [birds-base] contrast in bird experts with the same contrast for all bird novices (mineral experts and control participants). Analyses revealed a large bilateral cluster in lateral ventral temporal cortex that was significantly more active for bird experts compared to novices (Figure 2.6A). MNI coordinates for the peak voxels in left and right hemisphere were (-51, -57, -20) and (37, -55, 20) respectively. Furthermore, some more scattered effects could be found in left prefrontal cortex. The latter effects disappeared when the threshold was increased to $p < 0.05$ corrected for family-wise error. When comparing bird experts to the group of control participants in itself, the distribution of effects was largely the same.

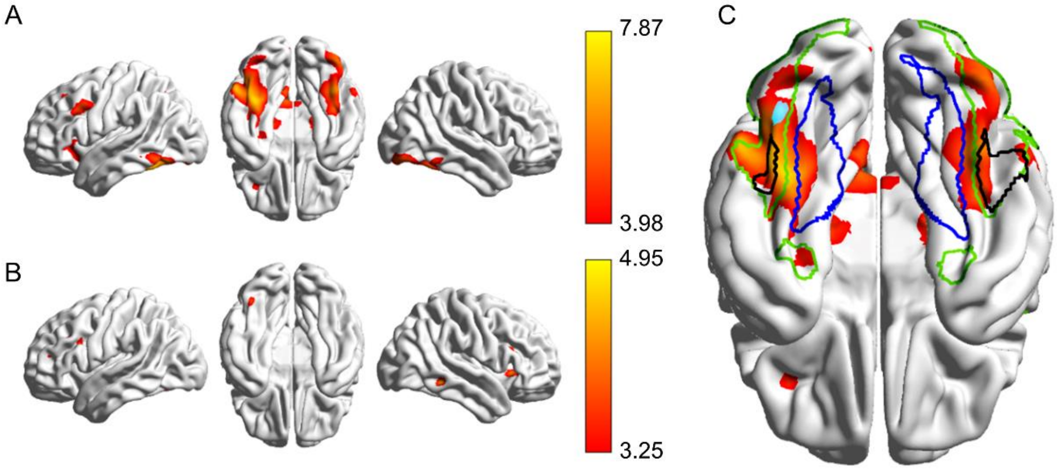


Figure 2.6. Overview of the univariate bird and mineral expertise effects. *(A) Left hemisphere, ventral and right hemisphere view of the univariate bird expertise effect: heightened activation for birds in bird experts compared to bird novices (uncorrected threshold of $p < 10^{-4}$, minimum cluster size of 10 voxels). (B) Left hemisphere, ventral and right hemisphere view of the mineral expertise effect: heightened activation for minerals in mineral experts compared to mineral novices (uncorrected threshold of $p < 10^{-3}$, minimum cluster size of 10 voxels). (C) Ventral view of the bird expertise effect (orange – yellow) and the mineral expertise effect (light blue). Dark blue outlines delineate the functional regions with a preference for nonliving objects, green outlines indicate regions selective for living objects and black outlines indicate the bilateral FFA. The figures were created using BrainNet Viewer (*(Xia, Wang, & He, 2013) *http://www.nitrc.org/projects/bnv/) and custom Matlab code.*

Ventral temporal cortex is known to house a complex functional organization. Figure 2.6C shows a ventral cortical view of the bird expertise effect and the mineral expertise effect in combination with outlines of the most relevant empirically measured regions with a functional preference for living objects, nonliving objects, as well as the fusiform face area. The spatial distribution of the bird expertise effect does not align with any of these functional divisions.

In addition, we quantified the bird expertise effects in 6 bilateral fROIs (FFA, PPA, pLOC, aLOC, a Living and a Nonliving region) that were manually delineated in individual participants using functional data from the conditions of faces, living objects, nonliving objects, scrambled and scenes. The expertise effect for birds was tested by comparing the mean activation for the contrast [birds – base] in ornithologists with the mean activation in bird novices (mineralogists and control participants). For each fROI, the results were averaged across the left and right hemisphere. The results are depicted in Figure 2.7A. In all 6 fROIs we found significantly heightened activation for birds in ornithologists compared to bird novices. This included FFA ($N_1 = 19$, $N_2 = 34$, $p < 0.0001$) and the Living region ($N_1 = 20$, $N_2 = 36$, $p < 0.0001$), which are most informative and most responsive to the domain of birds (which are living objects), but also the less responsive regions like pLOC ($N_1 = 20$, $N_2 = 37$, $p = 0.001$), aLOC ($N_1 = 20$, $N_2 = 37$, $p < 0.0001$), PPA ($N_1 = 20$, $N_2 = 37$, $p = 0.005$) and the Nonliving region ($N_1 = 20$, $N_2 = 35$, $p = 0.003$). Nevertheless, we found a significant positive correlation (Pearson's $r = 0.584$, $p = 0.046$) between the fROIs' general sensitivity for birds (average activation for the [birds-base] contrast in bird novices) and the difference in [birds - base]-activation between bird experts and bird novices (Figure 2.7C). In other words: the expertise effect for birds was most pronounced in those fROIs that already showed a higher specificity for birds (FFA and Living region). To make sure that the bird expertise effect in the Living region was not driven by the FFA, we excluded FFA voxels from the Living region for each participant and repeated the analysis for all participants for which the bilateral fROIs consisted of more than 20 voxels (Living - FFA left: 42 subjects, average size of 60 voxels; Living - FFA right: 42 subjects, average size of 73 voxels; given that the Living region was restricted to ventral cortex, it is to be expected that voxels responsive to animal bodies would overlap substantially with the FFA, see e.g. Schwarzlose et al. (2005)). Again, we found significantly heightened activation for birds in ornithologists compared to bird novices ($N_1 = 11$, $N_2 = 24$, $p = 0.005$) and the size of the effect was very similar to the effect in the original Living region.

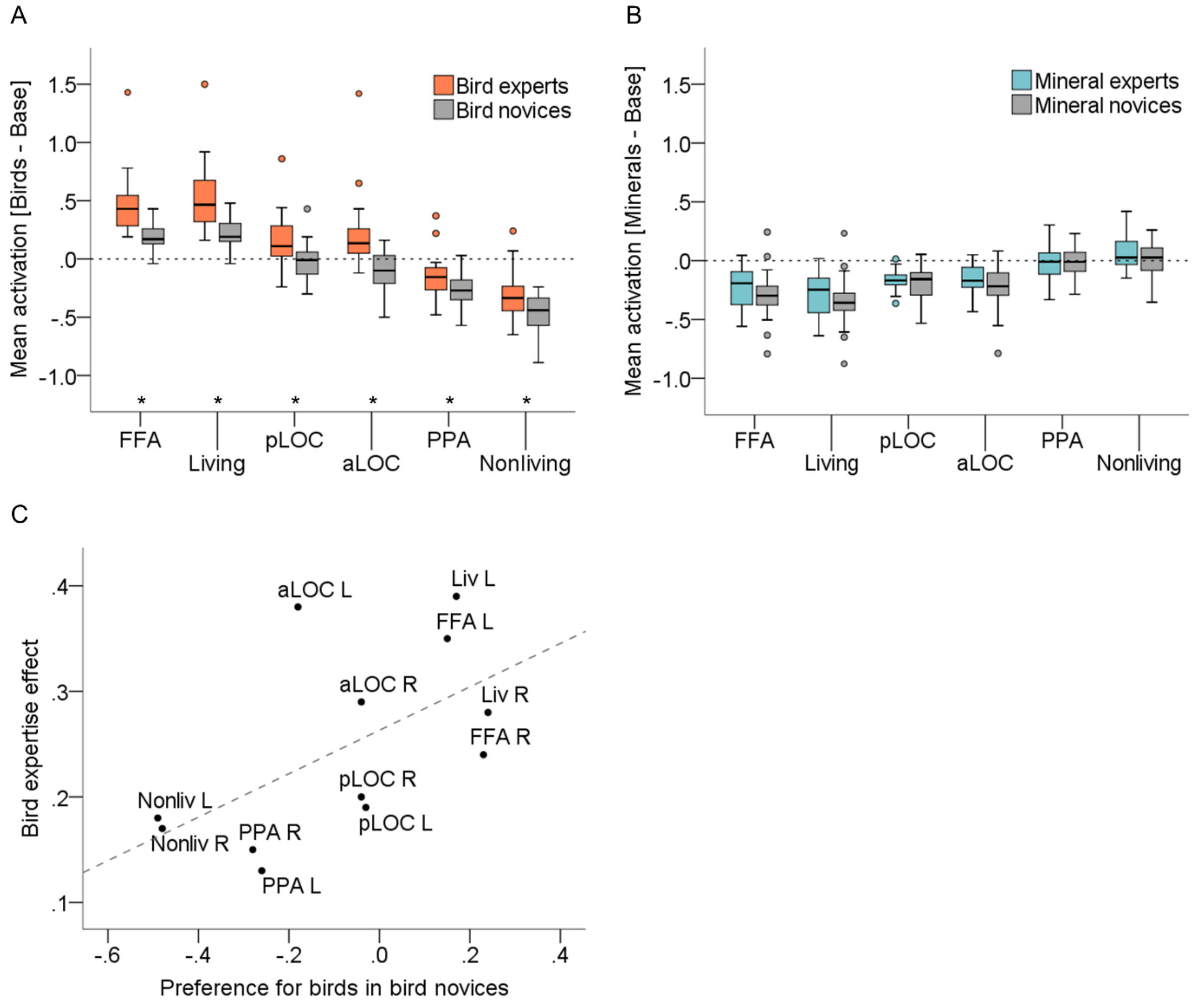


Figure 2.7. Results for the univariate ROI-analyses. *(A) Mean activation for the [Birds - Base] contrast for bird experts and bird novices (mineralogists and control participants) in 6 functionally defined ROIs (activation was averaged across hemispheres, only subjects with both left and right hemisphere fROIs were included). Boxplots display median and interquartile range, whiskers indicate the minimum and maximum values, dots represent outliers (> 1.5 x interquartile range) and significance is indicated by an asterisk. In all 6 fROIs, there was a significant difference between experts and novices. (B) Mean activation for the [Minerals - Base] contrast for mineral experts and mineral novices (ornithologists and control participants). Unpaired t tests revealed no significant differences. In supplementary material (section 2.5.4, Figure 2.11) we have broken down the single difference bars depicted in panels A and B into the constituting two bars (activation for expert condition and activation for base condition separately). (C) Scatterplot displaying a significant positive correlation (Pearson's r = 0.584, p = 0.046) between the general preference for birds (mean activation for birds in bird novices) and the expertise effect for birds (heightened activation in bird experts compared to novices) across left (L) and right (R) hemisphere fROIs. The dotted line depicts the linear line of best fit (y = 0.26 + 0.21x).*

Expertise effects for minerals were measured by comparing activation between mineral experts and mineral novices (ornithologists and control participants) for the contrast [minerals – base]. No effects survived a stringent FWE-corrected threshold. At a lower uncorrected threshold of $p < 0.001$ (with a minimum cluster size of 10 voxels, see Lieberman and Cunningham (2009)), small, distributed effects in left and right prefrontal and ventral temporal regions emerged (Figure 2.6B). Here again, the effects were largely the same when comparing mineral experts with the group of control participants in itself.

As illustrated in Figure 2.6C, the peak voxel of the cluster of significant activation in left ventral temporal cortex was located more posterior compared to the bird expertise effect in that same region (MNI coordinates of peak voxel (-38, -70, -20)). The absence of effects at an FWE-corrected threshold shows that expertise effects are distributed in a manner that is more convenient for a multi-voxel approach. Nevertheless, the small univariate peaks could still underlie the multi-voxel effects. We performed the same multivariate subject classification analysis as described above in this left ventral temporal cluster, to check whether the effects in this cluster could explain the multivariate results shown above. The resulting decoding accuracy (44.4%) was not significant, meaning that the multi-voxel responses for minerals in this particular cluster did not differ between mineralogists and control participants. This also indicated that the significant subject classification between mineralogists and control participants in the high-level visual aROI (67.4%) was not driven by a very local effect in this left ventral temporal cortex, but signified a more distributed effect across a larger part of high-level visual cortex.

We also performed fROI-based analyses for mineral expertise. The mineral expertise effect was tested by comparing the mean activation for the contrast [minerals – base] in mineralogists with the mean activations in mineral novices. There were no significant differences between these two groups in any of the selected regions (Figure 2.7B). This finding further suggests that expertise for minerals induces small and distributed neural effects which are not confined to very specific (known) functional distinctions. Overall, in line with the MVPA findings, the univariate results suggest that the changes in selectivity underlying the MVPA findings are distributed, stronger in ornithologists than in mineralogists, and do not show an obvious overlap in spatial distribution in high-level visual cortex.

Here we restrict the investigation of expertise effects at the level of smaller ROIs to univariate analyses. A priori we decided to only perform the classification and generalization analyses in these three large aROIs because these are the optimal and most sensitive analyses to investigate questions about domain specificity. Post hoc we checked the results in the 6 smaller functional ROIs that were delineated in each participant for the purpose of ROI-based univariate analyses. Overall, the classification performances dropped compared to those in the larger aROIs (e.g. for classifying ornithologists vs. control participants based on the birds condition in the high-level visual cortex: drop from 91.3% to an average of 69.2% across fROIs), in some fROI x condition combinations falling below the statistical threshold. Given the lower sensitivity in these smaller fROIs we refrain from drawing strong conclusions. At best, the results suggest that the higher classification performances in the aROIs do not seem to be based upon one smaller sub-region. We also calculated the correlations between the behavioral scores and the “proportion decoded as expert” in the fROIs. The results confirm most of what we see in the aROIs but with some variability between the fROIs. These results are shown in supplementary material (section 2.5.2, Figure 2.9 and Table 2.3).

2.3.5 Expertise does not influence the representational similarity of object categories

After having shown that expertise changes the high-level visual multi-voxel activity patterns for objects of expertise in a domain-specific manner, the question emerges whether these changes might be related to a specific altered representation of these objects relative to other object categories. To test this, we applied multivariate correlational analyses to investigate potential differences between the two expert groups and the control participants in the representational similarity between the 7 conditions (faces, birds, living, nonliving, scrambled, minerals, scenes) in high-level visual cortex. Especially the relationship between the expertise condition on the one hand (birds for ornithologists, minerals for mineralogists) and the remaining conditions on the other hand could be informative.

The MDS-plots for the different subject groups can be found in Figure 2.8. The mutual relations between the different conditions were strikingly similar across the three subject groups, with a clear distinction between the animate and inanimate categories. The objects of expertise nicely followed this distinction, independently of expertise, and did not seem to suddenly turn up in an unexpected position in their experts. Of course, visual inspection of MDS plots does not substitute statistics, but at least such explorative inspection suggests no obvious effects of expertise which would warrant further statistical testing. More quantitative analyses also did not show any obvious and significant difference between subject groups. We also performed these MVPA-based MDS analyses using data from the low-level visual and frontal aROIs, to again find similar representational spaces in the three subject groups (results not shown).

To sum, expertise does not seem to have a strong influence on the representational similarity between the object category of expertise and other categories. Put bluntly: a mineral is (visually) similar to a rock, even to a mineralogist. (Note that mineralogists will fiercely argue that people should not confuse minerals with rocks.)

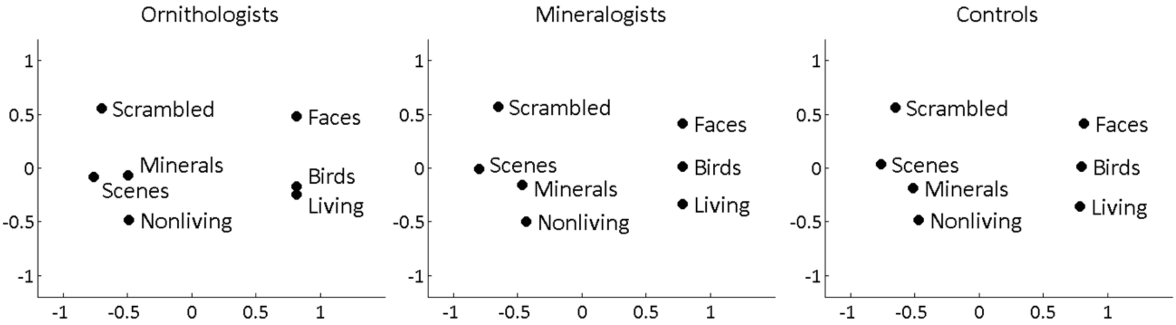


Figure 2.8. MDS-plots of the neural similarity between the 7 object categories. *Multi-dimensional scaling plots for ornithologists, mineralogists and control participants in the high-level visual aROI. The representational similarity between the different conditions is very similar across the three subject groups, with a clear distinction between living and nonliving object categories.*

2.4 DISCUSSION

2.4.1 Conclusions

In the present study, we compared the changes in neural processing that were associated with two very different types of visual expertise: ornithology and mineralogy. Multi-voxel analyses showed that both types of expertise influence neural object representations in high-level visual cortex, while the effects for bird expertise even extended to low-level visual regions and to the frontal lobe, displaying a distributed pattern of expertise effects. Univariate differences in response strength were only found for bird expertise, distributed across all included category-selective regions of interest. Importantly, a multi-voxel generalization analysis indicated that the expertise effects in high-level visual cortex were mostly specific to the domain of expertise. In the frontal lobe, in contrast, changes in object processing due to expertise overlapped significantly across the two different domains of expertise.

2.4.2 Top-down influences of expertise

In the one-back task that participants performed in the scanner, for both expert groups the ability to detect repetitions of images belonging to the domain of expertise was higher compared to images belonging to the other expert domain, with in addition better performances on a post-scan recognition task. These results are in line with an earlier study which showed that experts had a clear preference for pictures of objects related to their field of expertise (Hershler & Hochstein, 2009). The fact that objects of expertise appear to be more salient to experts may reflect the relevance of top-down attentional control in expertise. Harel et al. (2010) demonstrated that the level of engagement experts show for the objects of expertise affects the neural responses to these expert objects. Based on their findings, we would predict smaller or even no effects of expertise in tasks which do not tap into the expertise.

Frontal cortex would be the most likely source of this top-down attentional control (Corbetta & Shulman, 2002; Harel, 2015; Harel et al., 2010). Our analyses of the frontal lobe provide some insight into the nature of these top-down influences. By applying the multi-voxel generalization analysis, we demonstrated the presence of domain-general effects of expertise in frontal lobe. Several other studies, on various domains of expertise, have shown neural expertise-related changes in frontal lobe as well: e.g. for chess expertise (Krawczyk et al., 2011), radiological expertise (Bilalić et al., 2014), car expertise (Harel et al., 2010) and novel objects trained in the lab (Moore et al., 2006). However, the present study is unique in the sense that we demonstrate for the first time that these expertise effects in frontal lobe are similar across very different types of visual expertise. While our findings point towards the dominance of domain-general processes in frontal cortex, they do not pinpoint the exact processes that are involved. Probably it is a mixture of processes (attentional control, memory, arousal, …).

2.4.3 Informativeness

Expertise effects in high-level visual cortex did not generalize across different domains of expertise, indicating that expertise-related changes in the neural object representations in this region depend on the specific domain of expertise. We also showed that the peak activation (peak voxels of univariate activation) for both types of expertise did not overlap, possibly explaining the lack of generalization in MVPA. Note that the differences in effect size between the stronger bird expertise effects and the weaker mineral expertise effects is not by itself evidence for domain-specific effects of expertise. To the contrary, the situation that the effects in one domain would just be a stronger version of the effects in the other domain is exactly the situation that was simulated to estimate the maximal between-domain generalization possible given the within-domain decoding. Instead, the crucial evidence for domain specificity in high-level visual cortex was the lack of generalization between the two domains of expertise, significantly lower than the estimated maximal generalization.

Strikingly, we found that the expertise-related enhanced activation for birds was most pronounced in those functional regions that already showed a higher sensitivity for birds in bird novices, like the FFA and the Living region. This result is similar to the results in a recent study by Brants et al. (2016), who showed that training to discriminate between novel objects strengthens the responses in a pre-existing specificity map for the to-be-trained objects. It has been suggested that the extent to which neurons and brain regions are involved in a particular type of expertise depends on their informativeness for the domain of expertise and the task at hand (Brants et al., 2016; Op de Beeck, 2012; Op de Beeck & Baker, 2010). This concept of informativeness has its origin in the field of visual neuroscience (Raiguel et al., 2006; Schoups et al., 2001). However, we should note that in the current study, we also showed the presence of bird expertise effects in PPA and the Nonliving region (like other studies before us have found expertise effects in object-selective regions, see introduction), which are considered to be "noninformative" regions. Furthermore, we were not able to show similar effects in informative regions for mineralogists. Thus, informativeness is a partial but not a full explanation of the domain-specific distribution of expertise effects in visual cortex.

Apart from the domain in which subjects have acquired expertise, the type of training with the object category could also influence the neural effects of expertise. In the study by Brants et al. (2016), in which both type of training and expert object category were manipulated across a group of laboratory-trained participants, only object category influenced the reported neural expertise effects. However, some studies have shown differential changes in the neural representations of novel objects depending on the type of training participants received (Wong et al., 2009; Wong, Folstein, & Gauthier, 2012). Type of experience is of course very hard to control for when comparing two real-world domains of expertise. The way in which participants in the current study gained experience with birds or minerals could play a role in the resulting neural expertise effects, however, we did not take type of training into account when selecting participants for this study and therefore we cannot make statements on how this might have influenced our results.

This study fits into the bigger framework of ongoing discussions regarding the neural processes that underlie expert object recognition, in which two contrasting views play a major role. The perceptual process view sees expertise as a stimulus-driven, domain-general process, with expertise-related neural changes located in one specific region that encompasses the type of processing necessary for expert object recognition (Gauthier & Tarr, 1997). The expertise hypothesis, a more specific version, focuses on the relation between expertise and face processing. According to this hypothesis, FFA is the brain region in which "expert processing" takes place (Gauthier et al., 2000, 1999). Its selectivity for faces has arisen due to the fact that we are all experts in processing faces, and not because faces are a special category.

The interactive view on expertise on the other hand is domain-oriented and sees expertise as an interaction between bottom-up and top-down factors (Harel et al., 2013). The neural correlates of expertise are not limited to one specific region in the brain but depend upon the domain of expertise and the task demands. In line with this view is the idea of informativeness which was mentioned above. In the current study, expertise effects were found in FFA, as predicted by the expertise hypothesis, but also outside of FFA and even outside the visual cortex. Furthermore, the domain-specific effects that were found in high-level visual cortex point more towards the domain-oriented view on expertise: expertise-related changes in this region were localized differently depending on the domain of expertise.

2.4.4 Limitations and future directions

The present study provides a substantial advance in our understanding of how different domains of expertise change the brain. However, many questions remain. In terms of our own data, it is puzzling that the expertise effects show a strong difference in size between ornithology and mineralogy. The successful subject classification in high-level visual cortex and the significant generalization in frontal lobe show that mineral expertise effects are present, but they are smaller compared to effects of bird expertise. How can we explain this difference in effect sizes? There was a minor difference in the level of expertise between the two subject groups. We indicated that this difference is insufficient to explain the differential effect size at the neural level. A different possibility is that ornithology is a more visual expertise compared to mineralogy. In fact, both domains are only partially visual and also rely on other modalities (e.g., sound for birds and touch for minerals). The relative importance of the different modalities might differ between the domains of expertise. However, according to experts in the field, the shape of a mineral is still a very important determinant for identification and classification.

The results of the subject classification analyses showed a second curious finding. In high-level visual cortex, the interaction between domain of expertise and stimulus condition was as expected: ornithologists could be classified based on their neural response patterns for birds and mineralogists based on the neural responses to minerals. However, in the low-level visual ROI, mineralogists could be distinguished from control participants based on their response patterns for birds. This result was not related to behavior, given that mineralogists and control participants did not show convincing differences in performance on the behavioral tasks for birds. There was also no difference in univariate activation for the [birds - base] contrast between the two subject groups.

Following the major distinction underlying the large-scale organization of neural object representations, we chose to compare one animate and one inanimate domain of expertise. Therefore, differences in neural expertise effects between the two domains of expertise could be related to this animate-inanimate distinction, instead of the two domains in itself. To shed light on this issue, two different animate object categories of expertise should be compared (e.g., Tanaka and Taylor, 1991; Tanaka and Curran, 2001), as well as two inanimate expert object categories. Furthermore, the level of homogeneity of an object category influences discrimination of the objects at the subordinate level (individual objects that are perceptually very similar make discrimination harder, D'Lauro et al., 2008) and subsequently may influence the underlying neural expertise effects. Therefore, the selected expert object categories should also be matched based on their homogeneity. When comparing ornithology with mineralogy, it is possible that the categories of birds and minerals differ in their intra-category homogeneity (note that issues like these can never be completely avoided when comparing two very different real-world domains of expertise).

An important limitation of the present study is that expertise is manifested at the behavioral level in the ability to make fine-grained within-category distinctions (e.g., discriminating among birds), whereas at the neural level we investigated selectivity for between-category distinctions (e.g., discriminating birds from other objects). Important effects might be missed by this lack of specificity at the neural level. Further studies should be done to investigate the neural representation of more subordinate distinctions, although this approach might encounter the limits of multi-voxel analyses in terms of distinguishing fine object distinctions (see e.g. Brants et al. (2016)). Such studies could extend the present findings, which reveal domain-specific effects of expertise on between-category selectivity in high-level visual cortex combined with domain-general effects in the frontal lobe.

2.5 SUPPLEMENTARY MATERIAL

2.5.1 ROI sizes and MNI coordinates

ROI	# subjects	size (± sd)	MNI coordinates (± sd)
Anatomical ROIs			
Low-level visual ROI	57	7042	/
High-level visual ROI	57	5462	/
Frontal lobe	57	42017	/
Functional ROIs			
FFA (left)	54	109 (±74)	-42±3, -55±8, -19±4
FFA (right)	56	182 (±97)	44±4, -53±8, -19±4
OFA (left)	38	56 (±36)	-38±5, -88±4, -10±4
OFA (right)	44	64 (±56)	39±5, -87±3, -9±4
PPA (left)	57	179 (±101)	-25±5, -48±7, -9±4
PPA (right)	57	258 (±114)	27±5, -47±9, -10±4
pLOC (left)	57	286 (±150)	-41±5, -85±5, -6±7
pLOC (right)	57	299 (±166)	41±5, -84±5, -5±6
aLOC (left)	57	341 (±231)	-37±7, -54±10, -16±5
aLOC (right)	57	350 (±249)	40±7, -56±10, -16±6
Living (left)	57	111 (±73)	-43±3, -59±7, -17±4
Living (right)	56	158 (±79)	45±4, -56±7, -18±4
Living – FFA (left)	42	60 (±36)	-43±4, -60±7, -16±4
Living – FFA (right)	42	73 (±40)	45±4, -58±6, -16±4
Nonliving (left)	56	108 (±72)	-28±3, -52±7, -11±4
Nonliving (right)	56	108 (±78)	30±4, -50±7, -11±4

Table 2.2. ROI sizes. *Table displays for each ROI the number of subjects in which this ROI was outlined, the mean and standard deviation (sd) of the number of voxels and the mean and standard deviation of the MNI coordinates.*

2.5.2 Subject classification analyses in smaller ROIs

We a priori decided to perform MVPA in the larger anatomical ROIs, assuming that we would have more sensitivity to make inferences about domain specificity in these larger ROIs. Post hoc we also performed some of the analyses in the smaller functional ROIs. In the graphs below (Figure 2.9), we show the results of the subject classification analyses in the following smaller ROIs: the high-level visual regions (anterior and posterior LOC, PPA, FFA and the Living and Nonliving regions) and two subregions of the frontal lobe (dorsolateral prefrontal cortex (DLPFC) and inferior frontal gyrus (IFG)).

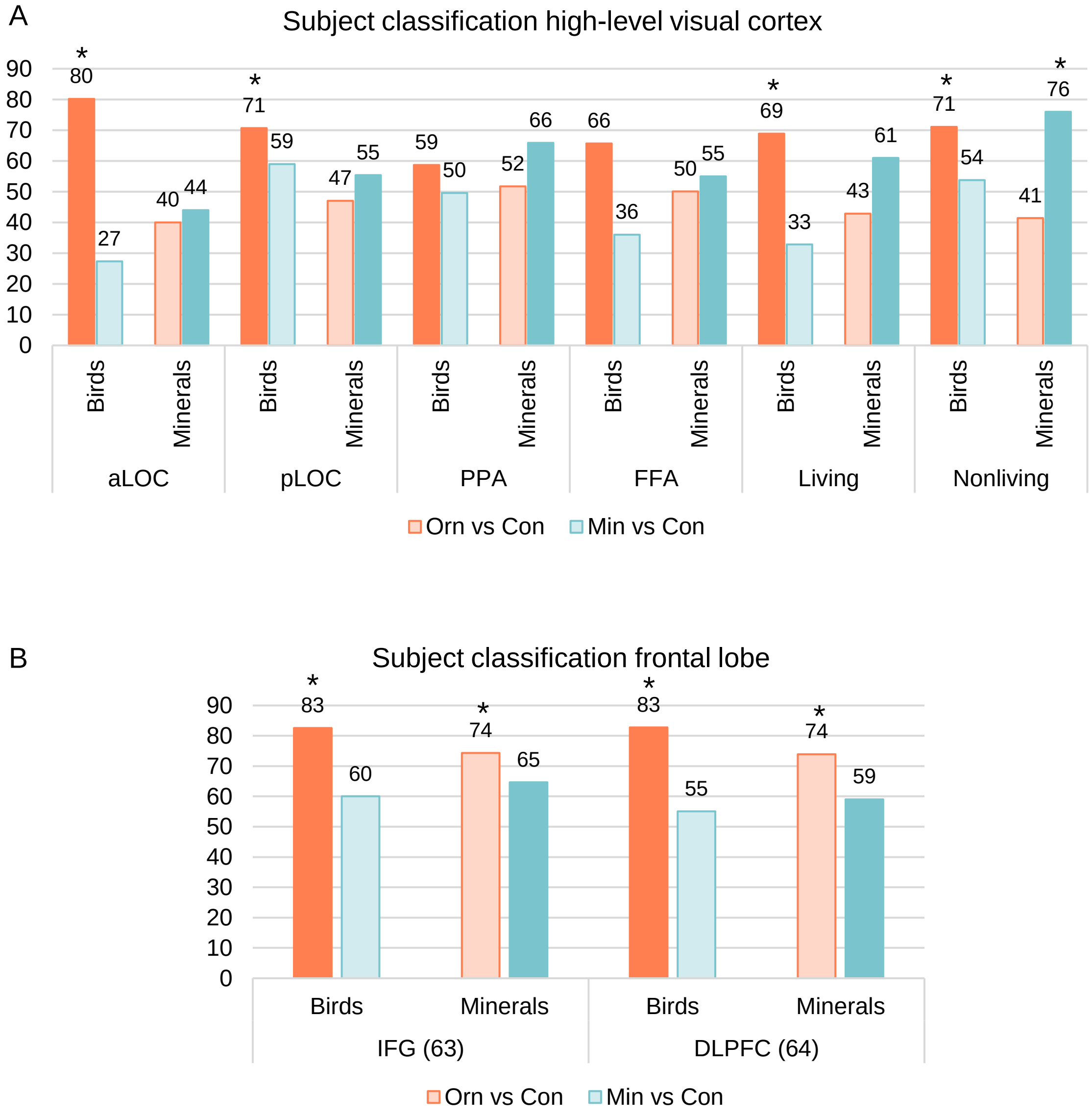


Figure 2.9. Subject classification results in smaller ROIs. *Results for the subject classification analyses in subregions of the high-level visual cortex (A) and the frontal lobe (B). Bars depict the classification accuracies in percentages. The dark bars indicate the potential expertise effects (e.g. classification of ornithologists (orn) vs controls (con) based on their activation for birds). Significant classification accuracy (after FDR correction) is indicated with an asterisk.*

Overall, the results suggest that the expertise effects that we have demonstrated in the larger anatomical ROIs seem to be distributed across the smaller subregions instead of localized within one specific (functional) ROI. In the high-level visual regions, bird expertise effects are present in aLOC, pLOC, the Living and the Nonliving region, while mineral expertise effects can only be found in the Nonliving region (when correcting for multiple comparisons), thus reflecting the whole-brain univariate results. In the frontal regions, bird expertise effects are present in both subregions while there are no mineral expertise effects (cfr. subject classification results in the frontal lobe). However, many of the effects hoover around the statistical threshold in these smaller ROIs (overall lower classification performance compared to the larger anatomical ROIs). Given the lower sensitivity in these smaller ROIs, we refrain from drawing strong conclusions.

We also included the brain-behavior correlations (correlations between the proportion of times each participant was decoded as an expert and the participants' scores on the behavioral tasks) for the smaller ROIs (Table 2.3). Again, given the lower sensitivity, it is hard to interpret these findings. The results for the smaller ROIs confirm most of what we see in the large ROIs, but with some variability between ROIs. Given that this variability might in large part be due to noise fluctuations in the data, which is why we prefer to restrict conclusions to the larger ROIs.

Classification	Behavioral task		aLOC	pLOC	PPA	FFA	Living	Nonliving	IFG	DLPFC
Orn. vs Con.	Discrimination birds	r	0.54	0.50	0.24	0.35	0.29	0.30	0.39	0.48
		p	0.000	0.001	0.131	0.027	0.074	0.059	0.012	0.002
	Semantic birds	r	0.54	0.55	0.26	0.39	0.35	0.43	0.53	0.61
		p	0.0004	0.0002	0.111	0.013	0.025	0.006	0.0004	< 0.0001
Min. vs Con.	Discrimination minerals	r	-0.12	0.16	0.26	-0.10	0.01	0.41	0.38	0.34
		p	0.491	0.353	0.121	0.562	0.968	0.011	0.019	0.042
	Semantic minerals	r	-0.20	0.06	0.25	0.09	0.21	0.45	0.33	0.24
		p	0.239	0.746	0.132	0.577	0.209	0.005	0.050	0.151

Table 2.3. Correlations between the "proportion decoded as expert" and behavioral scores for the high-level and frontal subregions. *The "proportion decoded as expert" represents the proportion of times a subject was either classified as an ornithologist (ornithologists and control participants) or as a mineralogist (mineralogists and control participants). Regions in which the subject classification accuracy was significant are indicated by a frame. Significant correlations are highlighted in green.*

2.5.3 Scatterplots depicting the relation between the "proportion decoded as expert" and behavioral tasks

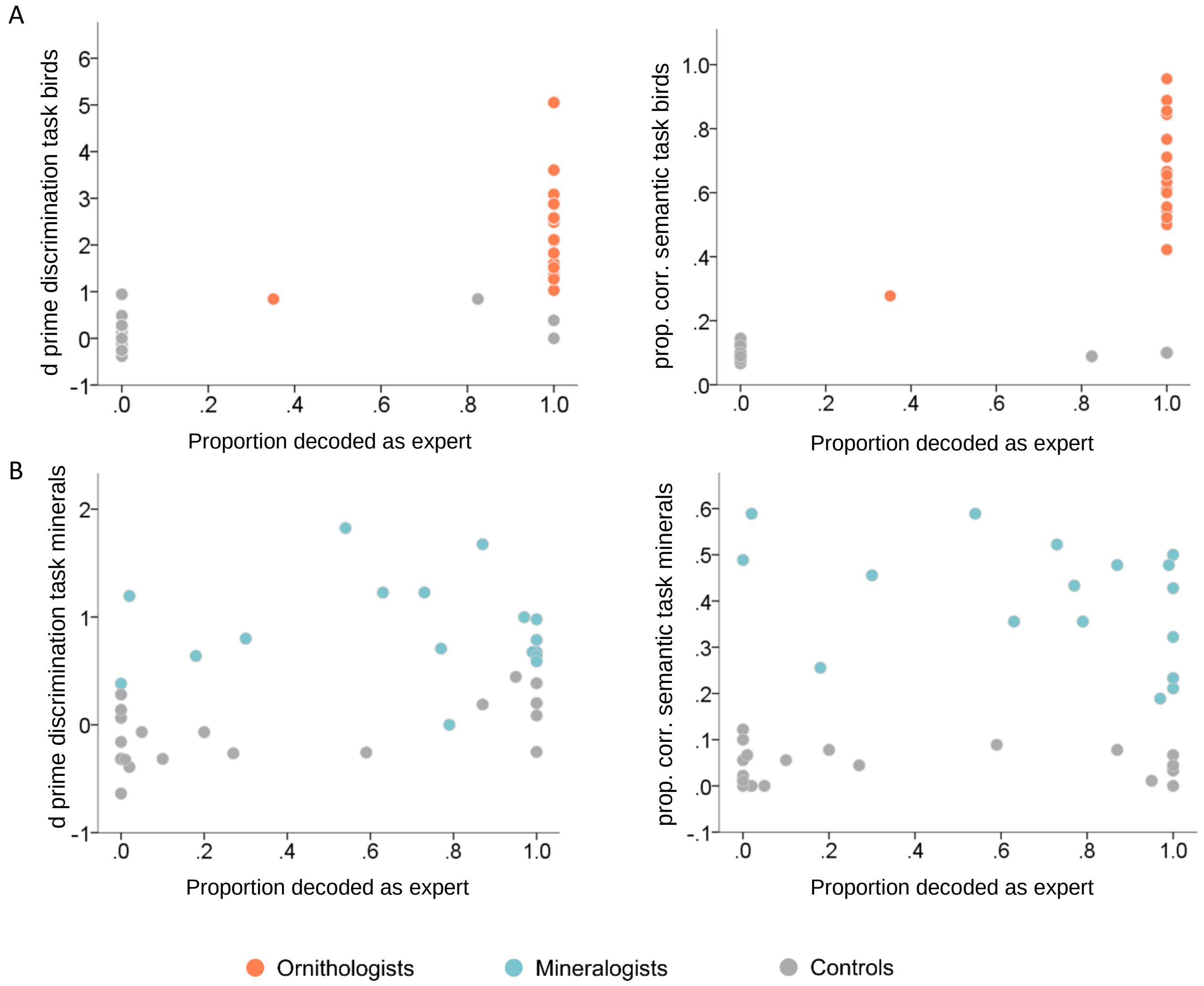


Figure 2.10. Scatterplots depicting relation between the "proportion decoded as expert" and behavioral tasks. *(A) Scatterplots depicting the relation between the ornithologists' and control participants' scores on the bird discrimination task and semantic task for birds on the one hand and the proportion of times each participant was classified as being an ornithologist in the high-level visual aROI on the other hand. (B) Scatterplots depicting the relation between the mineralogists' and control participants' scores on the mineral discrimination task and semantic task for minerals on the one hand and the proportion of times each participant was classified as being a mineralogist in the high-level visual aROI on the other hand.*

2.5.4 Univariate ROI-analyses: breakdown of activation for expert condition and base condition

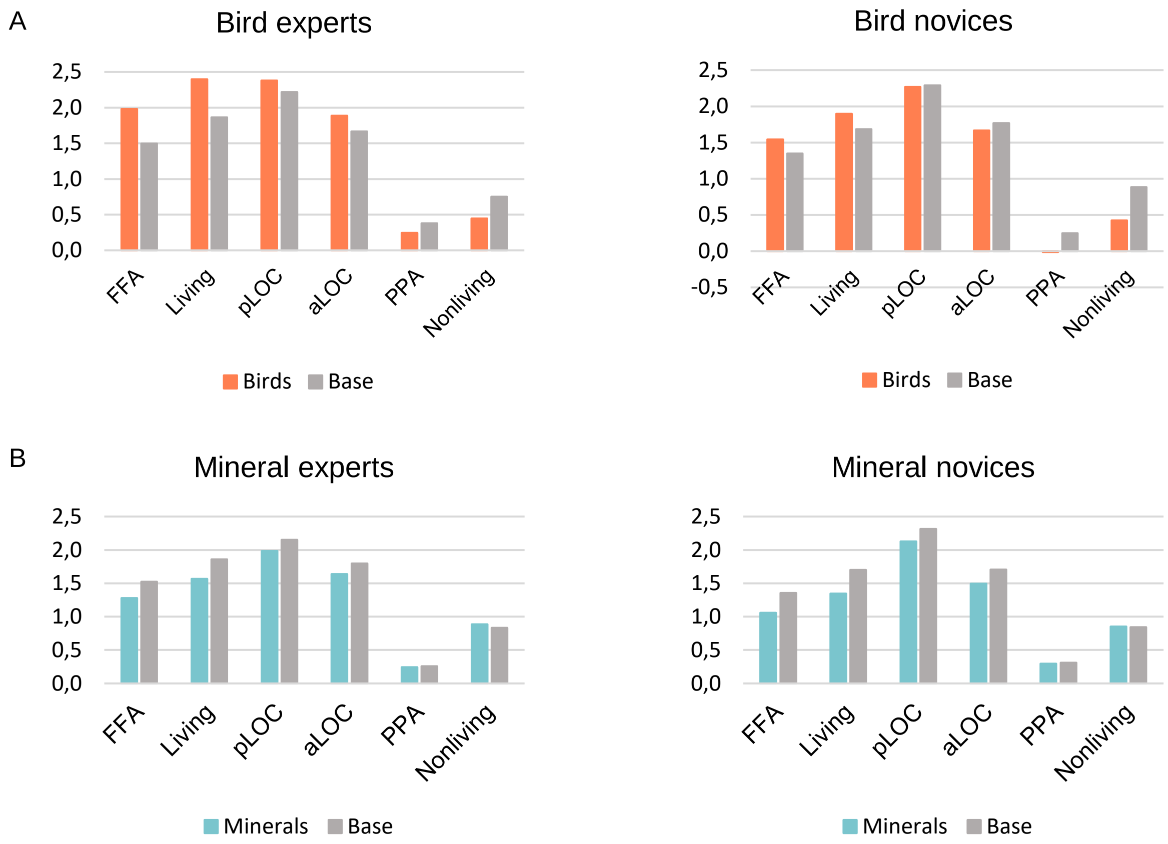


Figure 2.11. Univariate activation for expert condition and base condition. *This figure is related to Figure 2.7 which shows the mean activation for the [birds - base] contrast for bird experts and bird novices (2.7A) and the mean activation for the [minerals – base] contrast for mineral experts and mineral novices (2.7B). Bar graphs display the mean activation for the conditions birds and base separately in bird experts and bird novices (A) and the mean activation for the conditions minerals and base separately in mineral experts and mineral novices (B).*

In the bar graphs above (Figure 2.11) we have broken down the single difference bars depicting the mean activation for the contrast [*expert condition – base condition*] in experts and novices into the constituting two bars (activation for expert condition and activation for base condition). The base condition is calculated by averaging the activation for the living and nonliving conditions. The graphs show that both expert object categories (birds and minerals) elicit a response in (almost) all of the functional ROIs in both experts and novices. However, the response elicited by the base condition is higher than the response for minerals in both mineral experts and novices and the same is true for the bird activation in PPA and the

Nonliving region in bird experts and novices. This result is in line with the results found by McGugin et al. (2012), who show that activation for cars in car experts (in FFA) is actually negative when compared to an “animal” baseline. Nevertheless, they do show the presence of an expertise effect by calculating correlations between the activation for cars and a behavioral measure of car expertise. The neutral base condition that we have used is also a “high-level” condition, and it is not surprising that our ROIs show a high response for this condition. For example: when looking at the bird experts’ and novices’ response for the base condition in PPA and the Nonliving region, we see that this response is higher than the response for birds. However, since the base condition is partly made up out of activation for nonliving objects (the preferred object category for PPA and the Nonliving region), this finding is not surprising. The increased activation for birds (even when compared to a “high-level” base condition) in bird experts compared to bird novices is what indicates the presence of an expertise effect.

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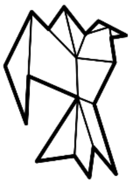

3

The mental representational space of objects of expertise

Visual experts are able to quickly and accurately identify individual exemplars belonging to the same visually homogeneous object category. We learn to recognize and categorize new exemplars by judging its similarity to a representation of the category that is stored in memory. However, the concept of perceptual similarity has not yet been investigated in the context of expertise, an ‘extreme’ form of perceptual learning. In the present study, we investigate the influence of expertise on the mental representations of objects of expertise. We applied a multiple object arrangement paradigm and representational similarity analyses to study the mental representational spaces of experts and compare it to those of novices. Results indicated a quantitative enhancement of the representational space of objects of expertise in experts compared to novices. Furthermore, we also demonstrated the presence of qualitative differences in the form of more fine-grained, subordinate-level distinctions in the experts’ mental representational spaces. Finally, the expression of these expertise effects was influenced by top-down factors.

3.1 INTRODUCTION

In daily life, we constantly interpret our surroundings by identifying and categorizing objects that appear in our visual field. For categorization, we must group physically different objects together, while identification requires us to discriminate between physically similar objects. When developing visual expertise in a specific domain, learning to identify individual exemplars is especially important.

Research on the behavioral aspects of visual expertise has, among other things, focused on the way in which objects of expertise are processed. It has been proposed that objects of expertise are processed in a configural or holistic manner (Curby & Gauthier, 2010; Gauthier & Tarr, 1997, 2002; Richler & Gauthier, 2014; Richler, Wong, & Gauthier, 2011; Rossion & Curran, 2010; Wong, Palmeri, & Gauthier, 2009). Holistic processing has originally been described as a hallmark of face perception (Tanaka & Sengco, 1997; Tanaka & Farah, 1993). Configural information, that is information about the way in which the different parts of an object relate to each other, is crucial to the representation of faces, and also plays a role in objects of expertise. Changes in the typical configuration of an object of expertise can disproportionately impair the recognition of the object (however, see Robbins & McKone, 2007).

Additionally, the type of training that is optimal to acquire expertise in a visual domain has been extensively studied. Tanaka and Taylor (1991) already showed that in contrast to novices, experts use subordinate-level names (e.g. ‘robin’ or ‘sparrow’) as frequently as basic-level names (e.g. ‘bird’), and they perform subordinate-level categorizations as fast as basic-level categorizations. Several studies have compared subordinate-level training with basic-level training and mere exposure in a specific visual domain (Gillebert, Op de Beeck, Panis, & Wagemans, 2008; Scott, Tanaka, Sheinberg, & Curran, 2006, 2008; Tanaka, Curran, & Sheinberg, 2005; Wong, Palmeri, Rogers, Gore, & Gauthier, 2009). In basic-level training, participants are trained to divide objects into broader categories at the basic level, while in subordinate-level training, they are required to identify and discriminate between visually similar objects belonging to the same category. Subordinate-level training leads to a better discrimination performance between exemplars and has long-term effects (Scott et al., 2008). Furthermore, subordinate-level training induces a greater generalization of subordinate discrimination to novel exemplars from learned categories and to exemplars belonging to new, but structurally related categories (Gauthier, Williams, Tarr, & Tanaka, 1998; Tanaka et al., 2005). It has become clear that subordinate-level categorization is the trademark of visual expertise and it is therefore important to study the way in which experts make fine-grained distinctions between individual exemplars within the expert object category.

The question of how we learn to categorize new objects is studied in the field of perceptual learning. To recognize, identify or categorize an object requires the comparison of its visual representation with some representation of stored knowledge. According to the exemplar-based model, categories are represented by individual exemplars that are stored in memory (Nosofsky, 1987, 2011; Nosofsky, Sanders, Gerdom, Douglas, & McDaniel, 2017; Nosofsky, Sanders, & McDaniel, 2017). New instances are categorized by judging the similarity to these exemplars: if the perceived stimulus holds many similarities with exemplars of a specific category, it is assigned to that category. For example, the mental representation of the category 'birds' is stored in memory by means of a collection of representations of robins, warblers, pigeons, ducks, ostriches and other birds which people have encountered. In the generalized context model, an exemplar-based view proposed by Nosofsky (1986), exemplars are represented as points in a multidimensional psychological space. The similarity between exemplars is inversely proportional to their distance in the psychological space. The exemplar-based view is contrasted by the prototype theory which states that categories are represented by an abstract summary or a prototype, which is derived by averaging experiences with exemplars (Mervis & Rosch, 1981; Posner & Keele, 1968; Smith & Minda, 1998). New stimuli are categorized by comparing their similarity to the category prototype.

Both theories emphasize the importance of similarity in categorization: only by resemblance to a prototype or to exemplars can a new stimulus be assigned to a category. It is thus key to study perceptual similarity and the way in which mental representations of categories and objects relate to each other in order to understand how we learn to categorize objects (Nosofsky, 1992). Several studies have used similarity spaces of object categories to investigate perceptual learning (Edelman, 1998; Shepard, 1987). In most studies, representational spaces or feature spaces were created by carefully manipulating a limited number of dimensions in an artificially created object class of very simple (Cohen, Nosofsky, & Zaki, 2001) or more complex stimuli (Folstein et al., 2012; Gillebert et al., 2008; Goldstone

& Steyvers, 2001; Panis, Vangeneugden, & Wagemans, 2008). This highly controlled experimental manipulation renders a feature-space representation that is a fairly direct reflection of the object category. Creating a representational space for a natural, real-world object category is more challenging. Natural stimuli are more complex and vary along a large number of dimensions that could be difficult to describe and that are not independent from each other (Mathy & Bradmetz, 2011). In a recent study in which novice participants were trained to classify pictures of rocks, a multidimensional feature space for rocks was used to test the exemplar-based model's predictions of categorization and generalization performances (Nosofsky, Sanders, & McDaniel, 2017; Nosofsky, Sanders, Meagher, & Douglas, 2018).

The traditional way to investigate perceptual similarity is by asking participants to make pairwise similarity judgments of the different objects and subsequently applying multidimensional scaling (MDS) to create a two-dimensional visualization of the mutual relations between the objects (Goldstone, Medin, & Gentner, 1991; Nosofsky, 1992; Nosofsky et al., 2018; Shepard, 1980; Steyvers, 2002). However, a more efficient multiple object arrangement (MOA) method has been proposed in which participants are asked to arrange a set of objects according to their similarity by placing them in a two-dimensional space (Goldstone, 1994a; Kriegeskorte & Mur, 2012). The farther the objects are placed from each other, the more dissimilar they are. From these arrangements, the pairwise dissimilarities between the objects are derived. This method is highly efficient because by positioning an object in the 2-D space, the participant gives information about multiple pairwise similarities at the same time. Additionally, it allows the context provided by the remaining items to be taken into account when judging the similarity between two objects (e.g. a hamster and a cat may seem more similar to each other when an elephant is added to the set of items). Furthermore, participants can, consciously or subconsciously, base their arrangements on multiple underlying dimensions, which do not have to be prespecified by the researcher.

Although mental representational spaces of object categories have been investigated in the field of perceptual learning, this technique has never before been applied to study the behavioral aspects of an 'extreme' form of learning: visual expertise. It is our goal to map out the representational similarity space of experts in a real-world domain and compare this to the representational space of novices for the same object category. In the current study, we will apply the MOA method to investigate the mental representational space of the expert object category of birds. To the best of our knowledge, the MOA method is new in the field of expertise. We aim to investigate the influence of extensive experience on the mental representations and the perceptual similarity of birds by comparing two subject groups: ornithologists or bird experts and novices. Moreover, we will implement one expertise-related MOA task and one non-related task. It has previously been shown that similarity relations between objects are not invariant but instead may change depending on the experimental task context (Nosofsky, 1987; Nosofsky, Sanders, & McDaniel, 2017; Van Gulick & Gauthier, 2014). Research on the behavioral aspects of expertise has also demonstrated the influence of top-down processes: experts show a clear attentional preference for their expert object category (Hershler & Hochstein, 2009). We therefore predict that effects of expertise on the mental representational space of the expert object category will be more pronounced in an attention grabbing expertise-related task.

3.2 METHODS

3.2.1 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, Bulthé, van Vliet, & Op de Beeck, 2018). One candidate bird expert was excluded due to a neurological background. To check their 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 results on these expertise tasks (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. The study was approved by the Medical Ethical Committee of KU Leuven.

3.2.2 Determination of expertise level

The behavioral experiment formed part of a larger fMRI study on expertise and lasted approximately 90 minutes for the new participants and 60 minutes for those who already took part in a previous study. The new participants first completed a perceptual discrimination task and a semantic task (see Martens et al., 2018). For the remaining participants, results 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 (with no background) that were selected with the help of a bird expert. Half of these pairs were made up out of birds that belonged to the same bird species, the other half consisted of birds belonging to different species. Participants had to decide for each pair whether both birds did or did not belong to the same species. The visual similarity of the birds within each pair varied, with some very easy trials (e.g. do a robin and a crow belong to the same bird species?) and some trials that were a lot more difficult (e.g. visually differing male and female exemplars of the same species). Participants with a knowledge of birds were considered to be experts when they reached a score of 65% on the discrimination task. No candidate bird experts or control participants had to be excluded based on their score on this task. 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).

3.2.3 Multiple object arrangement

All participants provided similarity judgments of 24 birds using a multiple object arrangement paradigm (Goldstone, 1994a; Kriegeskorte & Mur, 2012). The task was administered to the participants using Matlab R2013a. The specific birds that were selected for this task are discussed in detail in the next section. Participants were asked to arrange the different stimuli based on their similarity in a two-dimensional space on the computer screen (Figure 3.1). The distances between the stimuli were interpreted as (dis)similarities: the closer together they were placed, the more similar they were. First, participants performed a practice trial with unrelated images for three minutes, to get familiarized with the format of the task. Next, they performed the actual MOA task twice: first they were asked to arrange the 24 birds according to their taxonomy or similarity of bird species, this was an expertise-related task. In a second, non-related task for which no specific bird knowledge was required, participants 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. In the first trial, all the 24 birds were presented simultaneously. For the subsequent arrangements, different subsets of the stimuli were presented. The subsets were selected by an adaptive algorithm based on the information that was gathered in the previous trials: the estimated certainty for the (dis)similarity between each bird pair was calculated and pairs for which this certainty was the lowest were selected to be arranged again.

Figure 3.1. Example of multiple object arrangement task. *Participants are asked to arrange birds based on their similarity in a 2-D space by dragging and dropping the presented icons in the white circle. Birds that are more similar are placed closer together. Participants have unlimited time to perform an arrangement. After each arrangement is done, a different subset of birds is presented. Participants performed two MOA tasks: a species task and a visual task. Each task lasted 20 mins.*

At the end of the experiment, participants performed a familiarity test. They were asked to name the 24 birds they had seen in the MOA task, to ensure that the ornithologists were familiar with these specific bird species.

3.2.4 Stimuli

The 24 birds that were selected for the MOA tasks were all common European bird species. The birds were arranged into 8 triplets (Figure 3.2). 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 differing male and female or a species with differing 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). In the MOA tasks, all 24 birds were presented together in a random fashion.

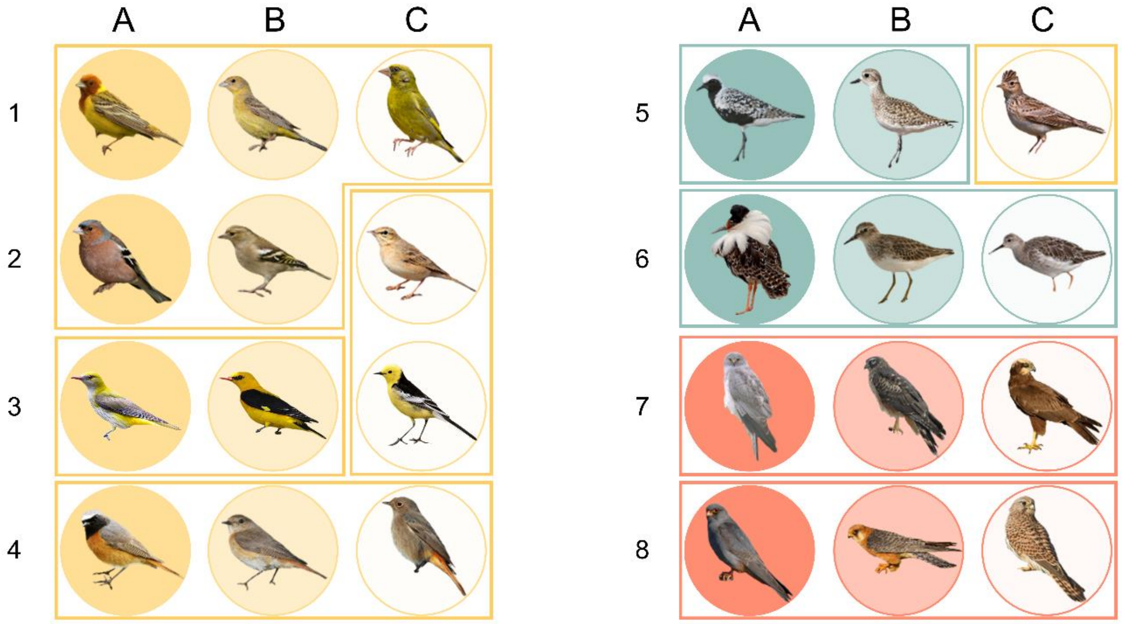

Figure 3.2. Stimuli. *The 24 birds that were selected for the MOA task consist of 8 triplets. In each triplet, birds A and B belong to the same species but are visually different, while birds B and C belong to different bird species but are visually similar. The bird species are grouped into bird families, which are indicated by rectangular frames. Furthermore, the bird families belong to three large bird orders: the birds in yellow are songbirds, the birds in blue are wading birds and the birds in red belong to the order of birds of prey.*

3.3. RESULTS

3.3.1 Measures of expertise

Twenty ornithologists and twenty control participants were selected to participate in this study based on their score on the perceptual discrimination task. Ornithologists reached an average score of 84% (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, $p < 0.0001$). Since the performance on this task was used as an inclusion criterion, this result is trivial. However, two other and statistically independent behavioral measures also demonstrated the clear difference in experience between experts and novices. On the semantic task, in which participants named 30 birds, ornithologists (68.6%, sd = 15.7%, min. = 42.2%, max. = 93.8%) outperformed the control participants (9.2%, sd = 3.4%, min. = 1.1%, max. = 16.7%), as a group (t(19) = 15.80, $p < 0.0001$) and even for all individual pairs of participants (minimum in ornithologists is clearly higher than the maximum in controls). Finally, with an average score of 83.5% on the familiarity test (sd = 14.1%, min. = 50%, max. = 100%), ornithologists demonstrated that they were overall familiar with the 24 specific birds that were presented to them during the MOA task, while control participants were not (average of 7%, sd = 5.4%, min. = 0%, max. = 20.8%; t(19) = 21.49, $p < 0.0001$). Within the group of ornithologists the different measures of expertise were associated with each other and with the self-reported level of expertise. For example, the ornithologists' self-reported years of experience were significantly correlated with their performance on the semantic task (Pearson's r = 0.47, p = 0.038) and on the familiarity test (Pearson's r = 0.46, p = 0.039), but not significantly with the performance on the discrimination task (Pearson's r = 0.37, p = 0.11).

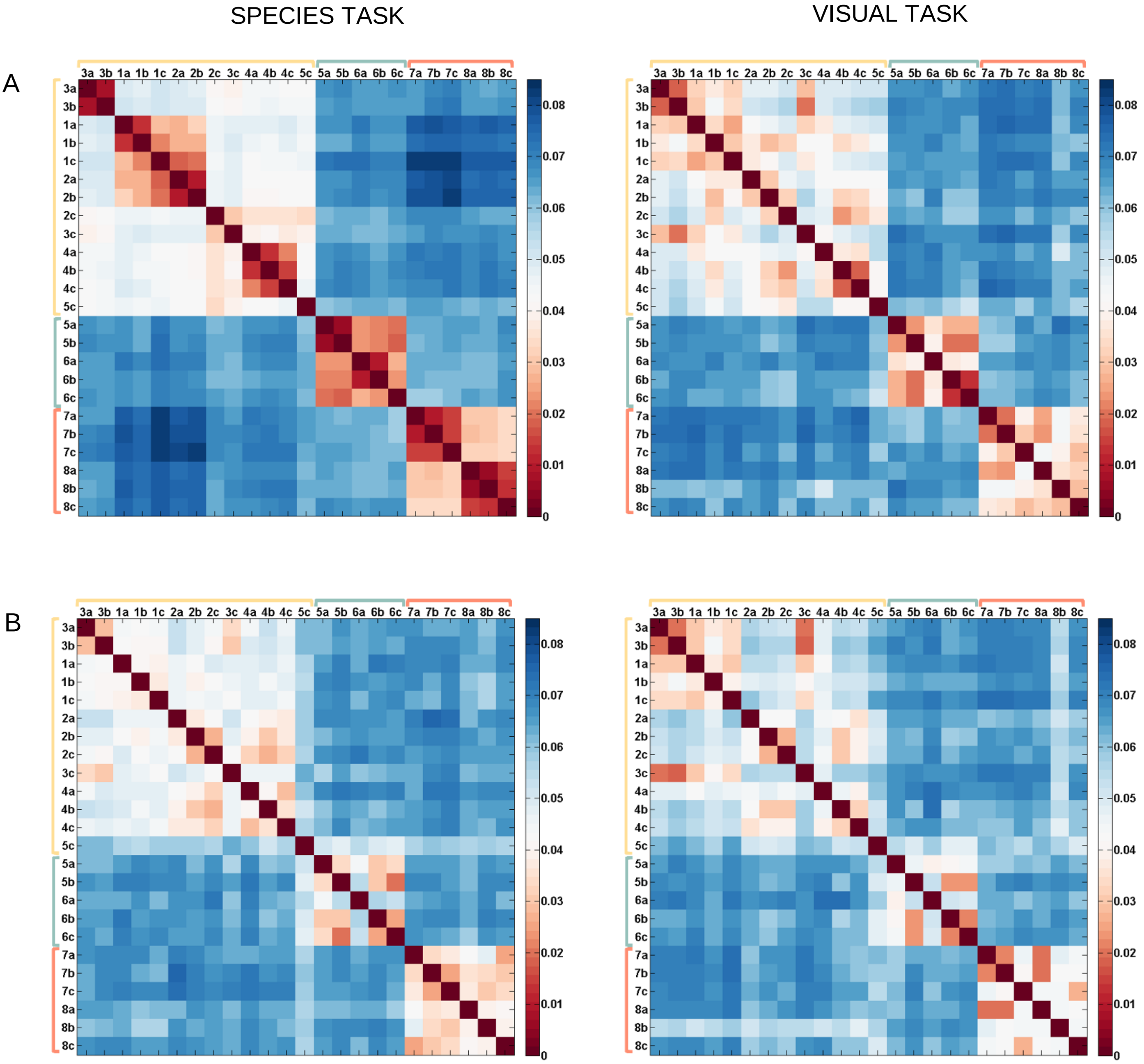

Figure 3.3. Representational dissimilarity matrices. *Matrices representing the average pairwise dissimilarities or distances between the 24 birds based on the MOA arrangements made by ornithologists (A) and control participants (B) in the species task (left) and the visual task (right). Smaller dissimilarities 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 brackets, wading birds by blue brackets and birds of prey by red brackets. The bird codes match the codes used in Figure 3.2.*

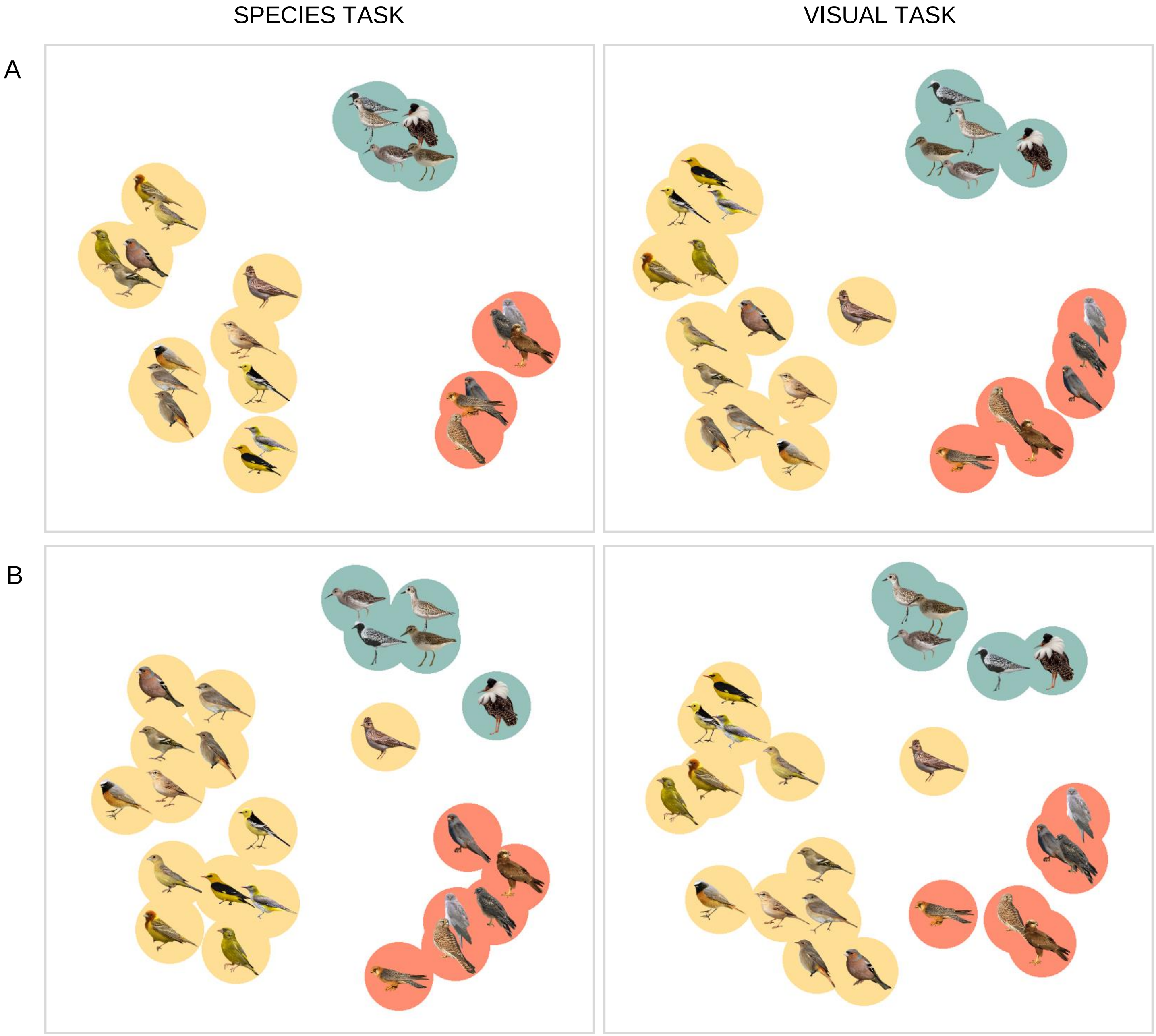

__Figure 3.4. MDS-plots of the MOA arrangements.__ Plots displaying the average arrangements made by ornithologists (A) and control participants (B) in the species task (left) and the visual task (right). Plots were visualized using 2-D multidimensional scaling with metric stress in Matlab R2013a. Birds in yellow are songbirds, blue birds are wading birds and birds in red are birds of prey.

3.3.2 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 (expertise-related task) and in a second task according to their visual similarity (non-related task). Based on these arrangements, the pairwise dissimilarities of the 24 birds were derived for both subject groups and both tasks, and presented in representational dissimilarity matrices (RDMs; Figure 3.3). The resulting arrangements were also visualized using multidimensional scaling (Figure 3.4). 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 (with one “odd bird out” in the control group: a songbird (5C) visually resembling a wading bird).

3.3.3 Consistency of arrangements

To compare how consistent the subjects within each group solved both tasks, we calculated within-group correlations for each task. Each subject’s 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 3.5). 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: $t(19) = 11.04$, $p < .0001$; visual task: $t(19) = 2.97$, $p = 0.008$). This effect was stronger for the species task than for the visual task ($t(19) = 7.04$, $p < .0001$).

Next we calculated the between-group correlations (each subject’s dissimilarity matrix was 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-group correlations (e.g., Op De Beeck, Deutsch, Vanduffel, Kanwisher, & DiCarlo, 2008). For the visual task, this benchmark was 0.44. The empirically measured between-group correlation (Pearson's r = 0.42) did not differ significantly from this reference value (t(19) = 1.04, p = 0.31), indicating that ornithologists and control participants solved the visual similarity arrangement task in a similar manner. However, for the expertise-related species task, the measured between-group correlation (Pearson's r = 0.43) was significantly lower than the reference value of 0.48 (t(19) = 5.26, p < 0.0001), signaling a qualitative difference between the bird arrangements performed by the two subject groups.

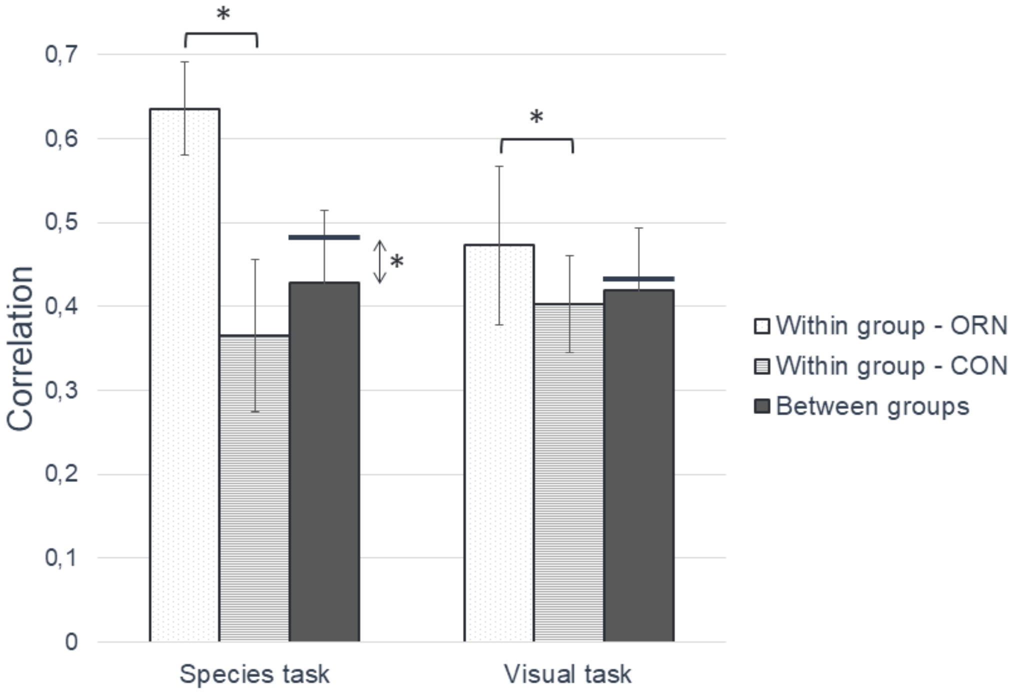

Figure 3.5. Consistency of arrangements. *Bar graph depicting the average within- and between-group correlations of the arrangements made by ornithologists and controls in the species task and the visual task. Error bars display the standard deviation (sd). The within-group correlation for ornithologists (ORN; in white) was in both tasks higher than the within-group correlation of control participants (CON; in light grey), indicating a higher consistency in the arrangements made by the experts. In the species task, the between-group correlation (dark grey) was significantly lower than the reference value (horizontal line), indicating a structural or qualitative difference between the arrangements made by the two subject groups.*

3.3.4 Structural differences in representational spaces of experts and novices

Visual inspection of the RDMs (Fig. 3.3) already gives an indication to what the qualitative difference between the ornithologists' and control participants' arrangements for the species task might have been. First of all the matrices suggest, like the MDS-plots, that information about the bird orders was present in the arrangements of both subject groups and for both tasks. To quantify this, we calculated the average within-order distance and the average between-order distance for both MOA tasks and both subject groups by calculating for each bird the average distance to all other birds belonging to the same order or belonging to a different order, respectively. Results are shown in Table 3.1. In both tasks and for both subject groups, the average within-order distance across orders was significantly smaller than the average between-order distance (Orn.: species task: $t(19) = 25.74$, $p < .0001$; visual task: $t(19) = 12.06$, $p < .0001$; Con.: species task: $t(19) = 11.28$, $p < .0001$; visual task: $t(19) = 10.20$, $p < .0001$). This was also the case for the three orders separately. This result confirmed what was already suspected based on the MDS-plots: birds belonging to the same bird order were indeed placed closer together by both subject groups and in both tasks.

Subject group	Task	Within-order distance	Between-order distance
Ornithologists	Species	0.028	0.067
	Visual	0.034	0.066
Controls	Species	0.039	0.065
	Visual	0.041	0.066

Table 3.1. Within- and between-order distances. *Average distances between birds belonging to the same order (within-order distance) and between birds belonging to different bird orders (between-order distance) for both subject groups and both tasks. The within- and between-order distances are averaged across the three orders. Both subject groups grouped birds belonging to the same order together in both tasks.*

Furthermore, the ornithologists' dissimilarity matrix for the species task clearly showed a more high level structure in the arrangement of the birds that did not seem to be present in the visual task of the ornithologists, nor in either of the two arrangements made by the control participants. We applied the same logic to test whether information at the higher level of the bird families (within the bird orders) was present in the way the two groups arranged the birds in both tasks. The within-family distance was for each bird defined as the average distance to all other birds belonging to the same bird family (and same bird order), while the between-family distance was calculated as the average distance to all birds belonging to different bird families, but still from the same bird order. The stimulus set consisted of 5 songbird families, 2 wading bird families and 2 families of birds of prey. For one songbird family we did not calculate the within-family and between-family distance, since it consisted of only one bird (bird 5C, see Figure 3.1).

Subject group	**Task**	**Within-family distance**			**Between-family distance**		
		Song	Wading	Prey	Song	Wading	Prey
Ornithologists	Species	**0.019**	**0.013**	**0.012**	**0.044**	**0.021**	**0.032**
	Visual	**0.034**	0.026	**0.031**	**0.043**	0.028	**0.036**
Controls	Species	**0.037**	0.039	0.036	**0.045**	0.036	0.035
	Visual	**0.040**	0.043	0.040	**0.046**	0.038	0.037

Table 3.2. Within- and between-family distances. *Average distances between birds belonging to the same bird family (within-family distance) and between birds belonging to different bird families but to the same bird order (between-family distance) for both subject groups and both tasks. The within- and between-family distances are averaged across the families within each bird order. Cases in which the within-family distances were significantly lower than the between-family distances are indicated in bold.*

The results confirmed that ornithologists indeed grouped birds belonging to the same bird family together in the species task (Table 3.2): the average within-family distance was significantly smaller than the average between-family distance for the songbird families ($t(79) = 14.72$, $p < 0.0001$), the wading bird families ($t(39) = 5.19$, $p < 0.0001$) and the bird of prey families ($t(39) = 13.86$, $p < 0.0001$). In the visual task, ornithologists still made a distinction between bird families belonging to the songbird order ($t(79) = 4.41$, $p < 0.0001$) and between birds of prey families ($t(39) = 2.67$, $p = 0.01$), but they no longer separated the two wading bird families ($t(39) = 1.27$, $p = 0.21$). Control participants did make a distinction between the songbird families in both the species task ($t(79) = 4.99$, $p < 0.0001$) and the visual task ($t(79) = 3.47$, $p = 0.0009$). However, there was no information on the wading bird families or on the bird of prey families in either of the tasks, since for these two orders the between-order distances were smaller than the within-order distances (Wading birds: species task: t(39) = 1.53, p = 0.13; visual task: t(39) = 2.55, p = 0.01; Birds of prey: species task: t(39) = 0.53, p = 0.60; visual task: t(39) = 2.21, p = 0.03). Overall, these results suggest that both subject groups arranged the birds in accordance with the bird orders, the finer structure in terms of the bird families however was significantly different between experts and novices.

3.3.5 Dissimilarities between same-species birds and visually similar birds

We designed the study to probe one specific qualitative difference between the groups in their mental representations. As mentioned in the Methods section (3.2.4), 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 3.2). 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 (Figure 3.6).

Paired-sample t-tests showed that 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 < 0.0001). 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 = 0.96), 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 = 0.048) and the same tendency was present in the species task, although the difference did not reach significance (t(19) = 2.09, p = 0.051). 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 (two-sample t-tests; species task: t(38) = 9.30, p < 0.0001; visual task: t(38) = 2.83; p = 0.007). Overall, these results indicate that ornithologists make fine-grained distinctions between birds at the level of the bird species and this effect is most pronounced in an expertise-related task.

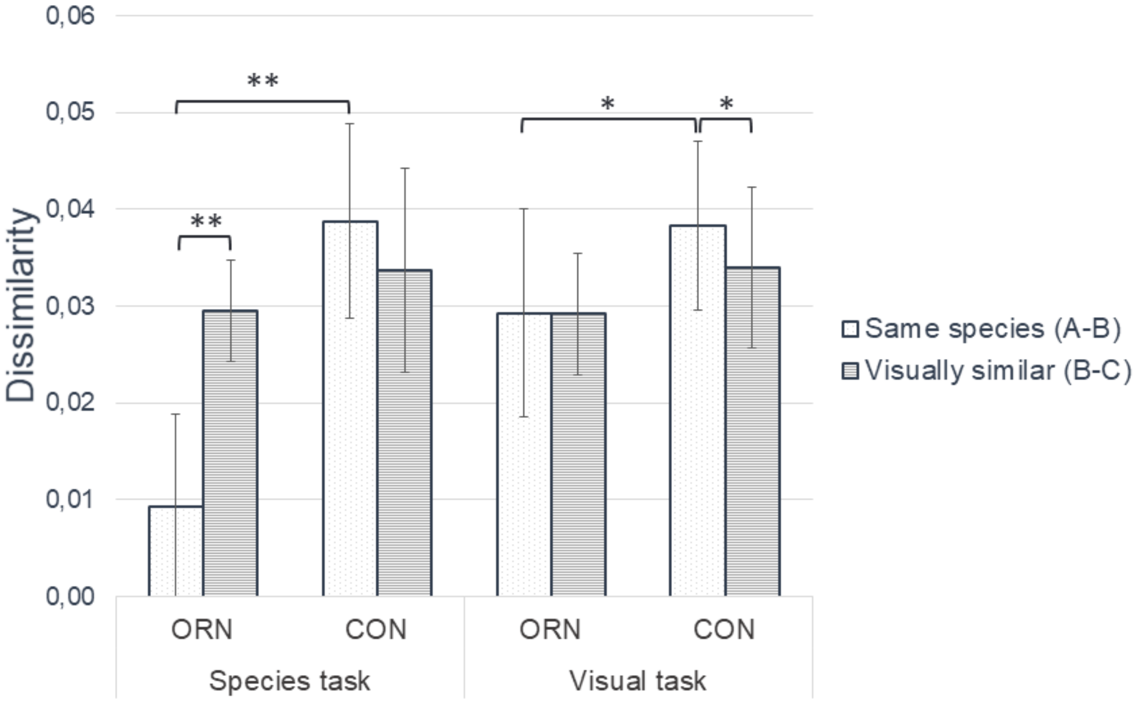

Figure 3.6. Dissimilarities between bird pairs. *Bar graph depicting the average pairwise dissimilarities or distances between bird pairs for ornithologists and control participants in the species task and the visual task. Birds A and B (white) belong to the same bird species but are visually different, and birds B and C (grey) are visually similar but belong to different bird species. Error bars display the standard deviation (sd). Significant differences are indicated by asterisks: * $p < 0.05$ and ** $p < 0.0001$.*

3.4 DISCUSSION

In the present study, we investigated the influence of visual expertise in ornithology on the mental representations of objects of expertise by comparing the similarity spaces created by experts and novices. The results indicated a quantitative enhancement of the representational space of objects of expertise; the similarity arrangements made by experts were more consistent compared to those made by novices. Furthermore, the results demonstrated the presence of qualitative differences between the similarity spaces of the two subject groups. Experts and novices have mental representations that share a lot of commonalities at the basic level (in this case: the bird orders). However, the more we go into finer details, the more qualitative differences we find. The influence of expertise on the mental representations of the birds was noticeable in the more fine-grained distinctions: where ornithologists were able to organize the birds according to the intermediate level of the bird families and even the subordinate level of the bird species, control participants were overall not able to make these systematic distinctions beyond the level of bird orders. Moreover, these effects were most pronounced in an expertise-related task.

3.4.1 Qualitative and quantitative expertise-related changes

This is the first study to investigate the mental representational space of a natural category in a real-world domain of expertise. In the past, many behavioral studies have shown that similarity plays a crucial role in perceptual category learning, whether it is similarity to exemplars or similarity to a prototype (e.g. Nosofsky, 1986; Posner & Keele, 1968). Mental similarity spaces are not only useful to investigate how perceptual learning or learning to categorize comes about, it is also important to explore what happens after the initial learning phase. In this study we show that years of extensive visual experience with a particular object category can bring about structural changes in the mental representational space of that specific category. These structural changes express themselves in the form of fine-grained subordinate-level distinctions. The idea that subordinate-level processing is an important aspect of expertise was first stated by Tanaka and Taylor (1991) and has been demonstrated in many different behavioral studies on expertise. Our study further confirms these observations by clearly showing that bird experts use a more subordinate level of organization (in this case: bird families and even the bird species) compared to novices when asked to perform an expertise-related task.

Apart from the structural changes in the mental representational space as a result of expertise, we also found that the coherence between the similarity spaces created by individuals was much higher in the group of experts compared to novices. The fact that ornithologists discriminate between birds in a very similar manner, indicates that they all go through a very similar learning process. This learning process very likely consists of subordinate-level training. As has been shown in previous studies (e.g. Scott et al., 2006, 2008), subordinate-level training leads to a better discrimination performance between individual exemplars, which is what the experts in this study demonstrated. Furthermore, this type of training allows for a greater generalization to new exemplars (Gauthier et al., 1998; Tanaka et al., 2005), which could facilitate learning about new bird species for experts.

3.4.2 Top-down influences

The effect of expertise on the structure of the representational space of birds was more pronounced in the expertise-related species task compared to the non-related visual task, indicating the influence of top-down factors. This result was in line with studies in the field of perceptual learning which have shown that task context can alter the similarity relations between objects (e.g. Nosofsky, 1987; Van Gulick & Gauthier, 2014). Perhaps this effect is even more pronounced in the context of visual expertise. We know that perceptual similarity is an important concept in the field of perceptual learning, however, the arrangements made by the experts suggest that past the initial learning phase, it is not just visual similarity that plays a role. This leads us to the following question: we draw lines between perceptual learning and visual expertise, but how 'perceptual' is visual expertise? In the expertise-related task, experts made more fine-grained distinctions between the birds compared to judgments based on visual appearance alone, clearly indicating the influence of semantic information or abstract knowledge. Even in the non-related visual task, experts were not able to discard species information when making judgments based on visual similarity.

To answer the question about how much perceptual, bottom-up effects contribute to acquiring visual expertise and to what extent top-down process play a role, we should investigate a domain of expertise in which (at least for a subset of the objects belonging to that category) perceptual information and semantic information are dissociated from each other. In the current study, we attempted to make this dissociation by creating the bird triplets, however, visual and semantic features were not orthogonal to each other. This was mainly because bird species belonging to the same bird order or bird family are not only related in the context of taxonomy, they also share visual features (e.g.: wading birds generally have long legs), which is likely also the reason why even novices were able to group the birds into their respective bird orders. Disconnecting perceptual from semantic information in order to assess the influence of semantic knowledge on the structure of the similarity space of an object category is a very difficult task to carry out with a real-world domain of expertise. Therefore it would be useful to revert to artificially created object categories (e.g. Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005; Gauthier & Tarr, 1997, 2002; Gauthier et al., 1998; Wong, Palmeri, & Gauthier, 2009). Participants can be extensively trained in a new category in which visual features and semantic characteristics (like name, family relations etc.) are orthogonal to each other. The drawback of this kind of approach is that subjects participating in training studies cannot reach the level of real-world experts. However, this could be a good way to study the intermediate step between the initial phase of perceptual learning and complete visual expertise; perhaps structural changes in a representational space due to expertise emerge gradually, or perhaps they appear abruptly.

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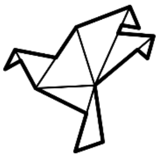


Neural expertise effects at the subordinate level

Visual expertise changes the neural representation and processing of objects of expertise. Studies investigating the neural correlates of visual expertise have focused on the neural response underlying the expert object category. However, behavioral research has demonstrated that experts are especially proficient at identifying and classifying objects within a specific category, at a more subordinate level compared to novices. In the present study, we apply multi-voxel pattern analyses to investigate the neural responses that are elicited by the individual objects of expertise, in both experts and novices. This way, we aim to investigate the influence of expertise on the neural representational space of objects of expertise in low-level visual cortex, high-level visual cortex and the frontal lobe. Results indicated quantitative enhancements of the representations of objects of expertise in experts compared to novices in the higher-level regions. Nevertheless, the overall structure of the neural representational space was not altered by expertise. Finally, we compared the neural representational spaces of both experts and novices to their mental representational spaces that were presented in chapter three.

4.1 INTRODUCTION

The effects of visual expertise, extensive visual experience with a specific category of objects, 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 exact location of these effects 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. For example, the neural activation elicited by images of cars in the brain of a car expert will differ from a novice’s neural response to those same images.

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. Gauthier et al., 2000; Xu, 2005; Haller and Radue, 2005; Harley et al., 2009; Wong and Gauthier, 2010; Harel et al., 2010; Bilalić et al., 2011, 2014; Hoenig et al., 2011; McGugin et al., 2012; Floyd et al., 2017; Martens et al., 2018). 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 correlation between neural activation and level of expertise. These effects have been found in visual regions like the lateral occipital complex (LOC, e.g. Jiang et al., 2007; Harel et al., 2010), the fusiform face area (FFA) and regions around it (e.g. Gauthier et al., 2000; Rhodes et al., 2004; Xu, 2005; van der Linden et al., 2008; Harley et al., 2009; McGugin et al., 2012), and early visual cortex (EVC, e.g. Harel, Gilaie-Dotan, Malach, & Bentin, 2010; Martens, Bulthé, van Vliet, & Op de Beeck, 2018), in areas outside of 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. Gauthier et al., 1999; Moore et al., 2006; Op de Beeck et al., 2006; Brants et al., 2011, 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, all 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). Several learning studies have shown that training participants to identify or categorize objects within a specific domain at the individual or subordinate level greatly improves their ability to discriminate these objects, in contrast to participants that were trained at the basic level. These effects have been found for real-world categories (e.g. birds, Tanaka et al., 2005; Scott et al., 2006) as well as for artificial objects (e.g. Ziggerins, 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, almost none of these studies 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 by a study on distinguishing subordinate object distinctions in general (Eger, Ashburner, Haynes, Dolan, & Rees, 2008). A few studies have resorted to the method of fMRI adaptation to resolve these problems

(Folstein et al., 2013; Gillebert et al., 2008; Panis, Vangeneugden, Op de Beeck, & Wagemans, 2008), but this indirect method of measuring neural selectivity has important interpretational problems.

In the current study, we aim to investigate through MVPA whether and how visual expertise changes the way in which *individual* objects of expertise are represented in the brain. Our goal is to gain insight into the effects of a real-world domain of visual expertise, in this case ornithology or bird expertise, on the neural representational space of objects of expertise, birds. To do this, we will use MVPA to distinguish the distributed neural responses to individual birds in object-selective cortex. These neural representations will be combined in a representational space, which we will then 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 (see chapter 3).

4.2 MATERIAL AND METHODS

4.2.1 Participants

The same 40 subjects that took part in the behavioral study on the mental representational space of objects of expertise (see chapter 3), also participated in this fMRI study. Twenty ornithologists (average age: 28.3 years, 5 females, 11.1 years of experience on average) and twenty control participants (average age: 28.6 years, 6 females, no experience with birds) were extensively tested for their level of knowledge concerning birds by means of a perceptual discrimination task and a semantic naming task. More details concerning the selection procedure can be found in section 3.2.1 of chapter three. The two subject groups consisted of healthy adults with normal or corrected-to-normal vision, without a neurological background. They provided a written informed consent for the fMRI scan. The study was approved by the Medical Ethical Committee of KU Leuven.

4.2.2 Stimuli

During the fMRI experiment, participants were presented with images of 24 birds that were also used in the MOA tasks of the behavioral experiment (see chapter 3). The selected birds consisted of 8 triplets (Figure 4.1). 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 differing male and female or a species with differing 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).

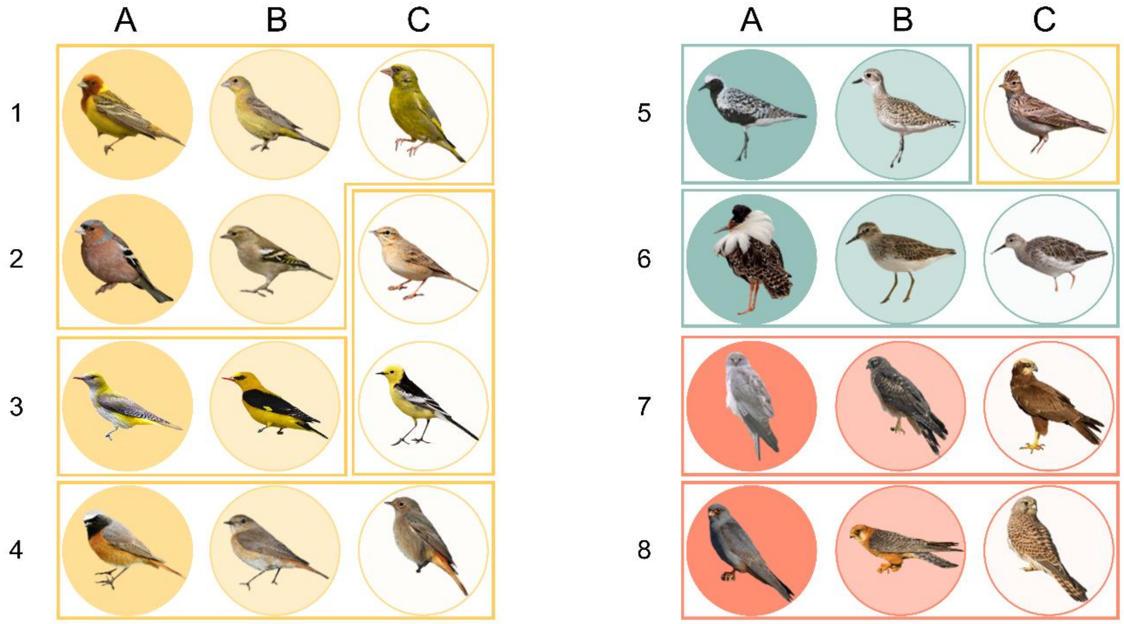


Figure 4.1. Stimuli. *The 24 birds that were presented to the participants during the scan task were the same as the birds that were selected for the MOA tasks (see chapter 3). The birds are arranged into 8 triplets. In each triplet, birds A and B belong to the same species but are visually different, 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: the birds in yellow are songbirds, the birds in blue are wading birds and the birds in red belong to the order of birds of prey.*

4.2.3 Apparatus

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^o 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.

4.2.4 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). Runs started with a 9 second fixation screen. Then each of the 24 conditions was presented 4 times per run, these 96 trials were interspersed with 96 fixation trials ranging from 1 to 9 seconds. We rapidly presented 4 different colored images of the same condition (bird) per trial: one of these 4 images was exactly the same image as was used in the MOA tasks, the other 3 images were pictures taken from different viewpoints (Figure 4.2). 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 1 to 4, 1 meaning “not at all similar” and 4 meaning “very similar”. The order of the buttons was counterbalanced across runs.

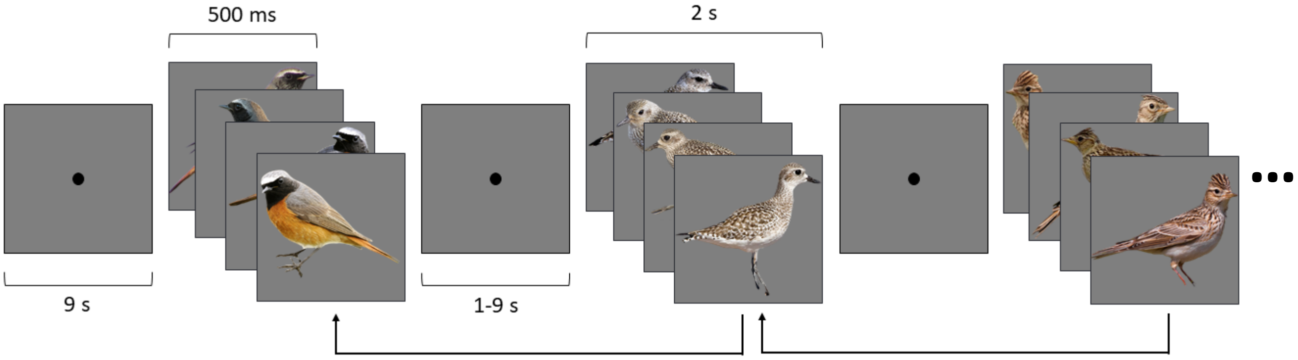


Figure 4.2. Schematic overview of the design of one experimental run. *Images of the 24 conditions (birds) were presented in an event-related design. In each trial, 4 different images of the same bird species were presented for 500 ms, resulting in a 2 s presentation per trial. Each condition was presented 4 times per run. Participants were asked to perform a one-back similarity judgment task.*

4.2.5 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 to the first slice, spatial realignment (to the mean image) to correct for head movements, coregistration of the anatomical image and the functional images (using the default SPM settings), 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 2.5 mm (1 voxel size), overall 1 run had to be discarded. For each participant, a general linear model (GLM) was fitted, including regressors for each of the 24 conditions (birds) and the 6 motion realignment parameters to control for signal variation due to head motion.

4.2.6 Regions of interest

We delineated three bilateral anatomically defined regions of interest (ROIs) in each participant: low-level visual cortex (LVC; Brodmann areas (BA) 17 and 18 which included V1 and nearby cortical regions, average size of 719 ± 205 voxels), high-level visual cortex (HVC; BA 36, 37 and 20, average size of 572 ± 132 voxels) and the frontal lobe (FL; average size of 4453 ± 2055 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 $p < 0.001$ for the contrast [all conditions - fixation].

4.2.7 Multi-voxel pattern analyses

We applied correlational multi-voxel pattern analyses (MVPA) to investigate the neural representational space of the 24 birds in the three selected ROIs in both 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 which was 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.

We applied representational similarity analyses (RSA) to compare the neural dissimilarity matrices of both subject groups to the behavioral dissimilarity matrices that were created based on the arrangements made by the participants in the MOA tasks (see chapter 3). We calculated partial correlations (Pearson’s r) between the group neural RDMs of the three ROIs on the one hand and the group behavioral RDMs of the species and visual MOA task on the other.

4.3 RESULTS

4.3.1 Distinctiveness and between-subject consistency of neural representations of objects of expertise

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 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 (FL).

First of all, we tested whether reliable information about the 24 conditions (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). 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 (pairwise t tests, for all comparisons: p < 0.0001), indicating that the multi-voxel patterns conveyed information about the presented conditions (Table 4.1).

	LVC		**HVC**		**FL**	
	within-con	between-con	within-con	between-con	within-con	between-con
Ornithologists	0.60 ± 0.10	1.02 ± 0.00	0.85 ± 0.08	1.01 ± 0.00	0.89 ± 0.06	1.00 ± 0.00
Controls	0.61 ± 0.13	1.01 ± 0.00	0.88 ± 0.06	1.01 ± 0.00	0.93 ± 0.05	1.00 ± 0.00

Table 4.1. Within- and between-condition dissimilarities. *Average within-condition dissimilarities (diagonal values) and between-condition dissimilarities (off diagonal values) of the neural representational spaces of ornithologists and control participants in low-level visual cortex (LVC), high-level visual cortex (LVC) and the frontal lobe (FL). Table shows averages across subjects ± sd. For both subject groups and in all three ROIs, the average within-condition dissimilarities were significantly smaller than the average between-condition dissimilarities (for all comparisons: p < 0.0001).*

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 (Figure 4.3). 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(19) = 0.38, p = 0.71; HVC: t(19) = 1.15, p = 0.26). However, in FL, the neural representations of the different birds were more distinct in the experts compared to the novices (t(19) = 2.15, p = 0.04).

Additionally, we asked ourselves how consistent the neural representational spaces of ornithologists and control participants were within and between groups. For each ROI, we calculated the within-group and between-group correlations between the neural RDMs for each participant. Results are shown in Figure 4.4. In LVC, there was no difference in consistency between the two subject groups (t(19) = 0.21, p = 0.83). However, in HVC and in FL, there was a significant difference between the within-group correlations of ornithologists and control participants (HVC: t(19) = 3.92, p = 0.0009; FL: t(19) = 7.94, p < 0.0001). 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.

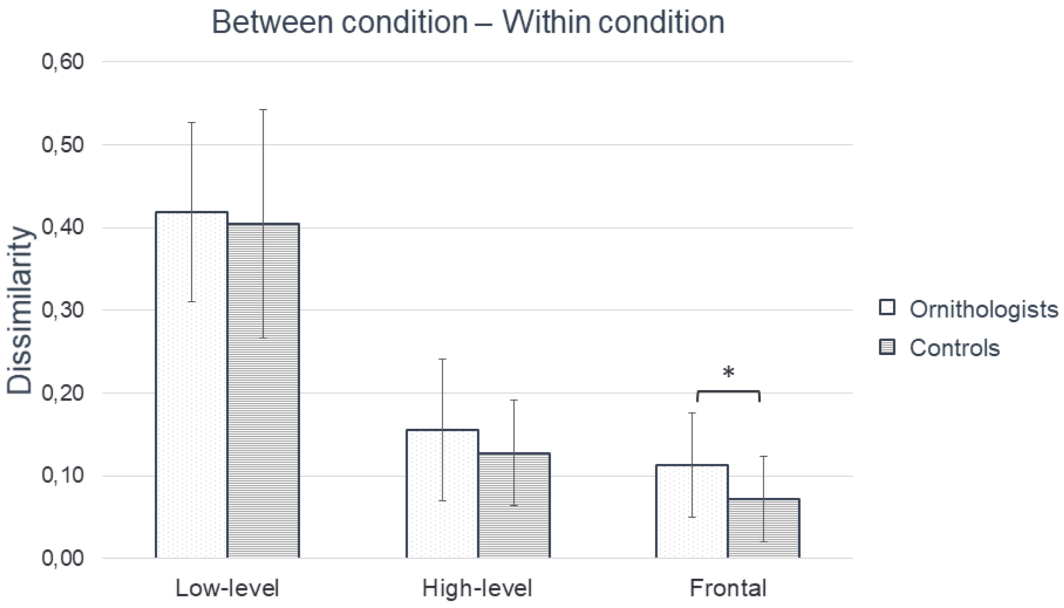


Figure 4.3. ***Distinctiveness of neural response patterns.*** *Bar graph depicting the average between-condition dissimilarity (off diagonal values of RDM) minus the average within-condition dissimilarity (diagonal values of RDM) for experts and novices in the three ROIs (low-level visual cortex, high-level visual cortex and frontal lobe). Error bars display the standard deviation. Significant differences are indicated by an asterisk.*

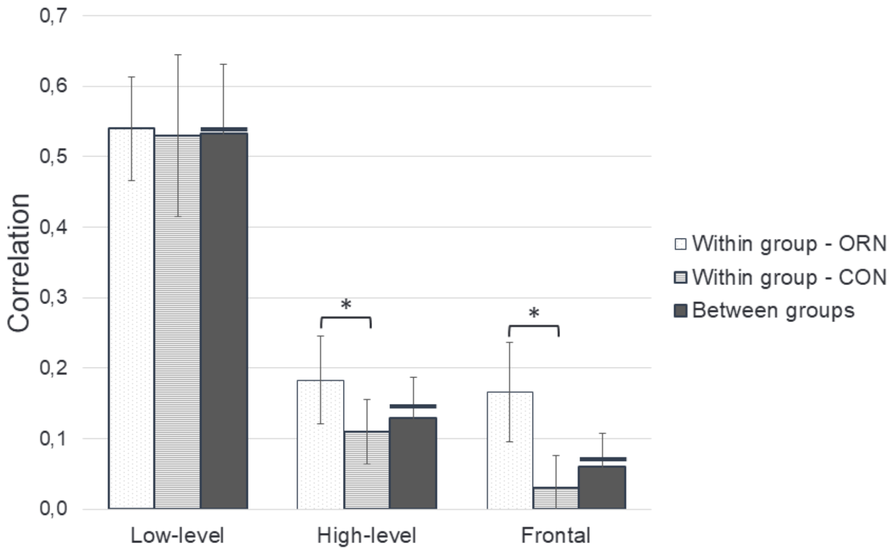


Figure 4.4. ***Consistency of neural representational spaces.*** *Bar graph depicting the average within- and between-group correlations of the neural representational spaces of ornithologists (ORN) and controls (CON) in the low-level visual cortex, high-level visual cortex and the frontal lobe. Error bars display the standard deviation. In the two higher-level regions, the neural representational space for the 24 birds was more consistent among ornithologists compared to control participants.*

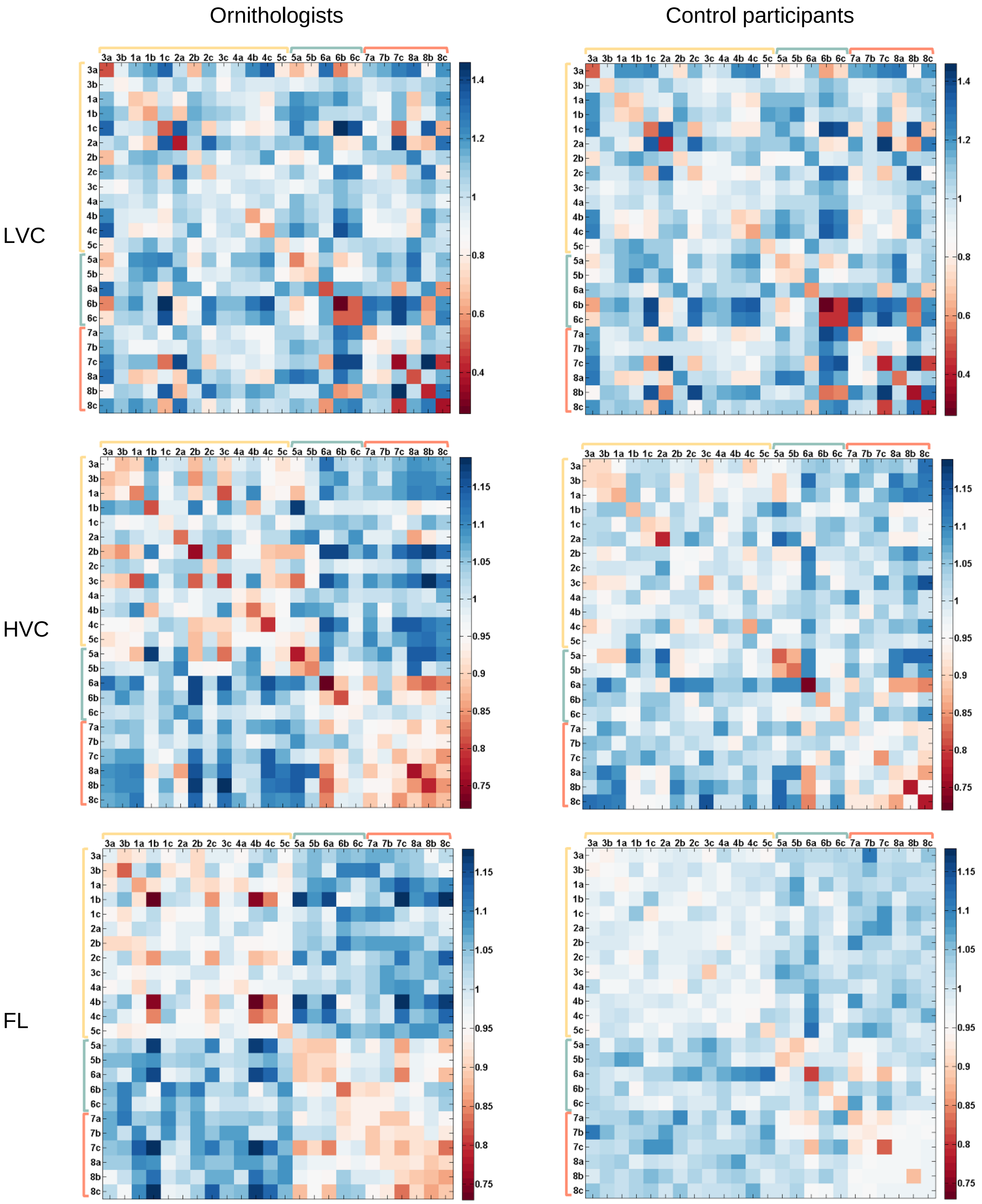


Figure 4.5. Representational dissimilarity matrices. *Matrices representing the average pairwise dissimilarities (1-correlation) between the neural response patterns underlying the 24 birds for ornithologists and control participants in the low-level visual cortex (LVC), the high-level visual cortex (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 brackets, wading birds by blue brackets and birds of prey by red brackets. The bird codes match the codes used in Figure 4.1.*

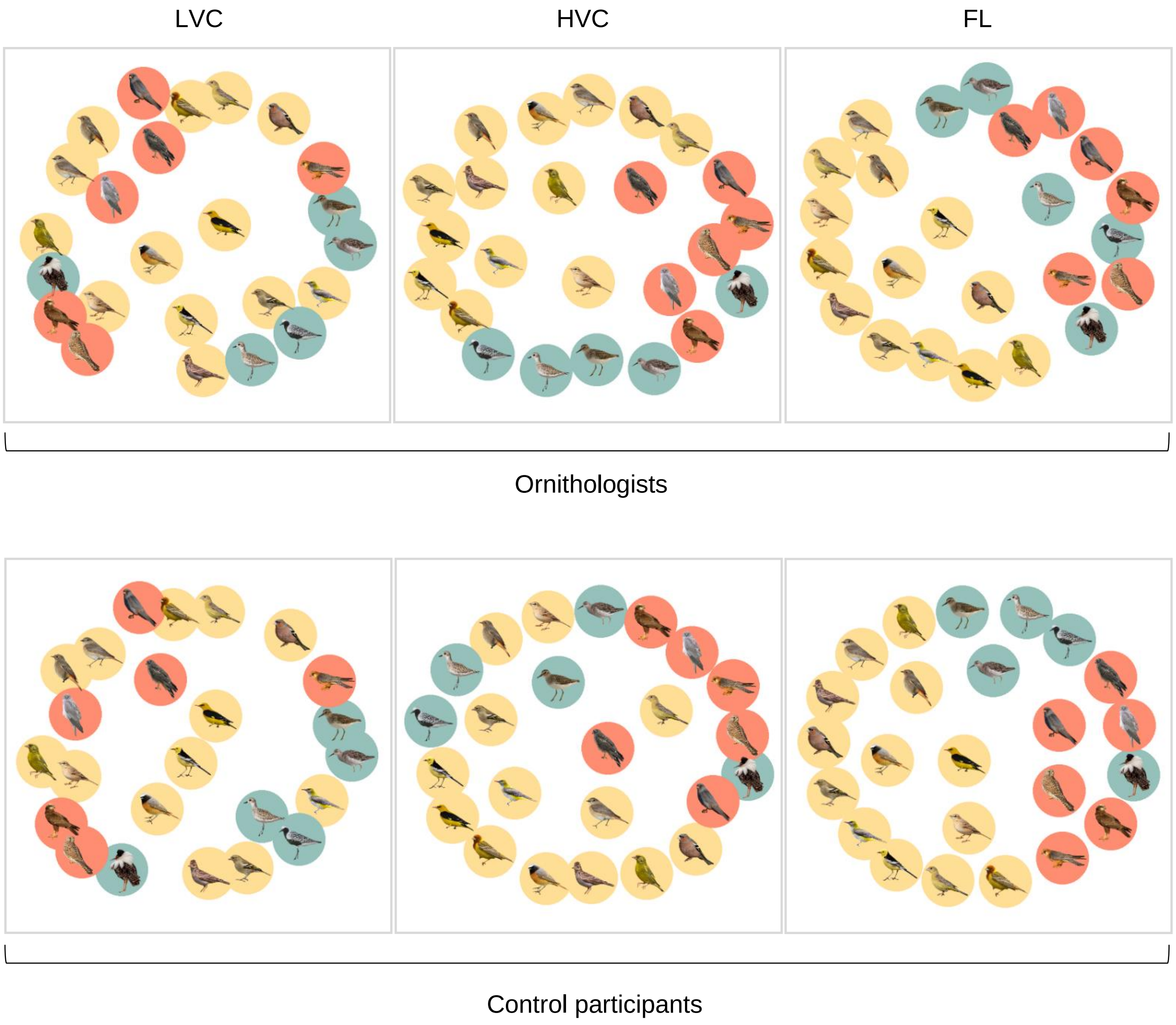


Figure 4.6. MDS-plots of the neural representational spaces. *Plots displaying the average neural representational space for ornithologists and control participants in low-level visual cortex (LVC), high-level visual cortex (LVC) and the frontal lobe (FL). Plots were visualized using 2-D multidimensional scaling with metric stress in Matlab R2013a. Birds in yellow are songbirds, blue birds are wading birds and birds in red are birds of prey.*

4.3.2 Neural representational space of objects of expertise

The RDMs showing the pairwise dissimilarities between the neural response patterns for the 24 birds are presented in Figure 4.5. Furthermore, we depicted the neural representational spaces in each ROI and for both subject groups using multi-dimensional scaling (Figure 4.6). Interestingly, visual inspection of the MDS-plots showed 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 FL, a distinction between songbirds on the one hand and wading birds and birds of prey on the other hand became visible.

We checked whether we could find evidence of a qualitative difference between the representational spaces of both subject groups. In the previous paragraph we reported two quantitative group differences: the neural representations of the 24 birds in FL were more reliable in experts compared to novices and the representational spaces of ornithologists were more consistent in HVC and FL. However, this tells us nothing about the structure of the neural representational spaces in the two subject groups. Expertise potentially influences the mutual relationships between the neural representations of the presented birds in one or more ROIs, in such a way that the representations of specific bird pairs move closer or further away from each other. Another possibility is that expertise simply enhances the neural representations (like we have shown in the frontal lobe) but leaves the structure of the representational space untouched. We compared the average correlation between groups to a reference value which lies in between the within-group correlations of the relevant ROI. This reference was calculated as the square root of the product of the two within-group correlations (e.g. Op de Beeck, Deutsch, Vanduffel, Kanwisher, & DiCarlo, 2008). If the structure of the representational spaces of the two subject groups would be different, we would expect the between-group correlation to be lower than the reference value (see also chapter 3). However, the between-group correlations did not differ from the expected reference value in any of the ROIs (see Fig. 4.4; LVC: $t(19) = 0.18$, $p = 0.86$; HVC: $t(19) = 0.96$, $p = 0.35$; FL: $t(19) = 1.33$, $p = 0.20$). This indicates that the structure of the neural representational space of the 24 birds was not influenced by expertise: the mutual relationships between the birds were similar for novices and experts. The absence of any group differences in this overall correlation does not give a reason to do further exploratory analyses at the level of bird order and bird family. For completeness we performed such analyses, but did not find any group differences.

In addition, we analyzed the similarity between birds at the level of the triplets. First of all, we checked whether the neural response patterns of the birds within each triplet were reliably distinct from each other. Per triplet, we compared the average within-condition dissimilarity (average dissimilarity when comparing each of the 3 birds with itself) to the average between-condition dissimilarity (which was the average dissimilarity between the neural representations of birds A and B, birds B and C, and birds A and C). The results were averaged across the 8 triplets (Table 4.2). In all three ROIs and for both subject groups, the within- and between-condition dissimilarities were significantly different, indicating that the multi-voxel patterns conveyed information about the different birds even within the triplets (pairwise t tests: LVC: Orn.: t(19) = 17.28, p < 0.0001; Con.: t(19) = 12.79, p < 0.0001; HVC: Orn.: t(19) = 5.46, p < 0.0001; Con.: t(19) = 6.61, p < 0.0001; FL: Orn.: t(19) = 3.58, p = 0.002; Con.: t(19) = 3.60, p = 0.002).

	LVC		**HVC**		**FL**	
	within-con	between-con	within-con	between-con	within-con	between-con
Ornithologists	0.60 ± 0.10	0.97 ± 0.04	0.85 ± 0.08	0.94 ± 0.03	0.89 ± 0,06	0.94 ± 0.04
Controls	0.61 ± 0.13	0.95 ± 0.04	0.88 ± 0.06	0.97± 0.03	0.93 ± 0,05	0.97 ± 0.03

Table 4.2. Within- and between-condition dissimilarities within the triplets. *Average within-condition dissimilarities (diagonal values for each triplet: A-A, B-B and C-C) and between-condition dissimilarities (off diagonal values for each triplet: A-B, B-C and A-C) averaged across the 8 triplets, for ornithologists and control participants in low-level visual cortex (LVC), high-level visual cortex (LVC) and the frontal lobe (FL). Table shows averages across subjects ± sd. For both subject groups and in all three ROIs, the within-condition dissimilarities were significantly smaller than the between-condition dissimilarities. Note that the within-condition dissimilarities are of course the same as the within-condition dissimilarities shown in Table 4.1.*

The fact that the multi-voxel patterns of the birds within the triplets were distinguishable from each other, allowed us to further investigate the relation between the neural representations of birds A and B (same species, visually different) on the one hand and of birds B and C (different species, visually similar) on the other hand in both ornithologists and control participants (Figure 4.7). We performed a three-way repeated measures ANOVA on the average distance between birds A and B and birds B and C with ROI (3 levels: LVC, HVC and FL) and bird pair (2 levels: pair A-B and pair B-C) as within-subjects factors and subject group (2 levels: ornithologists and controls) as between-subjects factor.

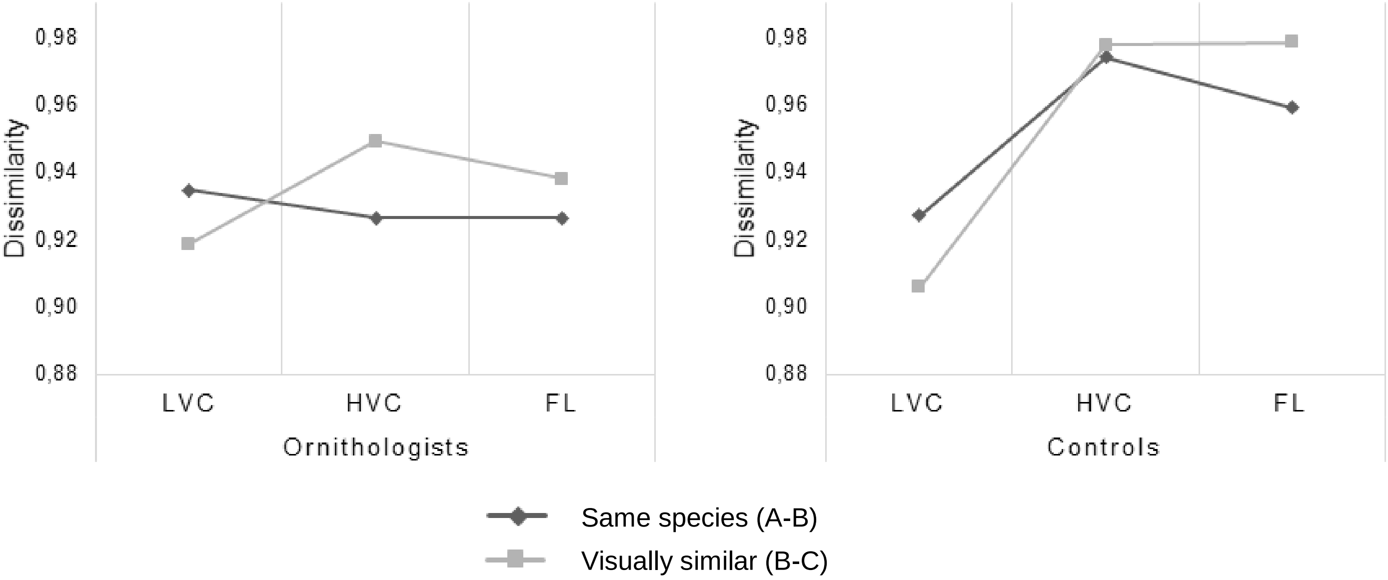


Figure 4.7. Dissimilarities between bird pairs. *Graph depicting the average pairwise dissimilarities between the neural response patterns underlying birds A and B (dark grey) and birds B and C (light grey) for ornithologists and control participants in low-level visual cortex (LVC), high-level visual cortex (HVC) and the frontal lobe (FL). Birds A and B belong to the same bird species but are visually different, and birds B and C are visually similar but belong to different bird species.*

Results showed a main effect of ROI (F(2,76) = 12.97, $p < 0.0001$); in general (across bird pairs and across subject groups) the neural representations in LVC were more similar compared to HVC and FL (average distances: LVC: 0.922, HVC: 0.957, FL: 0.950). We also found an interaction effect of ROI and subject group (F(2,76) = 6.86, $p = 0.002$): in the low-level visual ROI, the distances (across bird pairs) were larger in ornithologists than they were in control participants, while in the higher-level regions (HVC and FL), the opposite was true (Orn.: LVC: 0.927, HVC: 0.938, FL: 0.932; Con.: LVC: 0.917, HVC: 0.976, FL: 0.969). Most importantly, the analysis showed an interaction effect of ROI and bird pair (F(2,76) = 3.42, $p = 0.038$). In the low-level visual ROI, the neural representations of birds B and C were more similar compared to birds A and B, while in the high-level visual region and in the frontal lobe, the multi-voxel patterns of the birds A and B were more closely related (A-B: LVC: 0.931, HVC: 0.950, FL: 0.943; B-C.: LVC: 0.912, HVC: 0.963, FL: 0.958). This was true across the two subject groups. These results show that the manipulation of the visual appearance and the species of the birds was also reflected in their neural representations: visually similar birds were represented in a similar manner in low-level visual regions, while the “semantically” similar birds were represented more similarly in the higher-level regions. We were mostly interested in the interaction between subject group and bird pair: are the visually similar birds and the semantically similar birds represented differently in the brains of experts compared novices? Unlike the behavioral effect of expertise that was present in the species MOA task, we did not find differences between the neural representations of the two subject groups.

4.3.3 Correlations between neural and behavioral representational spaces

We applied RSA to investigate whether the neural representational spaces of both experts and novices were related to their respective behavioral dissimilarity matrices of the same 24 birds. These behavioral RDMs were created by having the participants perform two MOA tasks: one in which they judged the birds’ similarity based on their taxonomy or bird species (species task) and one in which they judged the birds’ visual similarity (see chapter 3). We calculated the correlation (Pearson’s r) between the group neural dissimilarity matrices of both groups in each of the three ROIs on the one hand and the behavioral dissimilarity matrices of both tasks on the other hand. To account for the variance explained by both tasks, we calculated partial correlations. We tested whether the resulting group correlations significantly differed from zero by also calculating the partial correlations for each subject separately and performing one-sample t-tests for each subject group, ROI and task. As shown in Table 4.3, the neural representational space of ornithologists in the low-level visual ROI was showing non-significant correlations with behavioral similarity in the two tasks (species: $t(19) = 1.22$, $p = 0.237$; visual: $t(19) = 1.98$, $p = 0.062$). The control participants’ neural RDM in LVC was significantly related to the behavioral RDM resulting from the species task ($t(19) = 4.47$, $p = 0.0003$), but there was no relation to the visual task ($t(19) = 1.97$, $p = 0.064$). This result was in accordance with the observation that there was no clear structure (no information about the bird orders) to the neural dissimilarity matrices of both subject groups in LVC. For the higher-level regions we found more consistent positive correlations between neural and behavioral similarity spaces. In HVC, the behavioral dissimilarity matrices of both tasks were significantly correlated with the neural dissimilarity matrix of experts and novices, respectively (Orn.: species: t(19) = 4.24, p = 0.0004; visual: t(19) = 4.17, p = 0.001; Con.: species: t(19) = 2.82, p = 0.011; visual: t(19) = 3.64, p = 0.002). The same was true for the frontal lobe (Orn.: species: t(19) = 3.91, p = 0.001; visual: t(19) = 4.86, p = 0.0001; Con.: species: t(19) = 2.34, p = 0.03; visual: t(19) = 2.50, p = 0.022). These results were likely due to the presence of bird order information that could be found in the neural representational spaces in the higher-level regions for both subject groups. We did not find an effect of expertise on the relation between the neural and the behavioral representational spaces.

		LVC		**HVC**		**FL**	
		Species	Visual	Species	Visual	Species	Visual
Ornithologists	group	-0.03	0.08	0.12	0.11	0.17	0.18
	per subject	0.03 ± 0.11	0.04 ± 0.08	**0.09 ± 0.10**	**0.07 ± 0.07**	**0.11 ± 0.13**	**0.10 ± 0.10**
Controls	group	0.10	-0.01	0.14	0.03	0.18	0.14
	per subject	**0.06 ± 0.06**	0.03 ± 0.07	**0.05 ± 0.08**	**0.05 ± 0.07**	**0.05 ± 0.10**	**0.05 ± 0.09**

Table 4.3. Partial correlations between neural and behavioral RDMs. *For both ornithologists and control participants, partial correlations (Pearson's r) are shown between the group neural RDMs in low-level visual cortex (LVC), high-level visual cortex (HVC) and the frontal lobe (FL) on the one hand and the behavioral RDMs of the species task and the visual task on the other hand. To test whether the group correlations significantly differed from zero, partial correlations were also calculated for each subject separately (table shows averages across subjects ± sd). Significant partial correlations are indicated in bold.*

4.4 DISCUSSION

In the present study, we investigated the influence of visual expertise in ornithology on the neural representations of individual objects of expertise. The results indicated a quantitative enhancement of the representations of objects of expertise in experts compared to novices. The neural representations 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. Nevertheless, the structure of the neural representational space was similar in the two groups.

4.4.1 Neural representations of individual objects of expertise

This is the first study to investigate neural expertise effects at the more detailed, subordinate level. So far, research on the neural basis of expertise has mostly focused on the neural activity underlying the expert object category instead of the individual objects of expertise (e.g. Bilalić et al., 2014, 2011; Floyd et al., 2017; Gauthier et al., 2000; Gauthier & Tarr, 2002; Harel et al., 2010; Harley et al., 2009; Martens et al., 2018; Mongelli et al., 2017). The reason for this is that the neural representations of visually similar exemplars within a specific category are very hard to differentiate. While selective neural responses to moving dot arrays (Larocque, Riggall, Emrich, & Postle, 2017) and to visually similar man-made objects have already been detected using multi-voxel analyses (Eger et al., 2008), the current study is the first to demonstrate that it is possible to distinguish individual objects belonging to the same animate category. Given this background, our findings are a very important step towards a fuller understanding of how expertise changes the representation of objects of expertise.

An important finding in this study is that the multi-voxel patterns that represent the objects of expertise in the frontal lobe are more distinctive in experts compared to novices, meaning that the individual birds are better distinguished from each other in the brains of experts. This result is in line with the idea of subordinate-level categorization, a behavioral hallmark of visual expertise which states that experts are very proficient at discriminating between visually similar objects within the same expert object category (Tanaka & Taylor, 1991). Our results show that experts do not only make more fine-grained distinctions between objects of expertise at the behavioral level (chapter 3), this feature can also be replicated with the neural data in the frontal lobe, pointing towards the influence of top-down factors in making these detailed distinctions (Harel et al., 2010; Martens et al., 2018).

Furthermore, the representational similarity spaces in the higher-level regions were more consistent among experts compared to novices. In other words: the relations between the neural response patterns representing the different birds (whether some birds are represented by very similar multi-voxel patterns while others are very different) are much more regular among the ornithologists. This result is in line with the behavioral results presented in chapter three, which showed that the experts created arrangements of the 24 birds that were more consisted compared to the arrangements made by novices, in both the species and the visual task. This might suggest that bird experts gain their knowledge or experience in a very similar manner. Again, the fact that this difference in consistency between experts and novices only occurred in the higher-level regions and not in the low-level visual area indicates that conceptual knowledge plays a role and that the representational spaces in these regions are not purely based on visual features (see also below).

We found no qualitative or structural differences between the neural representational spaces of experts and novices. This result seemingly indicates that expertise does not influence the structure of the neural representational space of the objects of expertise. However, two alternative factors might underlie this absence of an effect at the neural level. First of all, while in the scanner, participants were not specifically instructed to judge the birds' similarity based on their species, an expertise-related task, instead they were free to perform the task in a way that they deemed to be most fitting. The behavioral results that were presented in chapter three showed that when bird experts and novices are explicitly asked to judge the similarity between birds based on their bird species, a more subordinate-level structure emerges in the mental representational space of experts compared to those of novices. However, there were no structural differences between the mental RDMs of the two subject groups when they were asked to arrange the birds based solely on their visual similarity, a non-related task. It is possible that any potential structural changes in the neural representational space due to expertise could have been amplified by instructing the subjects to perform an expertise-related species task while in the scanner. 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. Even though we were able to distinguish the neural representations of the individual objects of expertise (even within the triplets of birds, which are especially selected for their visual and or semantic similarity), it is even more challenging to measure differences in those representations between subject groups. It could be the case that expertise-related structural changes to the neural representational space are present but that we simply cannot detect them using the multivariate methods and data quality that we currently have.

4.4.2 More structured representational spaces in higher-level regions

The neural data indicates that for both experts and novices, semantic information about the birds strengthens going from lower to more high-level cortical regions. We visualized the neural representational spaces of the birds using multi-dimensional scaling, for both subject groups and in the three ROIs: low-level visual cortex, high-level visual cortex and the frontal lobe. In LVC, no clear structure seems to be present in the neural representational space of either subject group. Given the established role of LVC in the representation of low-level physical dimensions such as contrast, color, and local spatial frequency content, this finding indicates that the representational structure in the other regions cannot easily be explained by such dimensions. However, in HVC and in FL, the overall structure of the representational spaces seems to be following the lines of the bird orders, indicating an emergence of more high-level information at the larger scale. This visual observation is further supported by the fact that also at the more fine-grained level of the bird triplets, semantic information becomes more important in the higher-level ROIs. In LVC, the neural response patterns to the visually similar birds (B-C) were more similar, while in HVC and FL the representations of the semantically similar birds (A-B) were more alike. Again, this was true for both subject groups, we found no effect of expertise in this regard.

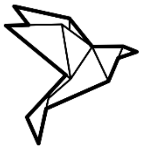
4.4.3 Relation between mental and neural representations

Finally, we also investigated the relation between the neural representational spaces and the mental (behavioral) spaces of the same individual objects of expertise, that were presented in chapter three. For both subject groups we found significant partial correlations between the similarity judgments of the visual *and* the species task on the one hand, and the neural representational spaces in the two higher-level regions on the other. Previous studies have already demonstrated the relation between participants' scores on tasks measuring their level of expertise and their neural responses to the expert object category (e.g. Gauthier et al., 2000; Gauthier & Tarr, 2002; Harley et al., 2009; Martens et al., 2018). However, none of these studies investigated the mental representational space of the individual objects of expertise in such detail, nor did they try to relate behavioral similarity judgments to the neural similarities between the response patterns of the individual objects.

In this case, we found not only a correlation between the mental (species and visual task) and neural (LVC and FL) representational space for the experts, but also for the novice group. One possible hypothesis was that the neural representational space of experts would be more related to their behavioral similarity judgments in the expertise-related species task, compared to when they performed the (unrelated) visual task. For novices the opposite could be expected, since they are guided more by the visual aspects of the birds than by species information, as was indicated by the behavioral results from chapter three. However, the demonstrated correlations reflect the presence of the large-scale bird order information that is present in the neural representational spaces of HVC and FL, of experts and novices. The absence of a difference between the two subject groups, particularly in terms of which ROIs were correlated with the mental representational spaces, suggests that the brain areas responsible for the representation of birds in bird experts already had the same overall representational content among novices. The representations become more distinctive and more consistent in experts, but show no qualitative change in what they represent. These effects might again be contingent upon the non-expertise-related task that participants were performing 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). In this case, the neural representational space resulting from the expertise-related task might be more related to the behavioral similarity judgments from the expertise-related task and vice versa. This approach would be time consuming, since enough neural data needs to be collected for each individual object of expertise in each of the two tasks.

5



General Discussion

The study of expertise helps us to understand how our neural functioning is altered by experience and learning. Experts in visual object recognition provide an excellent foundation to examine the way in which learning modifies our visual perception, both at the behavioral and the neural level.

Previous research has shown that visual expertise changes the representation of objects in the brain. These neural changes have been found in many different brain regions inside and outside of the visual cortex, with varying results across different studies. A first aim of this thesis (chapter 2) was to clarify the interaction between the specific domain of visual expertise under investigation and the underlying neural expertise effects. To this end, we compared the neural expertise-related changes for two different domains of expertise: ornithology and mineralogy.

Visual experts are very skilled at the identification of and discrimination between individual objects belonging to the same, visually homogeneous, object category. In this thesis, both behavioral and neural effects of visual expertise were examined at this more detailed level of processing. In chapter three, the influence of expertise on the perceived similarity between individual objects of expertise was explored. We compared the mental representational spaces of objects of expertise, birds, for both bird experts and novices. The final objective of this thesis was to investigate the representational space of the objects of expertise at the neural level (chapter 4). We compared the neural responses elicited by the individual objects of expertise in both experts and novices. This was the first study in which neural effects of visual expertise were examined at such a fine scale. Moreover, we compared the neural representational spaces of both experts and novices to their mental representational spaces that were presented in chapter three.

In the first part of this general discussion I will present the main findings and implications of the studies described above, as well as the strengths of the applied methodology and the limitations. Furthermore, a broader view of neural effects of expertise in general will be discussed. Finally, some suggestions for future research are offered.

5.1 MAIN FINDINGS AND IMPLICATIONS

5.1.1 Expertise-related neural changes for different domains of expertise

In the first study presented in this dissertation, we conducted a large-scale fMRI study to systematically compare the neural expertise effects related to two domains of visual expertise: ornithology and mineralogy. Both univariate and multivariate analyses were used to probe the neural responses to the respective expert object categories (birds and minerals) and to compare these responses to each other and to a third group of control participants. These neural changes were investigated at the whole-brain level, so as not to miss any potential expertise effects.

Both univariate and multi-voxel pattern analyses demonstrated the presence of large-scale distributed effects of expertise for ornithology. These effects were spread out across low-level and high-level visual areas, including all of the functionally defined ROIs, and extended into the frontal lobe. In comparison, the expertise effects underlying the domain of mineralogy were far more modest: multivariate effects were found in high-level visual areas, but univariate analyses did not indicate a general expertise-related increase of response anywhere in the brain. The bird and mineral expertise effects did not only differ in effect size, we also found that the peak voxel of activation for the two domains were in different locations in the high-level visual cortex. Moreover, a multivariate generalization analysis indicated that the effects for the two domains of expertise that were found in the high-level visual area were domain-specific. These results indicate that different domains of expertise induce different expertise-related neural changes. Therefore, it is not surprising that the large body of literature investigating the neural correlates of many different domains of visual expertise has generated such widely differing results (for reviews, see: Curby & Gauthier, 2010; Harel, Kravitz, & Baker, 2013; McKone & Kanwisher, 2005).

Contrary to the domain-specific expertise effects in the high-level visual area, we found evidence for domain-general effects in the frontal lobe, meaning that the neural changes elicited by the two different domains of expertise in this ROI significantly overlapped. The fact that the expertise effects even extended into the frontal lobe, indicates that expertise causes changes in neural processing that are widespread and distributed inside and outside of visual regions, rather than inducing dramatic local changes in neural responses. This contradicts the expertise hypothesis, which predicts that expertise-related neural changes are restricted to local populations of neurons, more specifically in the FFA (Gauthier et al., 2000, 1999; Gauthier & Tarr, 1997; Sigala & Logothetis, 2002). The results of this study are more in line with the interactive view on expertise; not only did we demonstrate the presence of widespread neural changes, both inside and outside the FFA, the effects in the frontal lobe also suggest the involvement of top-down factors. Furthermore, the fact that different domains cause different kinds of expertise effects signifies that expertise-related neural changes are at least in part domain-specific and are therefore not (solely) process-specific, as suggested by the expertise hypothesis. Note that this does not exclude the involvement of a specific type of expert processing, like for example holistic processing. We did not explicitly test the two expert groups for holistic processing of their expert object category.

5.1.2 Mental representational space of objects of expertise

In chapter three, we examined the influence of expertise on the mental representational space of objects of expertise by comparing the similarity spaces of these objects created by both experts and novices. Perceptual similarity between exemplars is an important notion in the field of categorization and perceptual learning and has been extensively studied. Nevertheless, this is the first study to examine perceptual similarity of objects belonging to a real-world domain of expertise.

Both experts and novices provided similarity judgments of a select set of birds in two multiple object arrangement tasks: an expertise-related task in which participants were asked to arrange the birds based on their taxonomy and a non-related task in which the birds had to be arranged according to purely visual features. Based on these similarity judgments we created representational dissimilarity matrices for the two tasks and for both subject groups.

First of all, we found a quantitative effect of expertise: the arrangements made by experts were more consistent compared to those made by novices, and this was true for both tasks. It is remarkable that even in the non-related visual task, for which no special knowledge of birds was necessary, experts judged the similarity between the different birds in a more consistent manner compared to novices. Research has shown that naming or labelling objects can affect the perceptual similarity and categorization of these objects (e.g. Hendrickson, Kachergis, Gureckis, & Goldstone, 2010; Lupyan, 2009; Winawer et al., 2007). The label can be seen as a feature of the object which influences similarity judgments in a quantifiable manner (Sloutsky, Lo, & Fisher, 2001). Furthermore, it has been proposed that domain-specific knowledge about relevant dimensions is necessary to discern similarity between objects (Sloutsky et al., 2001; Wellman & Gelman, 1992). In our experiment, we tested whether experts and novices were able to name the birds that were included in the MOA tasks. Experts were familiar with the large majority of the used stimuli, while novices were not able to label the birds. The fact that experts possessed knowledge of the labels of the stimuli could have influenced their similarity judgments, even in a purely perceptual task. This could explain the discrepancy in consistency of the arrangements between the two groups in the non-related task.

Apart from the quantitative difference between the two subject groups, we also showed the presence of qualitative differences in the form of more fine-grained, subordinate-level distinctions in the experts’ mental representational space when performing an expertise-related task. Contrary to novices, experts were able to consistently distinguish between the birds at the intermediate level of the bird families and at the subordinate level of bird species. Subordinate-level processing is the (behavioral) signature of visual expertise (Tanaka & Taylor, 1991). Research has shown that training to discriminate stimuli belonging to different categories can induce a within-category perceptual effect: exemplars belonging to the same category but to differing sub-clusters within that category also become better distinguishable (Gureckis & Goldstone, 2008). Additionally, when learning to categorize objects, the stimulus dimensions that successfully predict categorization acquire distinctiveness, while other features that are less relevant are de-emphasized (Folstein, Palmeri, & Gauthier, 2014; Goldstone, 1994b, 1998; Livingston & Andrews, 1995; Nosofsky, 1986). In our study, experts appeared to attach less importance to a priori salient features such as color when performing the expertise-related task, and more importance to subtle features which discriminate between the birds based on their taxonomy and which were not evident to novices. It could be that these changes are entirely due to strategic choices. However, it could also be the case that they are not completely voluntary (Goldstone, 1998). The different use of dimensions by experts in the expertise-related task, resulting in structural changes in the mental representational space, appeared to not be a purely voluntary choice but also reflected a change in perception. We found evidence for this in the results of the non-related, visual task: experts still took taxonomy of the birds into account (at the level of the bird species) when they were asked to arrange the birds based on purely visual features, even though that was not particularly helpful, suggesting that they did so unknowingly.

5.1.3 Neural expertise effects at the subordinate level

In the final study presented in this dissertation, we applied MVPA and representational similarity analyses to investigate the neural representational space of objects of expertise for the two subject groups in low-level visual cortex, high-level visual cortex and the frontal lobe. This was not only the first study to investigate neural responses at the subordinate level in a real-world domain of expertise, it was also the first study to demonstrate that MVPA can be used to distinguish between individual objects belonging to the same animate category.

Similar to the mental representational spaces presented in chapter three, we found evidence for hierarchical representations of multiple levels (bird order and family) that differentiate birds and that differ between brain regions. The neural representations of objects of expertise were enhanced in a quantitative manner in experts compared to novices. The representational spaces in the higher-level regions showed a higher consistency in the expert group. This was in line with the behavioral results, which also showed a higher consistency between the similarity arrangements made by the experts. Furthermore, the experts' neural response patterns for the individual objects of expertise in the frontal lobe were more distinctive compared to those of novices. Several studies have suggested that perceptual expertise enables more efficient mental representations of information and enhances the ability to store more detailed representations in working memory (Gobet et al., 2001; Humphreys, Hodsoll, & Campbell, 2005; Scolari, Vogel, & Awh, 2008). Furthermore, Moore and colleagues (2006) have linked improved working memory performance for objects of expertise to increased responses in lateral prefrontal cortex. Therefore, the more distinctive neural representations that were found in the frontal lobe of experts could represent the more efficient mental representations in working memory for objects of expertise.

The overall structure of the neural representational spaces in the three ROIs was not altered by expertise. This was in line with results from the first study which showed that expertise did not influence the representational similarity between the expert object category and other non-expert categories. However, visual expertise consists of the ability to make detailed within-category discriminations instead of discriminating the expert object category from other, unrelated, categories. Furthermore, the mental representational spaces of the same birds created by the experts and novices did show a clear effect of expertise on the overall structure, particularly in the expertise-related task. In section 4.4.1 of this thesis, we discussed two factors that might explain the absence of structural changes in the neural representational spaces.

5.2 METHODOLOGICAL STRENGTHS AND LIMITATIONS

5.2.1 Methodological strengths

Throughout this dissertation we applied a wide array of different methods to probe the behavioral and neural correlates of visual expertise. The combination of behavioral and neuroimaging techniques ensured a high external validity (Gegenfurtner, Kok, Van Geel, De Bruin, & Sorger, 2017) and allowed us to significantly extend our current knowledge. In the second and third study (chapters 3 and 4) we implemented a very similar paradigm, one behavioral version and one neuroimaging version, and we used the exact same stimuli. This allowed us to make a direct comparison between the way in which visual expertise is expressed at the behavioral and the neural level. Several other studies have related the neural responses to the expert object category to behavioral measures of expertise, like we also did in the first study (e.g. Gauthier et al., 2000; Gauthier & Tarr, 2002; Harley et al., 2009; McGugin, Gatenby, Gore, & Gauthier, 2012; McGugin, Van Gulick, Tamber-Rosenau, Ross, & Gauthier, 2015). However, never before has such a linear comparison been made between the behavioral and neural representations of objects of expertise.

Particularly at the neural level, we introduced some methodological innovations into the field of visual expertise. So far, most studies that looked into the neural basis of visual expertise have used univariate techniques to measure the average neural response to a specific expert object category (e.g. Bilalić, Langner, Ulrich, & Grodd, 2011; Gauthier et al., 2000; Gauthier & Tarr, 2002; Haller & Radue, 2005; Harel, Gilaie-Dotan, Malach, & Bentin, 2010; Harley et al., 2009; McGugin, Gatenby, Gore, & Gauthier, 2012; McGugin, Newton, Gore, & Gauthier, 2014; Xu, 2005). More recently, some studies have also applied multivariate methods to compare the neural response patterns of experts and novices (e.g. Bilalić, 2016; Bilalić, Grottenthaler, Nagele, & Lindig, 2014; Floyd, Santander, & Weimer, 2017). In the first study described in this dissertation, we used a combination of both univariate and multivariate analyses to probe the neural activation underlying bird and mineral expertise (other studies that also combined univariate and multivariate methods are: Bilalić, 2016; Bilalić et al., 2014). As already described in the introduction (section 1.3.3): multivariate analyses provide an answer to the limitations of univariate analyses, they can uncover effects that would otherwise remain undetected. This was also the case in our study: using univariate analyses, we were not able to indicate the presence of expertise-related neural changes underlying mineral expertise. However, multi-voxel pattern analyses, in the form of a subject classification and generalization paradigm, clearly showed an effect of mineral expertise on the neural response patterns underlying the expert object category in the high-level visual region and in the frontal lobe.

Some of the analyses we used to investigate expertise-related neural activation were never before applied in the field of visual expertise. This was true for the subject classification analysis and the generalization analysis (which have been used in different fields: e.g. Bulthé et al., 2018; Peters, Bulthé, Daniëls, Op de Beeck, & De Smedt, 2018). A similar approach to the subject generalization analysis was implemented in the study by Bilalić and colleagues (2014). They tested generalization across two different categories (faces and X-rays) within a group of radiologists (and a group of medical students) to uncover any shared processes. This method differed from our approach in the sense that we generalized across categories and across subject groups. Our results showed that the subject generalization analysis is a very promising method to uncover similar neural (multivariate) mechanisms that are at work in different subject groups and that might express themselves in a different way at the behavioral level.

A final methodological strength lies in the number of participants that were included in the different studies. Our first study consisted of three subject groups of 20, 20 and 17 participants respectively, creating a total of 57 participants. Also in the remaining two studies, two subject groups of 20 participants each were compared. The sample sizes of a lot of studies investigating the neural correlates of expertise were smaller (between 6 and 15 participants per subject group; e.g. Bilalić et al., 2011; Gauthier et al., 2000; Harel et al., 2010; Harley et al., 2009; Krawczyk, Boggan, McClelland, & Bartlett, 2011; Xu, 2005). Only in more recent years a trend towards larger sample sizes has become evident (between 12 and 24 participants per group; e.g. Bilalić, 2016; Bilalić et al., 2014; Mongelli et al., 2017). Increasing the sample size improves the power of the study (Button et al., 2013; Zandbelt et al., 2008). Even so, it remains important to carefully select participants and to ensure that the collected data is of high quality (e.g. discard runs with too much motion), as well as applying the correct corrections (Lieberman & Cunningham, 2009).

5.2.2 Limitations

In the discussion sections of the experimental chapters (2, 3 and 4), we already described limitations that are specific to the presented study. In this section, limitations that are relevant for multiple chapters are discussed.

Throughout this dissertation we described several results pointing towards top-down influences of expertise, both at the behavioral and at the neural level. In chapters 2 and 4 we demonstrated the presence of neural expertise effects in the frontal lobe, suggesting the involvement of attentional control and conceptual knowledge (Corbetta & Shulman, 2002; Harel, 2015, 2016; Harel et al., 2010). However, these results can only provide indirect evidence, since we did not explicitly test the influence of top-down factors on the neural responses underlying objects of expertise. A few studies have applied task manipulations to investigate whether top-down controlled mechanisms modulate the neural expression of expertise; they compared tasks in which objects of expertise were either task-relevant or -irrelevant (Harel et al., 2010), tasks with a high or low cognitive load (McGugin et al., 2014) or tasks with or without added clutter (McGugin et al., 2015). Overall, these studies showed that neural expertise effects were still present when attention was diverted away from the objects of expertise, albeit to a (far) lesser extent compared to when objects of expertise were directly attended. In the studies presented in this dissertation, we were not able to implement task manipulations due to practical constraints. However, it would have added a very interesting aspect, especially in the study described in the fourth chapter. Our results indicated that the structure of the neural representational space of objects of expertise was no different in experts compared to novices. However, the participants were not explicitly asked to perform an expertise-related task. One possibility would have been to ask both experts and novices to perform two separate tasks: one expertise-related task in which attention would be maximally engaged by the actual objects of expertise (e.g. judge the similarity between two subsequent birds based on their taxonomy). The second task would have served to divert attention away from the actual objects of expertise (e.g. judge the similarity of size between two subsequently presented stimuli).

This brings us to the second limitation: the apparent null results that were found (or not found) in the two neuroimaging studies. One of these null results was just mentioned; the absence of expertise-related structural changes in the neural representational space of experts. However, absence of evidence does not necessarily mean evidence of absence. In the case of the lack of structural changes in the neural representational space, different possible explanations have already been addressed. A second analysis which apparently demonstrated a null result were the whole-brain and ROI-based univariate analyses of mineral expertise effects described in chapter two. These analyses seemed to demonstrate that there were no expertise-related neural changes for mineral expertise present in the low-level visual region, the high-level visual region or the frontal lobe. Again, this absence of evidence did not mean evidence of absence, as was demonstrated by the significant multivariate changes related to mineral expertise in (some of) these brain regions. These apparent null results might be a consequence of a lack of power. Even though we tried to include a large number of participants in the different studies, research has shown that the statistical power of studies in the neurosciences is very low, partly because the effect size of relatively complex cognitive processes is rather small (Button et al., 2013; Ioannidis, 2005).

This emphasizes the importance of replication studies and systematic reviews. Up until now, no large-scale meta-analyses have been performed in the field of visual expertise.

5.3 THE BIGGER PICTURE

In this dissertation, we focused on the neural changes underlying visual expertise. In chapter two, we demonstrated the presence of domain-specific neural changes in high-level visual cortex as well as domain-general neural changes in the frontal lobe, for two domains of visual expertise. However, as was already described in the introduction, many other types of (perceptual) expertise exist outside of the visual domain and they all leave their specific neural marks (Bilalić, 2017; Bilalić, Langner, Campitelli, Turella, & Grodd, 2015). In this section, I will demonstrate by means of some examples that the finding that visual expertise is supported by a combination of domain-specific and domain-general changes in neural processing, can be extended to other domains of expertise.

Different fields of expertise can be found in all the sensory modalities (vision, hearing, smell, taste and touch). In most of these widely varying domains neural expertise effects can be found in those brain regions that are relevant for the specific domain (domain-specific effects) as well as in brain-regions that support more general high-level cognitive functions like attentional control and retrieval of conceptual knowledge. These domain-general effects are generally situated in prefrontal cortex.

Auditory expertise is, besides visual expertise, one of the more extensively researched domains. Researchers investigating auditory expertise have mainly focused on musicians, both at the behavioral and at the neural level (e.g. overviews: Peretz & Zatorre, 2003, 2005; Sloboda, 1991). Research has shown that musicians with absolute or relative pitch (the ability to identify a tone) engage the superior temporal sulcus (STS) and the inferior frontal gyrus, which are part of the dorsal and ventral auditory streams respectively, when performing an expertise-related task (Zatorre, Perry, Beckett, Westbury, & Evans, 1998). Neural responses when listening to piano tones are larger in the auditory cortex of musicians compared to nonmusicians, and this domain-specific effect appears to be more pronounced for tones from each musician's own type of instrument (Pantev, Engelien, Candia, & Elbert, 2003; Tervaniemi, 2003). Neural effects of musical expertise that reflect more domain-general processes were found in DLPFC (Zatorre et al., 1998). This region has, among other things, been associated with attributing a verbal label, in this case to a musical note (Bermudez & Zatorre, 2005; see also section 5.1.2). Furthermore, level of musical improvisation training was associated with functional connectivity of DLPFC, premotor cortices and presupplementary areas. This last finding demonstrates that musical expertise is not purely restricted to the auditory domain, it can also induce expertise-related changes in motor performance and in visual regions (reading of musical notation; e.g. Mongelli et al., 2017; Wong & Gauthier, 2010).

A second domain in which neural expertise-related changes are found is olfactory expertise (for an overview of behavioral and neural effects, see Royet, Plailly, Saive, Veyrac, & Delon-Martin, 2013). Plailly, Delon-Martin and Royet (2012) compared expert perfumers to novices while they were imagining odors. They found that expertise was negatively correlated with activation in the piriform cortex (primary olfactory cortex) as well as in brain regions involved in memory and the formation of complex sensory associations (OFC and hippocampus).

Gustatory expertise is closely related to olfactory expertise and very few studies have focused on the neural correlates of expertise in taste. Castriato-Scanderbeg and colleagues (2005) demonstrated that brain regions involved in taste, like the insula and orbitofrontal cortex (OFC) were activated in both sommeliers and in novices when tasting wine. However, effects of expertise were mainly expressed through a higher activation of DLPFC. The only other study to ever compare the neural activations of experts in wine tasting (or any other domain of gustatory expertise) to those of novices found expertise-related activations in a whole set of brain regions, including the insula (Pazart, Comte, Magnin, Millot, & Moulin, 2014). Furthermore, they showed an overall reduction of activated brain regions in experts compared to novices.

Finally, tactile expertise in itself is difficult to investigate, since touch perception is usually accompanied by or even dominated by visual perception. Therefore, expertise in touch perception is usually studied in the blind. However, the perception of tactile stimuli by blind people does not primarily activate the somatosensory cortex like in sighted people, it also elicits activation in the low-level and high-level visual cortex (e.g. Sadato et al., 1996; Sadato, Okada, Kubota, & Yonekura, 2004), and the same is true for auditory stimuli (van den Hurk, Van Baelen, & Op de Beeck, 2017). Reading Braille, which requires fine-grained discriminations between tactile dot patterns, is a specific domain of tactile expertise in which blind people are very proficient. Therefore, the differences in neural activation in the visual cortex between blind participants and blindfolded sighted participants that discriminate tactile dot patterns represent domain-specific effects of tactile expertise. For example: increased activation has been found in lateral occipital cortex and fusiform cortex (Cattaneo et al., 2014). Furthermore, domain-general neural effects have also been found in DLPFC, which showed a more extensive activation in the blind compared to sighted people (Cattaneo et al., 2014). A recent study in which sighted participants underwent a short-term tactile training of Braille reading and were scanned before and after training, indicated that the strongest domain-specific effects of expertise were to be find in primary somatosensory cortex, contrary to the results shown in the blind (Debowska et al., 2016). Outside of the somatosensory system, they also demonstrated changes in the fusiform gyrus, the medial frontal gyri and inferior parietal lobule.

This short overview illustrates that also for very different fields of expertise, domain-specific and domain-general expertise effects can be found in the brain. The presence of domain-general effects were indicated by the expertise-related neural changes that can be found in prefrontal cortex. However, note that none of the above-mentioned studies explicitly tested whether the expertise effects in prefrontal cortex represented similar or overlapping processes between different types of expertise, like we demonstrated for ornithology and mineralogy in chapter two.

5.4 SUGGESTIONS FOR FUTURE RESEARCH

In this dissertation we used a variety of different paradigms and state-of-the-art analyses to improve our understanding of the neural basis of visual expertise. However, some questions remain unexplored and form the basis of potentially fruitful further research.

5.4.1 Additional examination of subordinate-level neural effects

In chapter four we provided significant new insights into the influence of expertise on the neural representational space of objects of expertise in low-level visual cortex, high-level visual cortex and the frontal lobe using methods that are novel to the field. Inevitably, our findings also raised new questions. It would be interesting to extend the current findings in two different ways. The first way to extend the study was already described in the limitations section (5.2.2): the implementation of a task manipulation to directly investigate the influence of top-down factors on the neural representational space of objects of expertise. To increase the chances of finding top-down expertise-related changes, it is important to maximize the difference in attentional engagement and relevance of conceptual knowledge between the expertise-related task and a non-related task, for example by using a non-related task that does not revolve around the actual objects of expertise (e.g. Harel et al., 2010).

Secondly, it would be interesting to investigate potential quantitative or qualitative neural changes in the representations of individual objects of expertise in different category-selective ROIs. In chapter two, we already demonstrated that FFA, LO, pFs, PPA, a Living and a Nonliving region all show neural expertise effects for the expert object category of birds and are therefore relevant to investigate. Even though all these regions were influenced by expertise, it could be the case that expertise effects at the more fine-grained, subordinate level are more pronounced in those regions that are the most informative for the domain of expertise. This would be in line with the finding that the heightened activation for the bird category in bird experts compared to novices was positively correlated with the general selectivity for birds across the different ROIs (see Fig. 2.7C). Note that discriminating between neural representations of different objects that are visually homogeneous using multi-voxel analyses is a difficult task that has only been accomplished in very few studies. As we already demonstrated in chapter two (section 2.5.2), applying MVPA in smaller ROIs with a limited number of voxels generates less reliable results compared to larger ROIs, meaning that this analysis might encounter the limits of MVPA.

A different way to identify smaller brain regions where quantitative or structural changes in the neural representational space of objects of expertise can be found, is by using a searchlight analysis (Kriegeskorte, Goebel, & Bandettini, 2006). Bilalić and colleagues (2014) used the searchlight technique to identify brain regions related to radiological expertise. They found a large number of brain areas that showed expertise effects, in occipitotemporal regions (e.g. fusiform gyrus, middle temporal gyrus, middle occipital gyrus), frontal regions (e.g. inferior frontal gyrus) and others. In their study, the neural activation underlying the expert object category (X-rays) was investigated, while in the case of our study, we would apply a searchlight analysis to examine the neural representations of the individual objects of expertise. The searchlight analysis could also be used to differentiate between brain regions in experts where the correlation between the neural representational space and the mental representational space of the expertise-related task is higher compared to the non-related task and vice versa.

5.4.2 Expertise-related functional connectivity

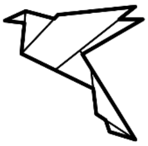
In this dissertation, we only focused on expertise-related neural changes in separate brain regions, without taking into account that the interplay between different brain regions might be influenced by expertise as well. With functional connectivity analyses it is possible to investigate the way in which neural responses in different brain regions are related to each other, by calculating the correlation between the timeseries of the neural responses in the different regions. Functional connectivity analyses can be performed on resting-state fMRI data (e.g. Fauvel et al., 2014; Lotze, Erhard, Neumann, Eickhoff, & Langner, 2014), as well as on task-related activation.

Mongelli and colleagues (2017) compared the task-related functional connectivity of expert musicians and control participants looking at stimuli with musical notation. They demonstrated that a set of fronto-temporo-parietal regions was functionally connected to a region in visual cortex selective for musical notation, and that this network was stronger and more extensive in musicians compared to control participants. They concluded that musical expertise ensured the development of functional connectivity between a visual “music region” and areas involved in auditory, semantic or motor knowledge. Furthermore, expertise in musical improvisation was also found to be positively associated with functional connectivity of DLPFC, dorsal premotor cortices and presupplementary areas (Pinho, de Manzano, Fransson, Eriksson, & Ullen, 2014). Similar results, meaning an increase in functional connectivity in experts compared to novices among task- and domain-related brain regions and frontal regions, were also found for professional race-car drivers (Bernardi et al., 2013, 2014).

The influence of a domain of visual expertise on the functional connectivity between domain-related brain regions has not been studied often, even though functional connectivity seems to be prominent in other domains of expertise. Therefore, it would be interesting to investigate whether visual expertise increases the task-related functional connectivity between brain regions that are relevant for the specific domain of expertise. It is important to identify a set of brain regions that might be relevant for the domain of expertise in visual cortex, e.g. LOC, FFA and early visual regions, as well as frontal regions like DLPFC, which has popped up in many different studies of (visual) expertise. Furthermore, an additional task manipulation (expertise-related vs. non-related task) might offer additional insights into the mechanisms of functional connectivity in visual expertise: it could be the case that increases in connectivity are more prominent and more extensive for task-related neural activation induced by an expertise-related task compared to a non-related task. Finally, it is important to note that since functional connectivity is essentially a correlation between the neural activation in different brain regions, no conclusions can be made about the direction or the causality of the connectivity between two brain regions.

5.4.3 Conclusion

These suggestions for future research offer additional ways to increase our insights into the neural correlates of visual expertise, and to further our understanding of learning effects on the sensory cortices in general. Although research on expertise-related neural changes underlying the category of (visual) expertise has been well developed, we have only scratched the surface when it comes to subordinate-level neural changes of expertise. Furthermore, only by combining different behavioral and neural methods like behavioral discrimination, similarity judgments, univariate whole-brain and ROI analyses of neural data, correlational and decoding multivariate analyses, functional connectivity, searchlight analyses, structural analyses and so on, can we advance our comprehension of the neural basis of expertise and ultimately of the functionality of the brain in general.



References

Bartels, A., & Zeki, S. (2000). The architecture of the colour centre in the human visual brain: new results and a review. *The European Journal of Neuroscience*, *12*(1), 172–193. https://doi.org/DOI 10.1046/j.1460-9568.2000.00905.x

Bartlett, J. C., Boggan, A. L., & Krawczyk, D. C. (2013). Expertise and processing distorted structure in chess. *Frontiers in Human Neuroscience*, *7*(December), 1–11. https://doi.org/10.3389/fnhum.2013.00825

Behrmann, M., Marotta, J., Gauthier, I., Tarr, M. J., & McKeeff, T. J. (2005). Behavioral Change and Its Neural Correlates in Visual Agnosia After Expertise Training. *Journal of Cognitive Neuroscience*, *17*(4), 554–568.

Bermudez, P., & Zatorre, R. J. (2005). Conditional Associative Memory for Musical Stimuli in Nonmusicians: Implications for Absolute Pitch. *Journal of Neuroscience*, *25*(34), 7718–7723. https://doi.org/10.1523/JNEUROSCI.1560-05.2005

Bernardi, G., Cecchetti, L., Handjaras, G., Sani, L., Gaglianese, A., Ceccarelli, R., … Pietrini, P. (2014). It's not all in your car: functional and structural correlates of exceptional driving skills in professional racers. *Frontiers in Human Neuroscience*, *8*(November), 1–12. https://doi.org/10.3389/fnhum.2014.00888

Bernardi, G., Ricciardi, E., Sani, L., Gaglianese, A., Papasogli, A., Ceccarelli, R., … Pietrini, P. (2013). How Skill Expertise Shapes the Brain Functional Architecture: An fMRI Study of Visuo-Spatial and Motor Processing in Professional Racing-Car and Naïve Drivers. *PLoS ONE*, *8*(10), 1–11. https://doi.org/10.1371/journal.pone.0077764

Bilalić, M. (2016). Revisiting the Role of the Fusiform Face Area in Expertise. *Journal of Cognitive Neuroscience*, *28*(9), 1345–1357. https://doi.org/10.1162/jocn

Bilalić, M. (2017). *The Neuroscience of Expertise*. Cambridge University Press.

Bilalić, M., Grottenthaler, T., Nagele, T., & Lindig, T. (2014). The Faces in Radiological Images: Fusiform Face Area Supports Radiological Expertise. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhu272

Bilalić, M., Kiesel, A., Pohl, C., Erb, M., & Grodd, W. (2011). It takes two-Skilled recognition of objects engages lateral areas in both hemispheres. *PLoS ONE*, *6*(1), 20–21. https://doi.org/10.1371/journal.pone.0016202

Bilalić, M., Langner, R., Campitelli, G., Turella, L., & Grodd, W. (2015). Editorial: Neural implementation of expertise. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00545

Bilalić, M., Langner, R., Erb, M., & Grodd, W. (2010). Mechanisms and neural basis of object and pattern recognition: a study with chess experts. *Journal of Experimental Psychology: General*, *139*(4), 728. https://doi.org/10.1111/ijlh.12426

Bilalić, M., Langner, R., Ulrich, R., & Grodd, W. (2011). Many Faces of Expertise: Fusiform Face Area in Chess Experts and Novices. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.5727-10.2011

Bilalić, M., Turella, L., Campitelli, G., Erb, M., & Grodd, W. (2012). Expertise modulates the neural basis of context dependent recognition of objects and their relations. *Human*

Brain Mapping, *33*(11), 2728–2740. https://doi.org/10.1002/hbm.21396

Boggan, A. L., Bartlett, J. C., & Krawczyk, D. C. (2012). Chess masters show a hallmark of face processing with chess. *Journal of Experimental Psychology: General*, *141*(1), 37–42. https://doi.org/10.1037/a0024236

Bracci, S., Ietswaart, M., Peelen, M. V., & Cavina-Pratesi, C. (2010). Dissociable Neural Responses to Hands and Non-Hand Body Parts in Human Left Extrastriate Visual Cortex. *Journal of Neurophysiology*, *103*(6), 3389–3397. https://doi.org/10.1152/jn.00215.2010

Bracci, S., & Op de Beeck, H. (2016). Dissociations and Associations between Shape and Category Representations in the Two Visual Pathways. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.2314-15.2016

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*. https://doi.org/10.1163/156856897X00357

Brants, M., Bulthé, J., Daniels, N., Wagemans, J., & Op de Beeck, H. (2016). How learning might strengthen existing visual object representations in human object-selective cortex. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2015.11.063

Brants, M., Wagemans, J., & Op de Beeck, H. (2011). Activation of Fusiform Face Area by Greebles Is Related to Face Similarity but Not Expertise. *Journal of Cognitive Neuroscience*, *23*(12), 3949–3958. https://doi.org/10.1162/jocn_a_00072

Bulthé, J., De Smedt, B., & Op de Beeck, H. (n.d.). Visual Number Beats Abstract Numerical Magnitude: Format-dependent Representation of Arabic Digits and Dot Patterns in Human Parietal Cortex. https://doi.org/10.1162/jocn_a_00787

Bulthé, J., Prinsen, J., Vanderauwera, J., Duyck, S., Daniels, N., Gillebert, C. R., … De Smedt, B. (2018). Multi-method brain imaging reveals impaired representations as well as altered connectivity in adults with dyscalculia. *NeuroImage*. https://doi.org/10.1101/162115

Burton, A. M., Schweinberger, S. R., Jenkins, R., & Kaufmann, J. M. (2015). Arguments against a configural processing account of familiar face recognition. *Perspectives on Psychological Science*, *10*(4), 482–496. https://doi.org/10.1177/1745691615583129

Button, K. S., Ioannidis, J. P. A., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafò, M. R. (2013). Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, *14*(5), 365–376. https://doi.org/10.1038/nrn3475

Byers, A., & Serences, J. T. (2012). Exploring the relationship between perceptual learning and top-down attentional control. *Vision Research*, *74*, 30–39. https://doi.org/10.1016/j.visres.2012.07.008

Castriota-Scanderbeg, A., Hagberg, G. E., Cerasa, A., Committeri, G., Galati, G., Patria, F., … Frackowiak, R. (2005). The appreciation of wine by sommeliers: A functional magnetic resonance study of sensory integration. *NeuroImage*, *25*(2), 570–578. https://doi.org/10.1016/j.neuroimage.2004.11.045

Cattaneo, Z., Bona, S., Bauer, C., Silvanto, J., Herbert, A. M., Vecchi, T., & Merabet, L. B.

(2014). Symmetry detection in visual impairment: Behavioral evidence and neural correlates. *Symmetry*, *6*(2), 427–443. https://doi.org/10.3390/sym6020427

Chang, C.-C., & Lin, C.-J. (2011). LIBSVM. *ACM Transactions on Intelligent Systems and Technology*. https://doi.org/10.1145/1961189.1961199

Cohen, A. L., Nosofsky, R. M., & Zaki, S. R. (2001). Category variability, exemplar similarity, and perceptual classification. *Memory and Cognition*, *29*(8), 1165–1175. https://doi.org/10.3758/BF03206386

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.-A., & Michel, F. (2000). The visual word form area Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*, *123*, 291–307.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

Curby, K. M., & Gauthier, I. (2010). To the trained eye: Perceptual expertise alters visual processing. *Topics in Cognitive Science*. https://doi.org/10.1111/j.1756-8765.2009.01058.x

D’Lauro, C., Tanaka, J. W., & Curran, T. (2008). The preferred level of face categorization depends on discriminability. *Psychonomic Bulletin and Review*. https://doi.org/10.3758/PBR.15.3.623

Debowska, W., Wolak, T., Nowicka, A., Kozak, A., Szwed, M., & Kossut, M. (2016). Functional and structural neuroplasticity induced by short-term tactile training based on braille reading. *Frontiers in Neuroscience*, *10*(OCT), 1–13. https://doi.org/10.3389/fnins.2016.00460

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, *56*(2), 384–398. https://doi.org/10.1016/j.neuron.2007.10.004

Downing, P. E., Chan, A., Peelen, M. V., Dodds, C. M., & Kanwisher, N. G. (2006). Domain Specificity in Visual Cortex. *Cerebral Cortex*, *16*(10), 1453–1461. https://doi.org/10.1093/cercor/bhj086

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. G. (2001). A Cortical Area Selective for Visual Processing of the Human Body. *Science*, *293*(5539), 2470–2473. https://doi.org/10.1126/science.1063414

Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test : Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants, *44*, 576–585. https://doi.org/10.1016/j.neuropsychologia.2005.07.001

Edelman, S. (1998). Representation is representation in form of similarities. *Behavioral and Brain Science*, *21*(May 2018), 449–498.

Eger, E., Ashburner, J., Haynes, J.-D., Dolan, R. J., & Rees, G. (2008). fMRI Activity Patterns in Human LOC Carry Information about Object Exemplars within Category. *Journal of Cognitive Neuroscience*. https://doi.org/10.1162/jocn.2008.20019

Epstein, R., & Kanwisher, N. G. (1998). A cortical representation of the local visual environment. *Nature*, *392*, 598–601.

Ericsson, K. A., Krampe, R. T., & Tesch-Römer, C. (1993). The role of deliberate practice in the acquisition of expert performance. *Psychological Review*, *100*(3), 363–406. https://doi.org/10.1037//0033-295X.100.3.363

Ericsson, K. A., & Lehmann, A. C. (1996). Expert and Exceptional Performance: Evidence of Maximal Adaptation to Task Constraints. *Annual Review of Psychology*. https://doi.org/10.1146/annurev.psych.47.1.273

Fahle, M. (2005). Perceptual learning: Specificity versus generalization. *Current Opinion in Neurobiology*, *15*(2), 154–160. https://doi.org/10.1016/j.conb.2005.03.010

Fauvel, B., Groussard, M., Chételat, G., Fouquet, M., Landeau, B., Eustache, F., … Platel, H. (2014). Morphological brain plasticity induced by musical expertise is accompanied by modulation of functional connectivity at rest. *NeuroImage*, *90*, 179–188. https://doi.org/10.1016/j.neuroimage.2013.12.065

Fenske, M. J., Aminoff, E., Gronau, N., & Bar, M. (2006). Chapter 1 Top-down facilitation of visual object recognition: object-based and context-based contributions. *Progress in Brain Research*. https://doi.org/10.1016/S0079-6123(06)55001-0

Fine, I., & Jacobs, R. A. (2002). Comparing perceptual learning tasks: a review. *Journal of Vision*, *2*(2), 190–203. https://doi.org/10:1167/2.2.5

Floyd, B., Santander, T., & Weimer, W. (2017). Decoding the Representation of Code in the Brain: An fMRI Study of Code Review and Expertise. In *Proceedings - 2017 IEEE/ACM 39th International Conference on Software Engineering, ICSE 2017*. https://doi.org/10.1109/ICSE.2017.24

Folstein, J. R., Gauthier, I., & Palmeri, T. J. (2012). How category learning affects object representations: Not all morphspaces stretch alike. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(4), 807. https://doi.org/10.1037/a0025836.How

Folstein, J. R., Palmeri, T. J., & Gauthier, I. (2013). Category learning increases discriminability of relevant object dimensions in visual cortex. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhs067

Folstein, J. R., Palmeri, T. J., & Gauthier, I. (2014). Perceptual advantage for category-relevant perceptual dimensions: The case of shape and motion. *Frontiers in Psychology*, *5*(DEC), 1–7. https://doi.org/10.3389/fpsyg.2014.01394

Folstein, J. R., Palmeri, T. J., Van Gulick, A. E., & Gauthier, I. (2015). Category learning stretches neural representations in visual cortex. *Current Directions in Psychological Science*, *24*(1), 17–23. https://doi.org/10.1002/ar.20849.3D

Gauthier, I., & Curby, K. M. (2005). A Perceptual Traffic Jam on Highway N170 Interference Between Face and Car Expertise. *Current Directions in Psychological Science*, *14*(1), 30–33.

Gauthier, I., & Logothetis, N. K. (2000). Is Face Recognition Not So Unique After All? *Cognitive Neuropsychology*, *17*(1–3), 125–142.

https://doi.org/10.1080/026432900380535

Gauthier, I., McGugin, R. W., Richler, J. J., Herzmann, G., Speegle, M., & Van Gulick, A. E. (2014). Experience moderates overlap between object and face recognition, suggesting a common ability. *Journal of Vision*. https://doi.org/10.1167/14.8.7

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*(2), 191–197.

Gauthier, I., & Tarr, M. J. (1997). Becoming a “Greeble” expert: Exploring mechanisms for face recognition. *Vision Research*. https://doi.org/10.1016/S0042-6989(96)00286-6

Gauthier, I., & Tarr, M. J. (2002). Unraveling mechanisms for expert object recognition: Bridging brain activity and behavior. *Journal of Experimental Psychology: Human Perception and Performance*. https://doi.org/10.1037//0096-1523.28.2.431

Gauthier, I., Tarr, M. J., Anderson, a W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform “face area” increases with expertise in recognizing novel objects. *Nature Neuroscience*, *2*(6), 568–573. https://doi.org/10.1038/9224

Gauthier, I., Williams, P., Tarr, M. J., & Tanaka, J. (1998). Training “greeble” experts: A framework for studying expert object recognition processes. *Vision Research*, *38*(15–16), 2401–2428. https://doi.org/10.1016/S0042-6989(97)00442-2

Gegenfurtner, A., Kok, E. M., Van Geel, K., De Bruin, A. B. H., & Sorger, B. (2017). Neural correlates of visual perceptual expertise: Evidence from cognitive neuroscience using functional neuroimaging. *Frontline Learning Research*, *5*(3), 14–30. https://doi.org/10.14786/flr.v5i3.259

Gegenfurtner, A., & Seppänen, M. (2013). Transfer of expertise: An eye tracking and think aloud study using dynamic medical visualizations. *Computers and Education*, *63*, 393–403. https://doi.org/10.1016/j.compedu.2012.12.021

Gilaie-Dotan, S., Harel, A., Bentin, S., Kanai, R., & Rees, G. (2012). Neuroanatomical correlates of visual car expertise. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2012.05.017

Gilbert, C. D., Li, W., & Piech, V. (2009). Perceptual learning and adult cortical plasticity. *Journal of Physiology*, *587*(12), 2743–2751. https://doi.org/10.1113/jphysiol.2009.171488

Gillebert, R., Op de Beeck, H., Panis, S., & Wagemans, J. (2008). Subordinate Categorization Enhances the Neural Selectivity in Human Object-selective Cortex for Fine Shape Differences. *Journal of Cognitive Neuroscience*, *21*(6), 1054–1064.

Gobet, F., Lane, P. C. R., Croker, S., Cheng, P. C. H., Jones, G., Oliver, I., & Pine, J. M. (2001). Chunking mechanisms in human learning. *Trends in Cognitive Sciences*, *5*(6), 236–243. https://doi.org/10.1016/S1364-6613(00)01662-4

Goldstone, R. L. (1994a). An efficient method for obtaining similarity data. *Behavior Research Methods, Instruments, & Computers*, *26*(4), 381–386. https://doi.org/10.3758/BF03204653

Goldstone, R. L. (1994b). Influences of Categorization on Perceptual Discrimination. *Journal of Experimental Psychology: General*, *123*(2), 178–200. https://doi.org/10.1037//0096-3445.123.2.178

Goldstone, R. L. (1998). Perceptual learning. *Annual Review of Psychology*, *49*, 585–612. https://doi.org/10.1146/annurev.psych.49.1.585

Goldstone, R. L., Medin, D. L., & Gentner, D. (1991). Relational similarity and the nonindependence of features in similarity judgments. *Cognitive Psychology*, *23*(2), 222–262. https://doi.org/10.1016/0010-0285(91)90010-L

Goldstone, R. L., & Steyvers, M. (2001). The sensitization and differentiation of dimensions during category learning. *Journal of Experimental Psychology: General*, *130*(1), 116–139.

Goodale, M. a., & Milner, a. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(I), 20–25. https://doi.org/10.1016/0166-2236(92)90344-8

Greene, M. R., & Oliva, A. (2009). The briefest of glances: The time course of natural scene understanding. *Psychological Science*, *20*(4), 464–472. https://doi.org/10.1111/j.1467-9280.2009.02316.x

Greve, D. N. (2002). Optseq2.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience*. https://doi.org/10.1038/nn1224

Gureckis, T. M., & Goldstone, R. L. (2008). The effect of the internal structure of categories on perception. In *Proceedings of the 30th Annual Conference of the Cognitive Science Society* (pp. 1876–1881).

Haller, S., & Radue, E. W. (2005). What Is Different about a Radiologist's Brain? *Radiology*, *236*(3), 983–989.

Harel, A. (2015). A Neurocognitive Approach to Expertise in Visual Object Recognition. In *International Conference on Augmented Cognition* (pp. 426–436). https://doi.org/10.1007/978-3-319-20816-9_41

Harel, A. (2016). What is special about expertise? Visual expertise reveals the interactive nature of real-world object recognition. *Neuropsychologia*. https://doi.org/10.1016/j.neuropsychologia.2015.06.004

Harel, A., Gilaie-Dotan, S., Malach, R., & Bentin, S. (2010). Top-Down engagement modulates the neural expressions of visual expertise. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhp316

Harel, A., Kravitz, D., & Baker, C. I. (2013). Beyond perceptual expertise: revisiting the neural substrates of expert object recognition. *Frontiers in Human Neuroscience*. https://doi.org/10.3389/fnhum.2013.00885

Harley, E. M., Pope, W. B., Villablanca, J. P., Mumford, J., Suh, R., Mazziotta, J. C., … Engel, S. A. (2009). Engagement of fusiform cortex and disengagement of lateral occipital cortex in the acquisition of radiological expertise. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhp051

Haynes, J.-D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, *7*(523–534).

Hendrickson, A., Kachergis, G., Gureckis, T. M., & Goldstone, R. L. (2010). Is categorical perception really verbally mediated perception? In *Proceedings of the Annual Meeting of the Cognitive Science Society* (Vol. 32).

Hershler, O., & Hochstein, S. (2009). The importance of being expert: Top-down attentional control in visual search with photographs. *Attention, Perception, and Psychophysics*. https://doi.org/10.3758/APP.71.7.1478

Hoenig, K., Müller, C., Herrnberger, B., Sim, E. J., Spitzer, M., Ehret, G., & Kiefer, M. (2011). Neuroplasticity of semantic representations for musical instruments in professional musicians. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2011.02.065

Hsiao, J. H., & Cottrell, G. W. (2009). Not all expertise is holistic, but it may be leftist: The case of Chinese character recognition. *Psychological Science*, *20*(4), 455–463.

Humphreys, G. W., Hodsoll, J., & Campbell, C. (2005). Attending but not seeing: The “other race” effect in face and person perception studied through change blindness. *Visual Cognition*, *12*(1), 249–262. https://doi.org/10.1080/13506280444000148

Huth, A. G., Nishimoto, S., Vu, A. T., & Gallant, J. L. (2012). A Continuous Semantic Space Describes the Representation of Thousands of Object and Action Categories across the Human Brain. *Neuron*. https://doi.org/10.1016/j.neuron.2012.10.014

Ioannidis, J. P. A. (2005). Why most published research findings are false. *PLoS Medicine*, *2*(8), 0696–0701. https://doi.org/10.1371/journal.pmed.0020124

Ishai, a, Ungerleider, L. G., Martin, a, & Haxby, J. V. (2000). The representation of objects in the human occipital and temporal cortex. *Journal of Cognitive Neuroscience*, *12 Suppl 2*, 35–51. https://doi.org/10.1162/089892900564055

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences*, *96*(16), 9379–9384. https://doi.org/10.1073/pnas.96.16.9379

James, T. W., & James, K. H. (2013). Expert individuation of objects increases activation in the fusiform face area of children. *NeuroImage*, *67*, 182–192. https://doi.org/10.1016/j.neuroimage.2012.11.007

Jiang, X., Bradley, E., Rini, R. A., Zeffiro, T., VanMeter, J., & Riesenhuber, M. (2007). Categorization Training Results in Shape- and Category-Selective Human Neural Plasticity. *Neuron*. https://doi.org/10.1016/j.neuron.2007.02.015

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. *The Journal of Neuroscience*, *17*(11), 4302–4311. https://doi.org/10.1098/Rstb.2006.1934

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rstb.2006.1934

Kourtzi, Z., Betts, L. R., Sarkheil, P., & Welchman, A. E. (2005). Distributed neural plasticity for shape learning in the human visual cortex. *PLoS Biology*. https://doi.org/10.1371/journal.pbio.0030204

Krawczyk, D. C., Boggan, A. L., McClelland, M. M., & Bartlett, J. C. (2011). The neural organization of perception in chess experts. *Neuroscience Letters*. https://doi.org/10.1016/j.neulet.2011.05.033

Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 3863–3868. https://doi.org/10.1073/pnas.0600244103

Kriegeskorte, N., & Mur, M. (2012). Inverse MDS: Inferring dissimilarity structure from multiple item arrangements. *Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2012.00245

Kriegeskorte, N., Mur, M., Ruff, D. A., Kiani, R., Bodurka, J., Esteky, H., … Bandettini, P. A. (2008). Matching Categorical Object Representations in Inferior Temporal Cortex of Man and Monkey. *Neuron*. https://doi.org/10.1016/j.neuron.2008.10.043

Larocque, J. J., Riggall, A. C., Emrich, S. M., & Postle, B. R. (2017). Within-Category Decoding of Information in Different Attentional States in Short-Term Memory. *Cerebral Cortex*, *27*(10), 4881–4890. https://doi.org/10.1093/cercor/bhw283

Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center–periphery organization of human object areas. *Nature Neuroscience*, *4*(5), 533–539. https://doi.org/10.1038/87490

Li, S., Ostwald, D., Giese, M., & Kourtzi, Z. (2007). Flexible Coding for Categorical Decisions in the Human Brain. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.3795-07.2007

Lieberman, M. D., & Cunningham, W. A. (2009). Type I and Type II error concerns in fMRI research: Re-balancing the scale. *Social Cognitive and Affective Neuroscience*. https://doi.org/10.1093/scan/nsp052

Livingston, K. R., & Andrews, J. K. (1995). On the Interaction of Prior Knowledge and Stimulus Structure in Category Learning. *The Quarterly Journal of Experimental Psychology Section A*, *48*(1), 208–236. https://doi.org/10.1080/14640749508401385

Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology*, *5*(5), 552–563. https://doi.org/10.1016/S0960-9822(95)00108-4

Lotze, M., Erhard, K., Neumann, N., Eickhoff, S. B., & Langner, R. (2014). Neural correlates of verbal creativity: differences in resting-state functional connectivity associated with expertise in creative writing. *Frontiers in Human Neuroscience*, *8*(July), 1–8. https://doi.org/10.3389/fnhum.2014.00516

Lupyan, G. (2009). Extracommunicative functions of language: Verbal interference causes selective categorization impairments. *Psychonomic Bulletin and Review*, *16*(4), 711–718. https://doi.org/10.3758/PBR.16.4.711

Mahon, B. Z., & Caramazza, A. (2009). Concepts and Categories: A Cognitive Neuropsychological Perspective. *Annual Review of Psychology*. https://doi.org/10.1146/annurev.psych.60.110707.163532

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., … Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(18), 8135–8139. https://doi.org/10.1073/pnas.92.18.8135

Martens, F., Bulthé, J., van Vliet, C., & Op de Beeck, H. (2018). Domain-general and domain-specific neural changes underlying visual expertise. *NeuroImage*, *169*. https://doi.org/10.1016/j.neuroimage.2017.12.013

Martin, J. H. (2012). *Neuroanatomy text and atlas*. McGraw Hill Professional.

Mathy, F., & Bradmetz, J. (2011). An extended study of the nonindependence of stimulus properties in human classification learning. *Quarterly Journal of Experimental Psychology*, *64*(1), 41–64. https://doi.org/10.1080/17470218.2010.493972

McGugin, R. W., Gatenby, J. C., Gore, J. C., & Gauthier, I. (2012). High-resolution imaging of expertise reveals reliable object selectivity in the fusiform face area related to perceptual performance. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1116333109

McGugin, R. W., Newton, A. T., Gore, J. C., & Gauthier, I. (2014). Robust expertise effects in right FFA. *Neuropsychologia*. https://doi.org/10.1016/j.neuropsychologia.2014.08.029

McGugin, R. W., Richler, J. J., Herzmann, G., Speegle, M., & Gauthier, I. (2012). The Vanderbilt Expertise Test reveals domain-general and domain-specific sex effects in object recognition. *Vision Research*. https://doi.org/10.1016/j.visres.2012.07.014

McGugin, R. W., Van Gulick, A. E., Tamber-Rosenau, B. J., Ross, D. A., & Gauthier, I. (2015). Expertise effects in face-selective areas are robust to clutter and diverted attention, but not to competition. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhu060

McKone, E., & Kanwisher, N. (2005). Does the human brain process objects of expertise like faces? *From Monkey Brain to Human Brain: A Fyssen Foundation Symposium*.

Mervis, C. B., & Rosch, E. (1981). Categorization of Natural Objects. *Annual Review of Psychology*, *32*(1), 89–115. https://doi.org/10.1146/annurev.ps.32.020181.000513

Mongelli, V., Dehaene, S., Vinckier, F., Peretz, I., Bartolomeo, P., & Cohen, L. (2017). Music and words in the visual cortex: The impact of musical expertise. *Cortex*. https://doi.org/10.1016/j.cortex.2016.05.016

Moore, C. D., Cohen, M. X., & Ranganath, C. (2006). Neural Mechanisms of Expert Skills in Visual Working Memory. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.1873-06.2006

Mourão-Miranda, J., Bokde, A. L. W., Born, C., Hampel, H., & Stetter, M. (2005). Classifying brain states and determining the discriminating activation patterns: Support Vector Machine on functional MRI data. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2005.06.070

Naito, E., & Hirose, S. (2014). Efficient foot motor control by Neymar's brain. *Frontiers in Human Neuroscience*, *8*, 1–7. https://doi.org/10.3389/fnhum.2014.00594

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424–430. https://doi.org/10.1016/j.tics.2006.07.005

Nosofsky, R. M. (1986). Attention, Similarity, and the Identification-Categorization Relationship. *Journal of Experimental Psychology: General*, *115*(1), 39–57. https://doi.org/10.1037/0096-3445.115.1.39

Nosofsky, R. M. (1987). Attention and Learning Processes in the Identification and Categorization of Integral Stimuli, *13*(1), 87–108.

Nosofsky, R. M. (1992). Similarity Scaling and Cognitive Process Models. *Annual Review of Psychology*, *43*(1), 25–53. https://doi.org/10.1146/annurev.ps.43.020192.000325

Nosofsky, R. M. (2011). The generalized context model: an exemplar model of classification. In E. M. Pothos & A. J. Wills (Eds.), *Formal Approaches in Categorization* (pp. 18–39). Cambridge University Press. https://doi.org/10.1017/CBO9780511921322.002

Nosofsky, R. M., Sanders, C. A., Gerdom, A., Douglas, B. J., & McDaniel, M. A. (2017). On Learning Natural-Science Categories That Violate the Family-Resemblance Principle. *Psychological Science*, *28*(1), 104–114. https://doi.org/10.1177/0956797616675636

Nosofsky, R. M., Sanders, C. A., & McDaniel, M. A. (2017). Tests of an Exemplar-Memory Model of Classification Learning in a High-Dimensional Natural-Science Category Domain. *Journal of Experimental Psychology: General*, *147*(3), 328. https://doi.org/10.1037/xge0000369

Nosofsky, R. M., Sanders, C. A., Meagher, B. J., & Douglas, B. J. (2018). Toward the development of a feature-space representation for a complex natural category domain. *Behavior Research Methods*, *50*(2), 530–556. https://doi.org/10.3758/s13428-017-0884-8

Ogawa, S., Lee, T. M., Kay, A. R., & Tank, D. W. (1990). Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proceedings of the National Academy of Sciences of the United States of America*, *87*(24), 9868–9872. https://doi.org/10.1073/pnas.87.24.9868

Oosterhof, N. N., Tipper, S. P., & Downing, P. E. (2012). Visuo-motor imagery of specific manual actions: A multi-variate pattern analysis fMRI study. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2012.06.045

Op de Beeck, H. (2012). The distributed nature of visual object learning. In *Plasticity in Sensory Systems*.

Op de Beeck, H., & Baker, C. I. (2010). The neural basis of visual object learning. *Trends in*

Cognitive Sciences. https://doi.org/10.1016/j.tics.2009.11.002

Op de Beeck, H., Baker, C. I., DiCarlo, J. J., & Kanwisher, N. G. (2006). Discrimination Training Alters Object Representations in Human Extrastriate Cortex. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.2481-06.2006

Op de Beeck, H., Deutsch, J. A., Vanduffel, W., Kanwisher, N. G., & DiCarlo, J. J. (2008). A stable topography of selectivity for unfamiliar shape classes in monkey inferior temporal cortex. *Cerebral Cortex*, *18*(7), 1676–1694. https://doi.org/10.1093/cercor/bhm196

Op de Beeck, H., Haushofer, J., & Kanwisher, N. G. (2008). Interpreting fMRI data: maps, modules and dimensions. *Nature Reviews Neuroscience*, *9*(2), 123–135. https://doi.org/10.1038/nrn2314

Op de Beeck, H., Torfs, K., & Wagemans, J. (2008). Perceived Shape Similarity among Unfamiliar Objects and the Organization of the Human Object Vision Pathway. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.2511-08.2008

Panis, S., Vangeneugden, J., Op de Beeck, H., & Wagemans, J. (2008). The representation of subordinate shape similarity in human occipitotemporal cortex. *Journal of Vision*, *8*(10), 9.1-15. https://doi.org/10.1167/8.10.9

Panis, S., Vangeneugden, J., & Wagemans, J. (2008). Similarity, typicality, and category-level matching of morphed outlines of everyday objects. *Perception*, *37*(12), 1822–1849. https://doi.org/10.1068/p5934

Pantev, C., Engelien, A., Candia, V., & Elbert, T. (2003). Representational cortex in musicians. In I. Peretz & R. J. Zatorre (Eds.), *The cognitive neuroscience of music* (pp. 382–395). Oxford: Oxford University Press.

Pazart, L., Comte, A., Magnin, E., Millot, J.-L., & Moulin, T. (2014). An fMRI study on the influence of sommeliers' expertise on the integration of flavor. *Frontiers in Behavioral Neuroscience*, *8*(October), 1–15. https://doi.org/10.3389/fnbeh.2014.00358

Peretz, I., & Zatorre, R. J. (Eds.). (2003). *The cognitive neuroscience of music*. *The Quarterly Review of Biology* (Vol. 86). Oxford: Oxford University Press. https://doi.org/10.1086/659918

Peretz, I., & Zatorre, R. J. (2005). Brain Organization for Music Processing. *Annual Review of Psychology*, *56*(1), 89–114. https://doi.org/10.1146/annurev.psych.56.091103.070225

Peters, L., Bulthé, J., Daniëls, N., Op de Beeck, H., & De Smedt, B. (2018). Dyscalculia and dyslexia: Different behavioral, yet similar brain activity profiles during arithmetic. *NeuroImage: Clinical*, *18*(July 2017), 663–674. https://doi.org/10.1016/j.nicl.2018.03.003

Pinho, A. L., de Manzano, O., Fransson, P., Eriksson, H., & Ullen, F. (2014). Connecting to Create: Expertise in Musical Improvisation Is Associated with Increased Functional Connectivity between Premotor and Prefrontal Areas. *Journal of Neuroscience*, *34*(18), 6156–6163. https://doi.org/10.1523/JNEUROSCI.4769-13.2014

Plailly, J., Delon-Martin, C., & Royet, J. P. (2012). Experience induces functional reorganization in brain regions involved in odor imagery in perfumers. *Human Brain Mapping*, *33*(1), 224–234. https://doi.org/10.1002/hbm.21207

Posner, M. I., & Keele, S. W. (1968). On the genesis of abstract ideas. *Journal of Experimental Psychology*, *77*(3), 353–363. https://doi.org/10.1037/h0025953

Raiguel, S., Vogels, R., Mysore, S. G., & Orban, G. A. (2006). Learning to See the Difference Specifically Alters the Most Informative V4 Neurons. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.0457-06.2006

Rhodes, G., Byatt, G., Michie, P. T., & Puce, A. (2004). Is the Fusiform Face Area Specialized for Faces, Individuation, or Expert Individuation? *Journal of Cognitive Neuroscience*. https://doi.org/10.1162/089892904322984508

Richler, J. J., & Gauthier, I. (2014). A meta-analysis and review of holistic face processing. *Psychological Bulletin*. https://doi.org/10.1037/a0037004

Richler, J. J., Wong, Y. K., & Gauthier, I. (2011). Perceptual expertise as a shift from strategic interference to automatic holistic processing. *Current Directions in Psychological Science*, *20*(2), 129–134. https://doi.org/10.1177/0963721411402472

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, *103*(1), 34–79. https://doi.org/10.1016/j.cognition.2006.02.008

Rossion, B., Collins, D., Goffaux, V., & Curran, T. (2007). Long-term Expertise with Artificial Objects Increases Visual Competition with Early Face Categorization Processes. *Journal of Cognitive Neuroscience*, *19*(3), 543–555.

Rossion, B., & Curran, T. (2010). Visual expertise with pictures of cars correlates with rt magnitude of the car inversion effect. *Perception*. https://doi.org/10.1068/p6270

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M. J., & Crommelinck, M. (2002). Expertise training with novel objects leads to left-lateralized facelike electrophysiological responses. *Psychological Science*. https://doi.org/10.1111/1467-9280.00446

Royet, J. P., Plailly, J., Saive, A. L., Veyrac, A., & Delon-Martin, C. (2013). The impact of expertise in olfaction. *Frontiers in Psychology*, *4*(DEC), 1–11. https://doi.org/10.3389/fpsyg.2013.00928

Sadato, N., Okada, T., Kubota, K., & Yonekura, Y. (2004). Tactile discrimination activates the visual cortex of the recently blind naive to Braille: A functional magnetic resonance imaging study in humans. *Neuroscience Letters*, *359*(1–2), 49–52. https://doi.org/10.1016/j.neulet.2004.02.005

Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, V., Deiber, M. P., Dold, G., & Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature*, *380*(6574), 526–528. https://doi.org/10.1038/380526a0

Schlaug, G. (2001). The Brain of Musicians: A model for functional and structural adaptation. *Annals of the New York Academy of Sciences*, *930*(1), 281–299. https://doi.org/10.1093/acprof:oso/9780198525202.003.0024

Schoups, A., Vogels, R., Qian, N., & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, *412*(6846), 549–553. https://doi.org/10.1038/35087601

Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. G. (2005). Separate Face and Body Selectivity on the Fusiform Gyrus. *Journal of Neuroscience*, *25*(47), 11055–11059. https://doi.org/10.1523/JNEUROSCI.2621-05.2005

Scolari, M., Vogel, E. K., & Awh, E. (2008). Perceptual expertise enhances the resolution but not the number of representations in working memory. *Psychonomic Bulletin and Review*, *15*(1), 215–222. https://doi.org/10.3758/PBR.15.1.215

Scott, L. S., Tanaka, J. W., Sheinberg, D. L., & Curran, T. (2006). A Reevaluation of the Electrophysiological Correlates of Expert Object Processing. *Journal of Cognitive Neuroscience*. https://doi.org/10.1162/jocn.2006.18.9.1453

Scott, L. S., Tanaka, J. W., Sheinberg, D. L., & Curran, T. (2008). The role of category learning in the acquisition and retention of perceptual expertise: A behavioral and neurophysiological study. *Brain Research*. https://doi.org/10.1016/j.brainres.2008.02.054

Searston, R. A., & Tangen, J. M. (2017). Expertise with unfamiliar objects is flexible to changes in task but not changes in class. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0178403

Seitz, A. R., & Dinse, H. R. (2007). A common framework for perceptual learning. *Current Opinion in Neurobiology*, *17*(2), 148–153. https://doi.org/10.1016/j.conb.2007.02.004

Shen, J., Mack, M. L., & Palmeri, T. J. (2014). Studying real-world perceptual expertise. *Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2014.00857

Shepard, R. N. (1980). Multidimensional scaling, tree-fitting, and clustering. *Science*, *210*(4468), 390–398.

Shepard, R. N. (1987). Toward a universal law of generalization for psychological science. *Science*, *237*(4820), 1317–1323. https://doi.org/10.1126/science.3629243

Sigala, N., & Logothetis, N. K. (2002). Visual categorization shapes feature selectivity in the primate temporal cortex. *Nature*. https://doi.org/10.1038/415318a

Sigman, M., Pan, H., Yang, Y., Stern, E., Silbersweig, D., & Gilbert, C. D. (2005). Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron*. https://doi.org/10.1016/j.neuron.2005.05.014

Sloboda, J. A. (1991). Musical Expertise. In K. A. Ericsson & J. Smith (Eds.), *Toward a General Theory of Expertise: Prospects and limits* (pp. 153–171).

Sloutsky, V. M., Lo, Y. F., & Fisher, A. V. (2001). How much does a shared name make things similar? Linguistic labels, similarity, and the development of inductive inference. *Child Development*, *72*(6), 1695–1709. https://doi.org/10.1111/1467-8624.00373

Smith, J. D., & Minda, J. P. (1998). Prototypes in the mist: The early epochs of category learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *24*(6), 1411–1436. https://doi.org/10.1037/0278-7393.24.6.1411

Srihasam, K., Vincent, J. L., & Livingstone, M. S. (2014). Novel domain formation reveals proto-architecture in inferotemporal cortex. *Nature Neuroscience*, *17*(12), 1776–1783. https://doi.org/10.1038/nn.3855

Steyvers, M. (2002). Multidimensional scaling. In *Encyclopedia of cognitive science*.

Tanaka, J. W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychological Science : A Journal of the American Psychological Society / APS*, *12*(1), 43–47. https://doi.org/10.1111/1467-9280.00308

Tanaka, J. W., Curran, T., & Sheinberg, D. L. (2005). The Training and Transfer of Real-World Perceptual Expertise. *Psychological Science*, *16*(2), 145–151.

Tanaka, J. W., & Farah, M. J. (1993). Parts and Wholes in Face Recognition. *The Quarterly Journal of Experimental Psychology*, *46*(2), 225–245. https://doi.org/10.1080/14640749308401045

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory and Cognition*, *25*(5), 583–592. https://doi.org/10.3758/BF03211301

Tanaka, J. W., & Taylor, M. (1991). Object categories and expertise: Is the basic-level in the eye of the beholder? *Cognitive Psychology*, *23*, 457–482. https://doi.org/10.1016/0010-0285(91)90016-H

Tarr, M. J., & Gauthier, I. (2000). FFA: A Flexible Fusiform Area for Subordinate-Level Visual Processing Automatized by Expertise. *Nature Neuroscience*, *3*(8), 764–769. Retrieved from http://www.nature.com/neuro/journal/v3/n8/full/nn0800_764.html

Tervaniemi, M. (2003). Musical sound processing: EEG and MEG evidence. In I. Peretz & R. J. Zatorre (Eds.), *The cognitive neuroscience of music* (pp. 294–309). Oxford: Oxford University Press.

Tsao, D. Y., Freiwald, W. A., Knutsen, T. A., Mandeville, J. B., & Tootell, R. B. H. (2003). Faces and objects in macaque cerebral cortex. *Nature Neuroscience*, *6*(9), 989–995. https://doi.org/10.1038/nn1111

Ung, H., Brown, J. E., Johnson, K. A., Younger, J., Hush, J., & Mackey, S. (2014). Multivariate classification of structural MRI data detects chronic low back pain. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhs378

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. *Analysis of Visual Behavior*. https://doi.org/10.2139/ssrn.1353746

van den Hurk, J., Van Baelen, M., & Op de Beeck, H. P. (2017). Development of visual category selectivity in ventral visual cortex does not require visual experience. *Proceedings of the National Academy of Sciences*, *114*(22), E4501–E4510. https://doi.org/10.1073/pnas.1612862114

van der Linden, M., Murre, J. M. J., & van Turennout, M. (2008). Birds of a feather flock together: Experience-driven formation of visual object categories in human ventral temporal cortex. *PLoS ONE*, *3*(12). https://doi.org/10.1371/journal.pone.0003995

Van Gulick, A. E., & Gauthier, I. (2014). The perceptual effects of learning object categories that predict perceptual goals. *Journal of Experimental Psychology: Learning , Memory, and Cognition*, *40*(5), 1307–1320. https://doi.org/10.1037/a0036822.The

Weiss, N., Mardo, E., & Avidan, G. (2016). Visual expertise for horses in a case of congenital prosopagnosia. *Neuropsychologia*. https://doi.org/10.1016/j.neuropsychologia.2015.07.028

Wellman, H. M., & Gelman, S. A. (1992). Cognitive Development: Foundational Theories of Core Domains. *Annual Review of Psychology*, *43*(1), 337–375. https://doi.org/10.1146/annurev.ps.43.020192.002005

Winawer, J., Witthoft, N., Frank, M. C., Wu, L., Wade, A. R., & Boroditsky, L. (2007). Russian blues reveal effects of language on color discrimination. *Proceedings of the National Academy of Sciences*, *104*(19), 7780–7785. https://doi.org/10.1073/pnas.0701644104

Wong, A. C. N., Palmeri, T. J., & Gauthier, I. (2009). Conditions for facelike expertise with objects: Becoming a ziggerin expert - but which type? *Psychological Science*. https://doi.org/10.1111/j.1467-9280.2009.02430.x

Wong, A. C. N., Palmeri, T. J., Rogers, B. P., Gore, J. C., & Gauthier, I. (2009). Beyond shape: How you learn about objects affects how they are represented in visual cortex. *PLoS ONE*, *4*(12). https://doi.org/10.1371/journal.pone.0008405

Wong, Y. K., Folstein, J. R., & Gauthier, I. (2012). The nature of experience determines object representations in the visual system. *Journal of Experimental Psychology: General*. https://doi.org/10.1037/a0027822

Wong, Y. K., & Gauthier, I. (2010). A Multimodal Neural Network Recruited by Expertise with Musical Notation. *Journal of Cognitive Neuroscience*. https://doi.org/10.1162/jocn.2009.21229

Xia, M., Wang, J., & He, Y. (2013). BrainNet Viewer: A Network Visualization Tool for Human Brain Connectomics. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0068910

Xu, Y. (2005). Revisiting the role of the fusiform face area in visual expertise. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhi006

Zandbelt, B. B., Gladwin, T. E., Raemaekers, M., van Buuren, M., Neggers, S. F., Kahn, R. S., … Vink, M. (2008). Within-subject variation in BOLD-fMRI signal changes across repeated measurements: Quantification and implications for sample size. *NeuroImage*, *42*(1), 196–206. https://doi.org/10.1016/j.neuroimage.2008.04.183

Zatorre, R. J., Perry, D. W., Beckett, C. A., Westbury, C. F., & Evans, A. C. (1998). Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. *Proceedings of the National Academy of Sciences*, *95*(6), 3172–3177. https://doi.org/10.1073/pnas.95.6.3172