



Examining the neural correlates of within-category discrimination in face and non-face expert recognition

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ABSTRACT

While expert face discrimination develops naturally in humans, expert discrimination in non-face object categories, such as birds, cars and dogs, is acquired through years of experience and explicit practice. The current study used an implicit visual discrimination paradigm and electroencephalography (EEG) – Fast Periodic Visual Stimulation – to examine whether within-category discrimination of faces and non-face objects of expertise rely on shared mechanisms despite their distinct learning histories. Electroencephalogram was recorded while bird experts and bird novices viewed 60 s sequences of bird images or face images presented at a periodic rate of six images per second (i.e., 6.0 Hz). In the sequence, an adapting base image of a family-level bird (e.g., robin), a species-level bird (e.g., purple finch) or a face (e.g., Face A) was presented repeatedly for four consecutive cycles, followed by a different within-category “oddball” image at every fifth cycle (e.g., warbler, house finch, Face B). A differential response between the adapting base and the oddball images (6.0 Hz/fifth cycle = 1.20 Hz) provided an index of within-category discriminability.

The results showed that both experts and novices demonstrated a robust EEG signal of equal magnitudes to the 6.00 Hz base face and bird images at medial-occipital channels and to the oddball 1.20 Hz face and bird images at the more anterior occipito-temporal channels. To examine whether the responses to faces and birds were generated by shared neural mechanisms, we correlated the responses to birds and faces at the participant-level. For the base signal at medial-occipital channels, all object categories positively correlated in both the experts and the novices, as expected given that the base signal indexes visual responses that are shared by all object categories (e.g., low-level). In contrast, for the discrimination signal at the more anterior occipito-temporal channels, the response to family- and species-level birds positively correlated with faces for the experts, but no face-bird association was found for the novices. These findings indicate the existence of partially shared neural mechanisms for within-category discrimination of faces and birds in the experts, but not in the novices.

1. Introduction

After years of practice and experience, perceptual experts acquire the ability to quickly and accurately identify and discriminate objects in their domain of expertise. For example, an experienced bird watcher easily discriminates between different species of birds, a car aficionado quickly discriminates between car models, and a dog judge effortlessly discriminates dog breeds. In contrast, face recognition is a *naturally* occurring form of expertise where people learn, without the benefit of direct instruction or practice, to discriminate *individual* faces in a single glance (Tanaka, 2001). Although face expertise might be biologically based, as new born human infants prefer looking at human faces relative to non-face stimuli (e.g., Goren et al., 1975), it could also be influenced by the extensive within-category face experience that

humans accumulate throughout the course of their life times. Thus, while non-face and face expertise differ in their developmental trajectories and learning protocols, both share the behavioral characteristics of quick and accurate within-category discrimination. However, an open question is whether within-category discrimination of faces and non-face objects of expertise rely on different or shared neural mechanisms.

According to the *modular account* of object recognition, face recognition is supported by a system that is exclusively dedicated to faces whereas a different and independent system supports the recognition of non-face objects, including objects from expert categories (e.g., Kanwisher, 2000). In contrast, the *expertise account* states that the putative face-specific system is domain-general by processing any object domain with a fixed set of diagnostic features (i.e., visually

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homogenous), for which expertise at within-category discrimination exists (e.g., Bukach et al., 2006; Tarr and Gauthier, 2000). Although the latter account has accumulated substantial amount of evidence over the last decade, there is still an ongoing debate as to whether face selective mechanisms can be recruited by expert non-face object domains.

1.1. Category discrimination of faces and non-face expert objects

The human ventral temporal cortex (VTC) contains a network of cortical areas that are highly sensitive to stimuli from the face category. Studies using event related potentials (ERPs) have shown differential responses to faces relative to non-face objects biased in right occipito-temporal channels at approximately 170 ms after stimulus onset. This indicate that cortical areas located in the VTC discriminate faces from other object categories (e.g., cars) at around 170 ms (Bentin et al., 1996; Rossion et al., 2000; Rossion and Jacques, 2008). Studies using functional magnetic resonance imaging (fMRI) have shown differential responses to faces as compared to non-face objects in cortical areas localized in the inferior occipital gyrus (Occipital Face Area [OFA]: for review, see Pitcher et al., 2011), the lateral fusiform gyrus (Fusiform Face Area [FFA]; Kanwisher et al., 1997), and the anterior temporal lobe (ATL; Gao et al., 2018), all of which show a right hemispheric bias. These findings are taken as evidence to support a modular account whereby it is claimed that face and non-face objects are encoded by different neural mechanisms (e.g., Kanwisher, 2000).

However, a growing body of evidence have shown that the areas sensitive to face stimuli are also sensitive to objects from expert categories. Like faces, objects from expert categories (e.g., birds, cars, dogs) evoke an enhanced ERP response at around 170 ms in occipito-temporal channels relative to objects from non-expert categories (Busey and Vanderkolk, 2005; Rossion et al., 2002; Scott et al., 2006, 2008; Tanaka and Curran, 2001). Moreover, the N170 to faces diminish in the presence of objects of expertise, relative to control categories, suggesting that face and non-face expert categories recruit related neural mechanisms (Gauthier et al., 2003; Rossion et al., 2004, 2007). Studies using fMRI have shown that objects from non-face expert categories evoke a greater BOLD response in both the OFA and the FFA relative to non-face expert categories (e.g., Gauthier et al., 2000a; Gauthier et al., 1999; Gauthier and Tarr, 2002; McGugin et al., 2012; McGugin et al., 2015; Xu, 2005). Grey matter thickness in the FFA also predicts the ability to recognize objects from expert categories, showing an effect that cannot be attributed to attention (McGugin et al., 2016). Consistent with the expertise account, the putative face-selective mechanisms are similarly engaged by faces and non-face expert domains (e.g., Bukach et al., 2006; Tarr and Gauthier, 2000).

Despite the growing body of evidence for the expertise account, there is disagreement as to whether these mechanisms are modular or domain-general (Gauthier, 2017). On the one hand, a few studies have failed to replicate the expertise effect, which are often cited as evidence against the expertise account (Grill-Spector et al., 2004; Op de Beeck et al., 2006; Yue et al., 2006). For example, in an fMRI study, car experts failed to show a disproportionate response to cars in face-selective areas (Grill-Spector et al., 2004). On the other hand, all these studies have been criticized for their methodology (for a discussion, see Gauthier, 2017). For example, experts with *modern* cars were tested with *antique* cars in the scanner (Grill-Spector et al., 2004). Perhaps more importantly, the rate of replication of the expertise effect is substantially higher than the rate of non-replication, and the effect has been shown using a wide range of methods. However, given the lack of agreement, the current debate could be advanced by examining a novel and important prediction by the expertise account, namely, whether the neural code of subcategories in the face and a non-face expert domain rely on shared mechanisms.

1.2. Within-category discrimination of faces and non-face expert objects

Adaptation paradigms have played a crucial role in examining the neural mechanisms of *within-category* discrimination of faces. With this method, repeated presentations of the same stimulus dimension (e.g., face identity) attenuate the evoked neural response, arguably by decreasing the responsiveness in the neural units (i.e., columns) encoding that dimension. Importantly, a change in stimuli dimension (e.g., a different face identity) recovers the signal by presumably recruiting a different and nonadapted neural population (Grill-Spector and Malach, 2001; Kourtzi and Grill-Spector, 2005). Adaptation studies with ERPs have shown that faces, but not cars, produce a rebound from adaption in occipito-temporal channels at about 250 ms after stimulus onset (e.g., Schweinberger et al., 2004). This indicates that cortical areas in the VTC discriminate face identities at around 250 ms. Moreover, adaptation paradigms with fMRI have revealed neural sensitivity to different face identities in both the OFA and the FFA, but not in areas that do not show face selectivity (e.g., Gauthier et al., 2000b; Loffler et al., 2005; Natu et al., 2016). Thus, the same cortical areas are involved in category- and individual level discrimination of faces, albeit at different time scales; category discrimination occurs earlier than individual level discrimination.

Although no studies have directly compared *within-category* discrimination mechanisms of face and non-face expert categories, indirect evidence suggests similar mechanisms between the two. For example, multiple studies have shown a positive correlation between behavioral within-category discrimination performance (e.g., BMW 520 vs. BMW 335) and the magnitude of the neural response in the OFA and FFA to that category (e.g., cars vs. other object categories; McGugin et al., 2012; McGugin et al., 2014). Moreover, within-category discrimination training enhances the neural sensitivity to the trained category in face selective areas, while training to discriminate *between* categories increase neural sensitivity to the category more broadly outside face selective areas (Wong et al., 2009). Similarly, within-category discrimination training enhances the N170 and N250 ERP components to the trained category, whereas between-category discrimination only enhances the N170 ERP component (Scott et al., 2006, 2008). Thus, only experience making within-category discriminations produced face-like neural effects. Although these studies only measured the neural correlate at the categorical level (e.g., expert category vs all other categories), they suggest a relation between within-category discrimination mechanisms of face and non-face expert categories.

The current study directly measured a within-category discrimination response to faces and a non-face expert objects, using a novel and implicit visual discrimination paradigm (FPVS: Fast Periodic Visual Stimulation) coupled with electroencephalography (EEG). Specifically, a group of expert and novice bird watchers were shown sequences of birds or faces, whereby the same object image (Fig. 2: family-level birds; species-level birds; faces) were presented at a periodic rate of six images per second (i.e., 6.0 Hz), with size varying randomly at every cycle to prevent pixel-based adaptation (Liu-Shuang et al., 2014). A different within-category “oddball” was periodically interleaved at every 5th cycle (i.e., 1.20 Hz). Thus, while the base signal (6.0 Hz and harmonics) indexed neural mechanisms that responded similarly to the base and oddball objects, the oddball signal (1.20 Hz and harmonics) indexed the mechanisms that responded differently to the base and the oddball objects. Participants were instructed to fixate a cross, centred within the objects and detect random changes in colour from red to green. This task ensured that the participants maintained a constant level of attention in the center of the object, while performing a task orthogonal to the images, which have been shown to drastically reduce expertise effects related to selective attention (Harel et al., 2010; McGugin et al., 2014). This approach allowed us to obtain a behavior free (i.e., implicit) measure of within-category discrimination in *both* experts and novices that is based on the principles of neural adaptation (for review, see Norcia et al., 2015; Rossion, 2014).

The claim that objects of expertise and faces partly share neural mechanisms was tested based on the assumption that neural responses that are generated within the same neural mechanisms, will correlate more than neural responses that are generated by different mechanisms (Reeder et al., 2016; McGugin et al., 2017; Peelen et al., 2009). The bird oddballs were perceptually salient as they varied in both external contours and internal shapes, which ensured a robust discrimination signals in *both* the novices and the experts that could be correlated with that of the faces.¹ The family- and species-level bird conditions varied in their shape homogeneity (e.g., external contour overlap), rather than task demands, since there was no explicit categorization task associated with the images. The modular account, which states that two independent mechanisms are used for within-category discrimination of faces and non-face objects, predicts that for both the experts and the novices, the face and bird discrimination responses (1.20 Hz and harmonics) should not correlate, while family- and species-level birds should correlate despite differences in homogeneity and overall response magnitude (Fig. 1, top row). In contrast, the expertise account, which states that expert categories share discrimination mechanisms, predicts that the discrimination response to the birds and the faces would correlate to a larger degree in the experts than in the novices, while family- and species-level birds should correlate with each other in both groups despite differences in homogeneity and overall response magnitude (Fig. 1, middle row). Finally, both the modular and the expertise account predict that all object conditions (birds [family-level, species-level] and faces) in both the expert and the novices, should correlate in the base-response (6.00 Hz and harmonics), since these responses primarily originate in low-level systems that are shared by all categories (Fig. 1, bottom row). Thus, a dissociation between the experts and the novices should be specific to the *discrimination* response of faces and birds.

2. Methods

2.1. Participants

Sixteen expert participants, ranging in age from 20 to 57 years (5 females, $M = 33.25$, $SD = 13.66$) were selected based on nominations from their bird-watching peers. Sixteen additional age and education matched control participants ranging in age from 20 to 70 years (6 females; $M = 33.88$, $SD = 12.73$), were recruited from the community or University of Victoria's online recruitment system for undergraduates. The novice participants had no prior experience in bird watching. However, two out of the 12 novice participants had participated in previous experiments on bird recognition in our lab (Hagen et al., 2014, 2016). For the experts, nine out of the 12 participants had taken part in previous studies on bird recognition (Hagen et al., 2014, 2016). Power analysis indicated that we had 80% power to detect a between-groups effect of at least Cohen's $d = 1.02$. Following the approach of previous expert studies in the lab, the experts were recruited based on recommendations by other expert participants (Hagen et al., 2014, 2016; Tanaka and Curran, 2001; Tanaka and Taylor, 1991). In addition, the level of bird recognition performance in our participants were assessed with a bird recognition test (Hagen et al., 2014, 2016) in which participants judged whether two sequentially presented bird images belonged to the same or different species. Discrimination scores between experts and novices were compared with a Welch two-sample t -test due to unequal variances in the two groups. Discrimination scores for one expert and novice were lost due to technical issues. The experts obtained a higher discrimination score ($n = 15$, $d' = 2.10$, $SD = 0.55$,

¹ This approach is different than other studies using the FPVS oddball paradigm in the sense that the bird oddballs were easily perceived due to for example differences in external object contours (see video example of trial in supplemental material).

$range = 0.98$ – 2.77) compared to the novices ($n = 15$, $d' = 0.90$, $SD = 0.36$, $range = 0.36$ – 1.64), $t(24.14) = 7.14$, $p < 0.001$. The expertise score of four of the experts overlapped with the upper range of the scores of the novices. However, unlike studies that define experts based on a behavioral discrimination performance (e.g., McGugin et al., 2012), our test did not isolate domain-specific recognition skills controlling for recognition abilities in other domains, and so we considered the expertise score secondary to the nominations from their bird-watching peers. All expert participants were recruited from the off-campus community, whereas the novices were recruited either from the off-campus community or University of Victoria's online recruitment system for undergraduate students. Four additional novices were excluded from the data analysis because of technical issues with the EEG recording ($n = 4$: triggers were not recorded).

2.2. Stimuli

Stimuli from the Family-level Bird condition consisted of 12 grayscale bird images from different bird families (Fig. 2A: eagle, cardinal, seagull, woodpecker, pigeon, wren, crow, hummingbird, swallow, jay, sparrow, robin), while the stimuli in the Species-level Bird condition consisted of 12 grayscale within-family bird images (Fig. 2B: American Gold Finch, Black Headed Grosbeak, Brambling, Common Redpoll, Evening Grosbeak, Grey Crowned Rosy Finch, Hoary Redpoll, Pine Grosbeak, Pine Siskin, Purple Finch, House Finch, Red Crossbill). Although the species-level birds were more homogenous in their overall shape than family-level birds, the birds within each condition were heterogeneous enough so that difference were easily perceived (see video example of trial in the supplemental materials). Stimuli used in the face condition consisted of full-front grayscale photographs of 12 female and 12 male faces with neutral facial expression (Fig. 2C, D). Each face picture was taken under the same conditions of lighting and background and with the same face-to-camera distance. External features such as hair and ears were cropped out using Adobe Photoshop, and the isolated faces were put against a neutral grey background. Whereas all face images were cropped and scaled to fit within a frame of approximately 250×300 pixels, all bird images were cropped and centred with respect to the fixation cross within a frame of 300×300 pixels. All images were pasted on a grey background using Adobe Photoshop CS4. In addition, images within each object category were equated for overall luminance using the Shine Toolbox (Willenbockel et al., 2010). Face images subtended a visual angle of approximately 8.95° vertically and 6.88° horizontally. Bird images subtended a visual angle of approximately 5.99° vertically and 6.18° horizontally.

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2.3. Procedure

The experiment consisted of 6 sixty-second trials during which EEG was recorded. In a given trial, bird (family- or species-level) or human face (female or male) images were presented at a rate of 6 cycles per second (6.00 Hz = base stimulation frequency) through sinusoidal contrast modulation using a custom Matlab script (Fig. 3; Liu-Shuang et al., 2014; The Mathworks). In the presentation sequence, an adapting base image of a family-level bird (e.g., Robin), a species-level bird (e.g., Purple Finch) or a face (e.g., Face A) was presented repeatedly for four consecutive cycles, with each cycle lasting for 167.7 ms. A different within-category “oddball” image (e.g., family-level: Woodpecker; species-level: House Finch; face: Face B) was randomly selected from the remaining of the 11 category images and displayed at every 5th presentation cycle ($F/5 = 1.20$ Hz = oddball stimulation frequency). Importantly, the size of each image varied randomly between 80% and 120% in 2% steps at every cycle of presentation to ensure that the low-level visual properties (e.g., retinal position of edge information) varied at every cycle (Liu-Shuang et al., 2014). Thus, the change in birds (or

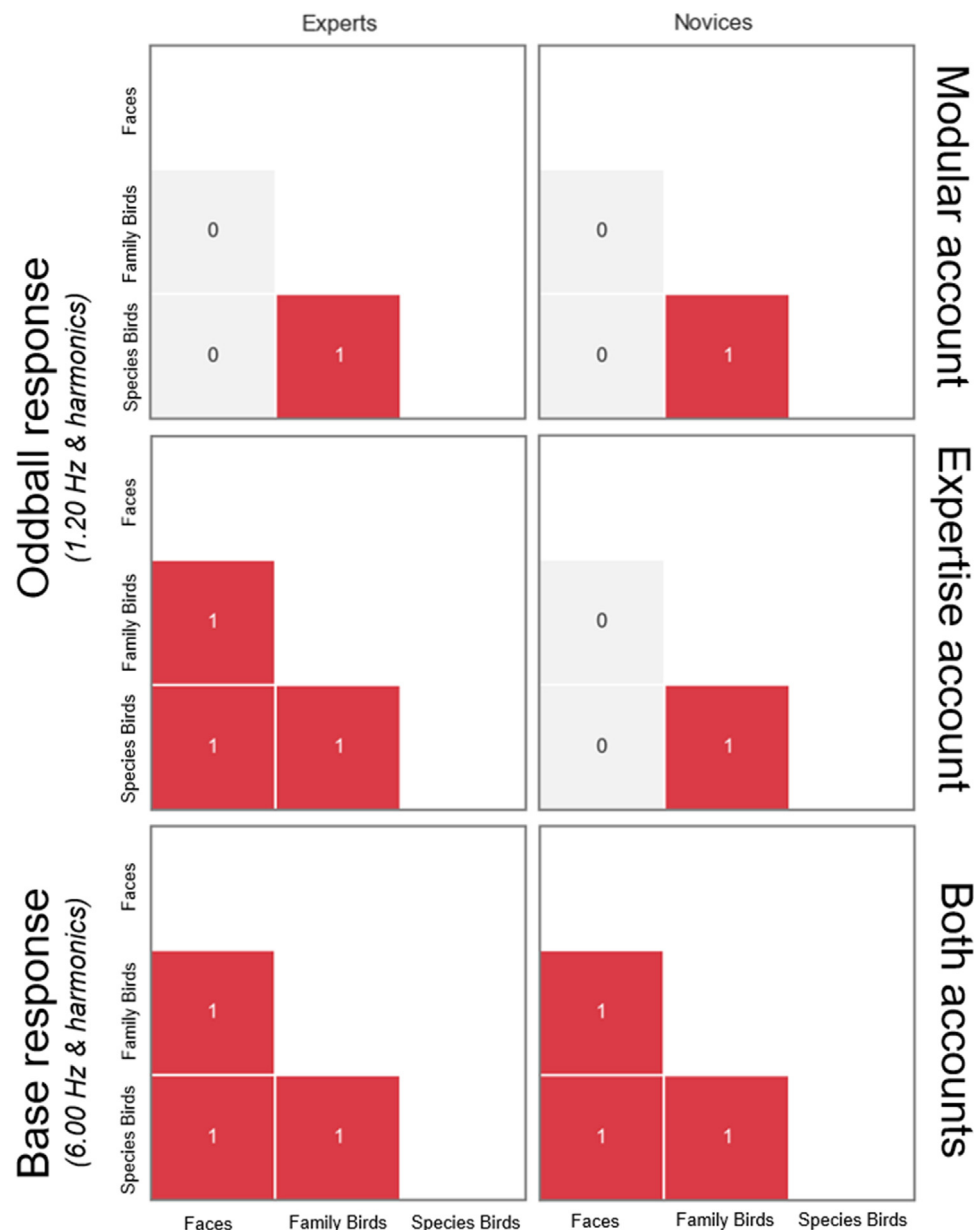


Fig. 1. *Top row*: predictions by the modular account for the oddball response (1.20 Hz and harmonics). *Middle row*: predictions by the expertise account for the oddball response (1.20 Hz and harmonics). *Bottom row*: predictions by both the modular and the expertise accounts for the base response (6.00 Hz and harmonics).

faces) at the oddball frequency ($F/5 = 1.20$ Hz) should evoke a periodic oddball response in higher-level mechanisms that are invariant to the change of object size, but not in lower-level mechanisms that are not invariant to stimuli size (e.g., retinotopically organized areas).

During the image presentation, participants were instructed to fixate a cross - centred in the birds and centred between the eyes of the faces - and press the space-bar every time it changed colour from red to green (duration of colour change: 200 ms). The colour-change occurred randomly. This task ensured that every participant maintained attention in the center of the object throughout each presentation cycle, while also performing an orthogonal task to the images, which have been shown to drastically reduce expertise effects related to selective attention (Harel et al., 2010; McGugin et al., 2014).

Two of the six trials displayed base and oddball birds that differed at the family level (e.g., base bird: robin, oddball bird: sparrow). Two of the six trials displayed base and oddball birds that differed at the species level (e.g., base bird: Gold Finch, oddball bird: House Finch). Two of the six trials displayed images of faces whereby one trial contained

base and oddball female faces (e.g., base face: female face A, oddball face: female face B) and one trial were composed of male faces (e.g., base face: male face A, oddball face: male face B). Thus, the entire experiment consisted of 240 s of image presentation. The order of the trials was counterbalanced across participants such that half of the participants were presented with birds followed by faces and the other half with faces followed by birds.

2.4. EEG acquisition

The electroencephalogram (EEG) was recorded using a montage of 36 electrode sites in accordance to the extended international 10–20 system (Jasper, 1958). Signals were acquired using Ag/AgCl ring electrodes mounted in a nylon electrode cap with an abrasive, conductive gel (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). Signals were amplified by low-noise electrode differential amplifiers with a frequency response of DC 0.017–67.5 Hz (90 dB–octave roll off) and digitized at a rate of 250 samples per second. Digitized signals were

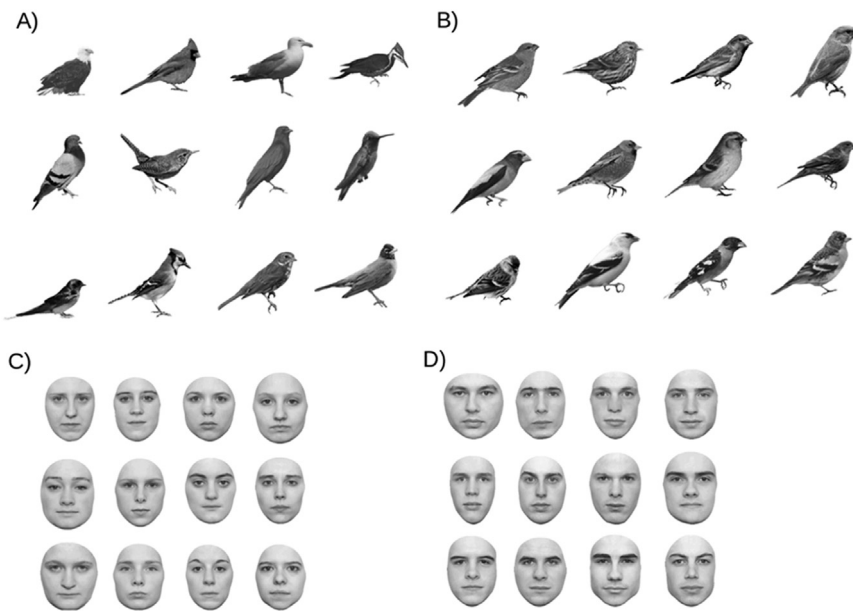


Fig. 2. Stimuli from the different object category conditions: (A) bird family, (B) bird species, (C) female faces differing across identity, and (D) male faces differing across identity.

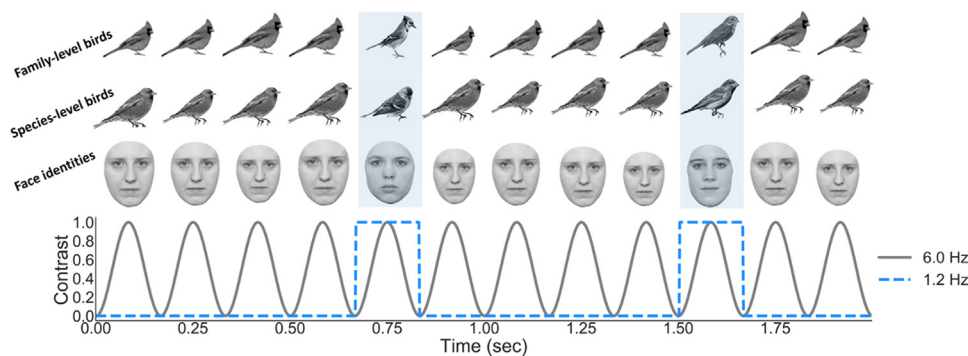


Fig. 3. Schematic illustration of the experimental paradigm. Objects were presented by sinusoidal contrast modulation at a rate of six images per second (6.00 Hz). A base object was presented 4 times with a different oddball object presented at every 5th cycle (1.20 Hz) of presentation. To avoid pixel-wise processing, object size was randomly varied between 80% and 120% at every stimulation cycle.

recorded to disk using Brain Vision Recorder software (Brain Products GmbH, Munich, Germany). The impedances were maintained below 10 k Ω . The EEG was recorded using the average reference.

2.5. Data analysis

Preprocessing was conducted with a customized software (Letswave 5: <http://nocions.webnode.com/letswave>) running in the Matlab environment (The Mathworks). EEG data was band-pass filtered (0.1–100 Hz zero-phase Butterworth filter, 24 dB/octet slope), and all channels were rereferenced to the common average reference. Filtered data was first cropped down to an integer number of 1.20 Hz that containing the start of the first presentation cycle and the end of the last presentation cycle (0–60 s, 72 oddball cycles, 15,000 time bins). The segmented sequences were averaged within each participant separately for each condition in the time domain to increase signal-to-noise by reducing EEG activity non-phase locked to the stimulation (e.g., Liu-Shuang et al., 2016). To extract amplitude spectra for all channels, a Fast Fourier Transform was applied to the averaged segments (frequency resolution, 1/60, i.e., 0.017 Hz). To consider noise variations across the EEG spectrum, signal-to-noise (SNR) was computed as the ratio of the amplitude in each frequency bin to the average amplitude of the 10 surrounding frequency bins in each direction, excluding the two directly neighbouring bins. Similarly, Z-scores were computed for each bin by subtracting its amplitude by the average signal of the 20 surrounding bins (excluding the neighbours) and dividing it by the

standard deviation of the 20 surrounding bins.

To determine the number of harmonics included in the statistical comparison between the experts and the novices in the face and bird conditions, the amplitude data from the frequency domain for each condition (group and object category) was averaged across participants and channels. Next, Z-scores for the base- and oddball stimulation rate, and its 8 harmonics were extracted and analyzed until they were no longer significant (Dzhelyova and Rossion, 2014; Liu-Shuang et al., 2014). A threshold of significance was placed at a Z-score of $z > 3.10$ ($p < 0.001$, one-tailed; i.e., signal > noise; e.g., Liu-Shuang et al., 2016, Xu et al., 2017). For the base frequency, the harmonics were analyzed up to the 6th harmonic ($6F = 36.0$ Hz). For the oddball frequency, the harmonics were analyzed up to the 7th harmonic ($7F/5 = 8.40$ Hz). The 5th harmonic of the oddball response ($5F/5 = 6.0$ Hz) was excluded from the oddball analysis because it overlaps with the fundamental frequency of the base response ($F = 6.0$ Hz).

3. Results

3.1. EEG data

3.1.1. Frequency domain analysis: group analysis

Distinct peaks were observed in the frequency domain at the exact rate of visual stimulation and associated harmonics (Fig. 4). Regions of interest (ROIs) for the base and oddball responses were defined based on the respective scalp topographies and by the channels with maximal

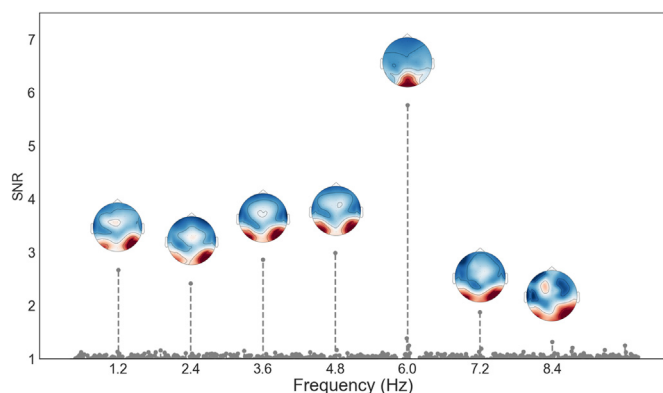


Fig. 4. EEG spectra from 0.37 to 9.83 Hz for the average across all electrodes, both groups, and three object conditions.

response (Fig. 4). The maximal response of the base stimulation rate (6.0 Hz) was located at medial occipital channels (Oz, POz) for every condition. This topography is similar to previous studies using the same task with faces (e.g., Liu-Shuang et al., 2014), words (Lochy et al., 2015), and objects (e.g., Jacques et al., 2016), and indicate that the visual system synchronized to the visual stimulation. In contrast to the base stimulation response, the maximal response of the oddball frequency (1.20 Hz) was located at occipito-temporal channels (PO7, PO8, P7, P8) for both the birds and face conditions. This topography is consistent with previous studies using the same task with faces (e.g., Liu-Shuang et al., 2014), words (Lochy et al., 2015), and objects (e.g., Jacques et al., 2016), and corresponds with cortical areas involved in high-level visual discrimination (e.g., Scott et al., 2006, 2008).

3.1.2. Base response (6.0 Hz and harmonics)

The visual response in each participant was quantified by aggregating the signal of the 6 first harmonics averaged across channels Oz and POz. We report uncorrected p-values for the post-hoc tests in this and subsequent analysis. Fig. 5 presents the aggregate SNR for the base stimulation rate in medial-occipital channels as a function object

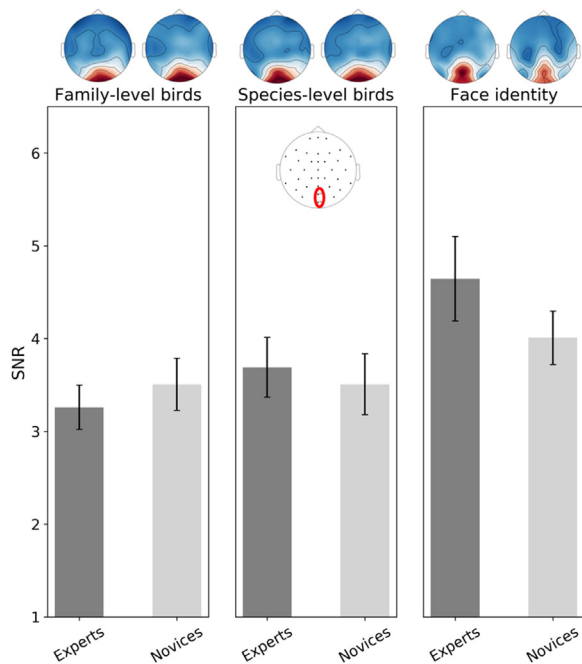


Fig. 5. SNR aggregated across the first 6 harmonics at medial-occipital channels (Oz, POz) and the associated scalp topography. Error bars represent 95% confidence intervals.

category and group. The SNR data for the base response were analyzed in a mixed-design analysis of variance (ANOVA) using object category (family-level bird, species-level bird, faces) as a within-subjects factor and group (experts, novices) as a between-subjects factor. There was no main effect of group, $F(1,30) = 0.22, p = 0.646, \text{generalized eta squared} = 0.0053$. The main effect of object category was significant, $F(2,60) = 11.21, p < 0.001, \text{generalized eta squared} = 0.09$. Post-hoc tests showed that Faces ($M = 4.33; SE = 0.40$) evoked a larger signal than both Family-level birds ($M = 3.38; SE = 0.27$) and Species-level birds ($M = 3.60; SE = 0.33, ps < 0.003$), and that Family- and Species-level birds evoked similar responses ($p = 0.255$). The two-way interaction between group and object category did not interact with object category, $F(2,60) = 2.24, p = 0.116, \text{generalized eta squared} = 0.0188$.²

3.1.3. Oddball discrimination response (1.20 Hz and harmonics)

The visual response in each participant was quantified by aggregating the signal of the 7 first harmonics, excluding the 5th harmonic ($5F/F = 6.00$ Hz) averaged across channels PO7, PO8, P7, and P8. Fig. 6 presents the aggregate SNR for the oddball stimulation rate in occipito-temporal channels as a function object category and group. The SNR data for the oddball response were analyzed in a mixed-design analysis of variance (ANOVA) using object category (family-level bird, species-level bird, faces) as a within-subjects factor and group (experts, novices) as a between-subjects factor. There was no main effect of group, $F(1,30) = 0.17, p = 0.687, \text{generalized eta squared} = 0.0037$. The main effect of object category was significant, $F(2,60) = 48.97, p < 0.001, \text{generalized eta squared} = 0.34$. Post-hoc tests showed that Family-level birds ($M = 3.01; SE = 0.26$) evoked larger signals than Species-level birds ($M = 2.41; SE = 0.19, p < 0.001$) and that both Family- and Species-level birds evoked larger signal than Faces ($M = 1.66, SE = 0.11, ps < 0.001$). The two-way interaction between group and object category was not significant, $F(2,60) = 2.52, p = 0.089, \text{generalized eta squared} = 0.026$.³

3.1.4. Correlation of the EEG response of each object category

To assess whether within-category discrimination of faces and birds shared neural processes in the experts, but not the novices, we correlated the neural responses (i.e., aggregated SNR values) associated with the different object categories (i.e., faces, family-level birds, species-level birds). Previous work has showed a positive correlation between neural responses that are generated by the same neural processes (McGugin et al., 2017; Peelen et al., 2009; Reeder et al., 2016).

For the base response (6.00 Hz and harmonics) at medial-occipital channels, a significant correlation was found across all object categories for both the experts ($r_{fb\&f} = 0.59, p_{fb\&f} = 0.016, 95\% \text{ CI}_{fb\&f} [0.14, 0.84]; r_{sb\&f} = 0.72, p_{sb\&f} = 0.002, 95\% \text{ CI}_{sb\&f} [0.35, 0.90]; r_{sb\&fb} = 0.82, p_{sb\&fb} < 0.001, 95\% \text{ CI}_{sb\&fb} [0.54, 0.94]$) and for the novices ($r_{fb\&f} = 0.62, p_{fb\&f} = 0.011, 95\% \text{ CI}_{fb\&f} [0.17, 0.85]; r_{sb\&f} = 0.53, p_{sb\&f} = 0.033, 95\% \text{ CI}_{sb\&f} [0.05, 0.81]; r_{sb\&fb} = 0.64, p_{sb\&fb} = 0.007, 95\% \text{ CI}_{sb\&fb} [0.22, 0.86]$), and there was no difference between the two groups ($p_{fb\&f} = 0.462, \text{one-tailed}; p_{sb\&f} = 0.209, \text{one-tailed}; p_{sb\&fb} = 0.321, \text{two-tailed}$) (Fig. 7). Thus, irrespective of the group, the responsiveness (6.00 Hz and harmonics) to one object category predicted the responsiveness to another category at the medial-occipital channels.

In contrast to the base response at medial-occipital channels, the oddball response (1.20 Hz and harmonics) at the more anterior occipito-temporal channels to Family-level birds correlated with Faces in the experts ($r = 0.76, p < 0.001, 95\% \text{ CI} [0.42, 0.91]$), but not in the

²Bayesian tests yielded a Bayes factor (BF) of 2.85 in favor of the model that only included the main effects, corresponding with the original analysis. The small value could indicate inadequate power.

³Bayesian tests yielded a Bayes factor (BF) of 1.89 in favor of the model that only included the main effects, corresponding with the original analysis. The small value could indicate inadequate power.

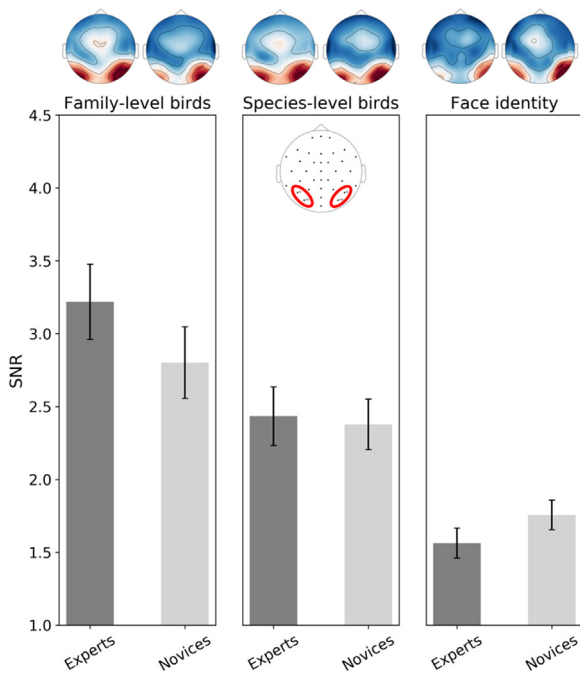


Fig. 6. SNR aggregated across the first 7 harmonics, excluding the 5th harmonic (5 F/F = 6.00 Hz) at occipito-temporal channels (PO7, P7, PO8, P8) and the associated scalp topography. Error bars represent 95% confidence intervals.

novices ($r = 0.10, p = 0.706, 95\% \text{ CI } [-0.42, 0.57]$), and importantly, the difference between the correlations was significant ($p = 0.012$, one-tailed) (Fig. 8). Similarly, the oddball discrimination response at occipito-temporal channels to Species-level birds correlated with Faces in the experts ($r = 0.69, p = 0.003, 95\% \text{ CI } [0.29, 0.88]$), but not in the novices ($r = 0.13, p = 0.638, 95\% \text{ CI } [-0.39, 0.59]$), and the difference between the correlations was significant ($p = 0.034$, one-tailed). In contrast, the oddball discrimination response at occipito-temporal channels to Family- and Species- level birds was significant in both the experts ($r = 0.76, p < 0.001, 95\% \text{ CI } [0.42, 0.91]$) and the novices ($r = 0.82, p < 0.001, 95\% \text{ CI } [0.54, 0.93]$), and there was no difference between the correlations in the two groups ($p = 0.708$, two-tailed). Thus, in the experts, the neural mechanism that discriminated different birds responded in a consistent manner with the neural mechanism that discriminated faces, while in the novices, the mechanism that discriminated different birds responded in a way that was not consistent with the mechanism that discriminated different faces.

The main findings were that the experts and novices showed similar overall base (6.00 Hz and harmonics) and oddball (1.20 Hz and harmonics) responses to birds (family- and species-levels) and faces. Moreover, for the base response, there was a strong positive correlation between all object categories (birds [family- and species-levels] and faces), which did not differ between the experts and the novices. However, for the base signal one should note the low precision as indicated by the large CIs. In contrast, for the oddball discrimination response, the experts showed a strong positive correlation across all object categories, while novices showed a strong correlation between

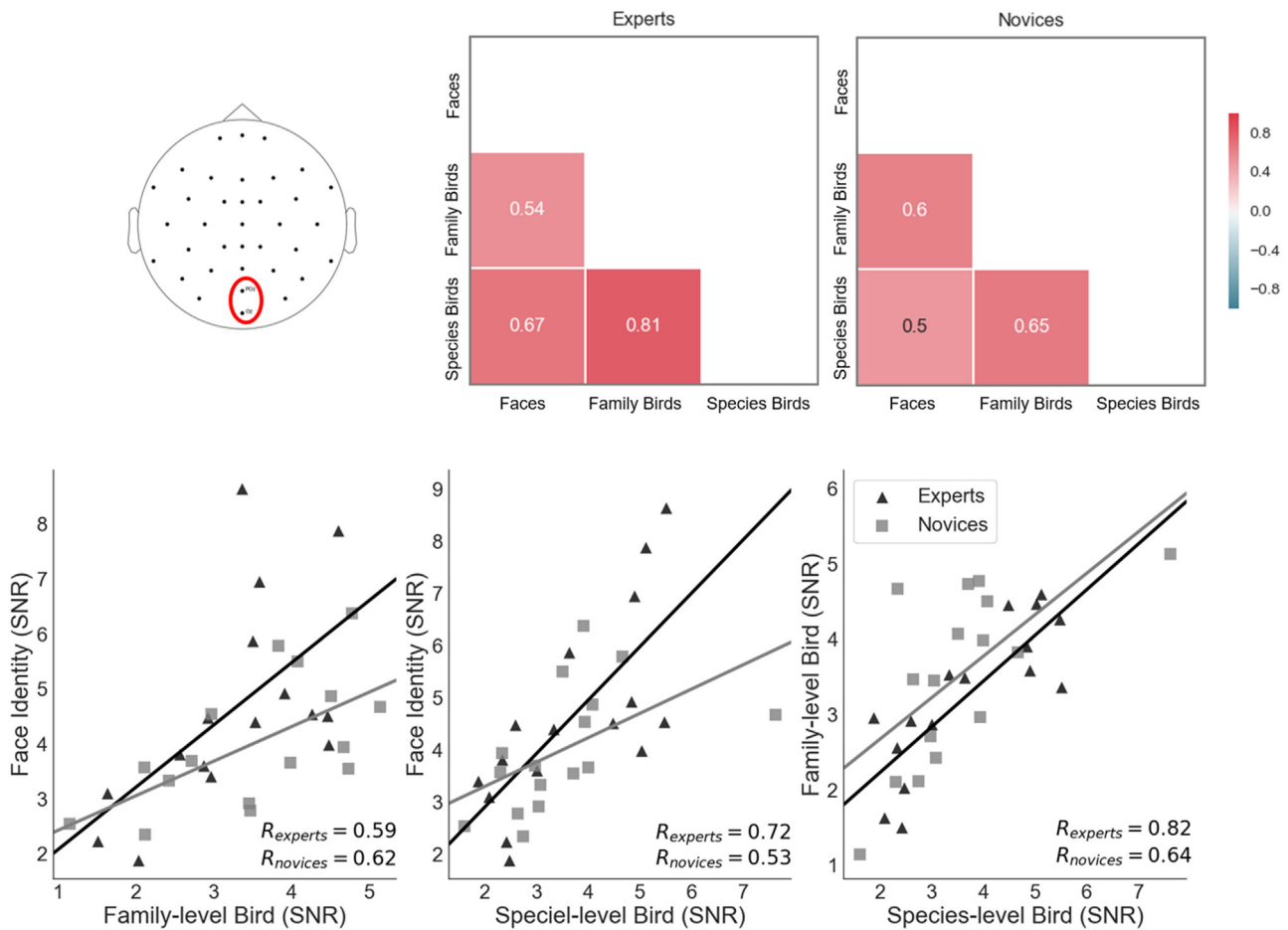


Fig. 7. Correlations of the base response (SNR) at medial-occipital channels to Face identity and Family-level birds, Face identity and Species-level birds, and Family-level birds and Species-level birds.

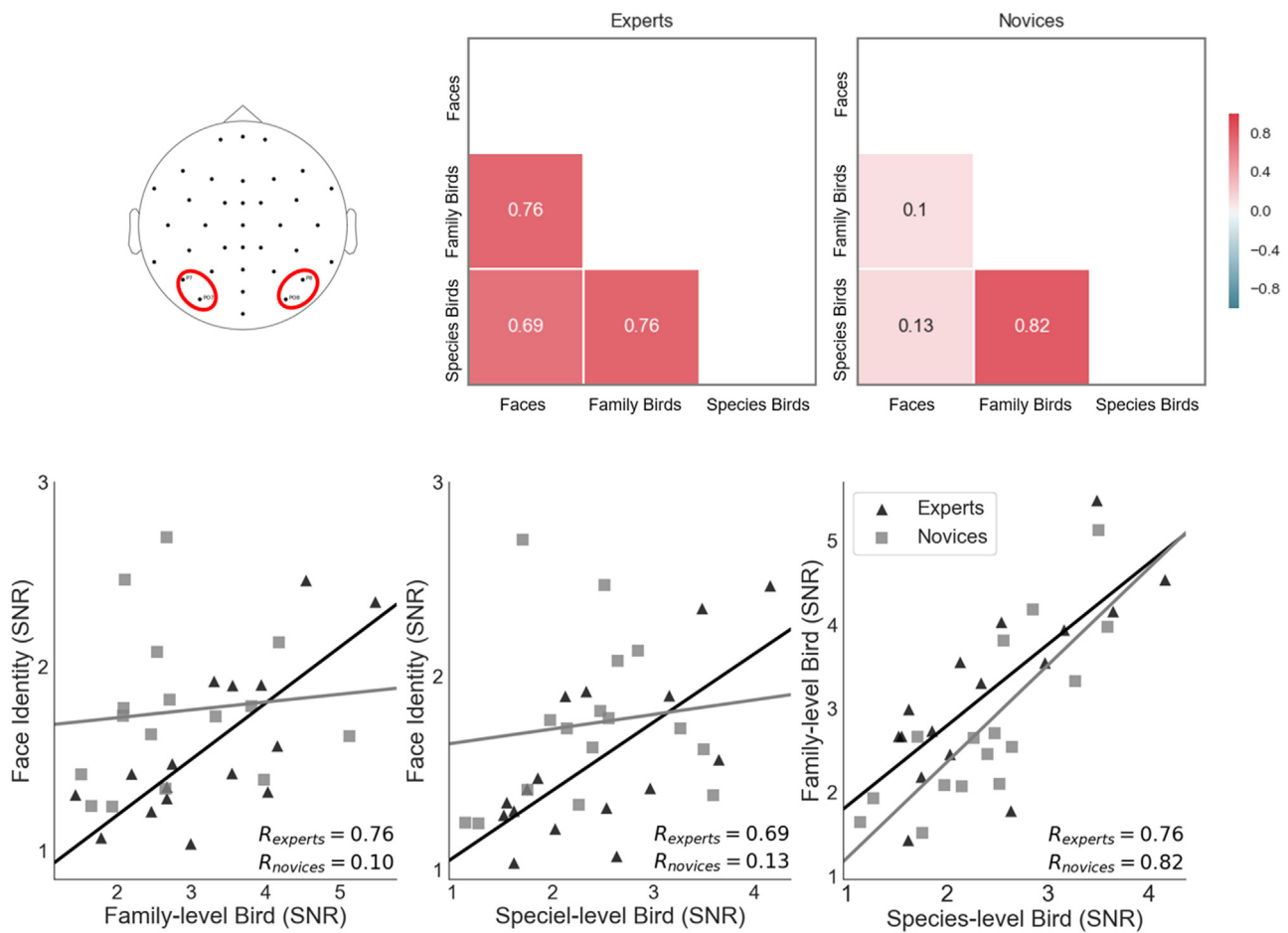


Fig. 8. Correlations of the discrimination response (SNR) at occipito-temporal channels to Faces and Family-level birds, Faces and Species-level birds, and Family-level birds and Species-level birds.

the birds (family-level vs species-level), but no correlation between birds and faces. The dissociation between experts and novices that was specific to the discrimination response for faces and birds is consistent with the claim of the expertise account that proposes a shared neural mechanism for faces and objects of expertise.

4. Discussion

The goal of the current study was to test whether the discrimination of faces and non-face objects of expertise relied on separable or shared neural discrimination processes. We presented bird experts and bird novices with faces and birds in a visual discrimination task where within-category discrimination responses were isolated and tagged to the frequency of 1.2 Hz. Both the birds and the faces evoked robust within-category discrimination responses (1.2 Hz and harmonics) in both the experts and the novices. Crucially, while the expertise account predicts that the bird discrimination responses in the experts are partly generated in face-selective mechanisms, the modular account predicts that they are generated in non-face selective mechanisms.

Frequency analysis of the EEG revealed distinct signal peaks that corresponded with the base rate stimulation (6.00 Hz and harmonics) and that was maximal at medial-occipital channels (Fig. 4). Faces evoked a larger base response at the medial-occipital channels than did the birds (family- and species- levels; Fig. 5). This difference could be caused by the larger visual angle of the faces than of the bird by evoking a larger retinotopic neural population response, or the faces could have attracted more attention than did the birds, as it has been shown that the responses at medial channels are influenced by selective attention (e.g., Morgan et al., 1996; Müller et al., 2006). Importantly, the experts

and the novices did not differ in their base response to the birds or to the faces, suggesting that the experts did not allocate more selective attention to the birds than did the novices (Fig. 5). The medial-occipital topography for the base response is consistent with previous studies examining face, non-face, and letter recognition, and the claim that it indexes neural processes shared by all object categories (e.g., low-level processes; Liu-Shuang et al., 2014; Lochy et al., 2015; Jacques et al., 2016).

Distinct signal peaks were also observed at the exact rate of within-category oddball stimulation (1.20 Hz and harmonics) in the family- and species-level bird and face categories (Fig. 4). However, unlike the base response, the oddball response was maximal at the occipito-temporal channels and was larger for the birds than the faces (Fig. 6). The larger response to the birds as compared to the faces is likely explained by the larger difference in external contour and internal features in the former as compared to the latter (Fig. 2). The discrimination responses to birds or faces did not differ in the expert and novices indicating that the face and bird oddballs were discriminated with equal ease by both groups. The same scalp topography has previously been reported in studies of face, non-face, and word recognition (Liu-Shuang et al., 2014; Lochy et al., 2015; Jacques et al., 2016), and is consistent with the claim that the oddball response is reflecting higher-level visual discrimination responses located in VTC.

To examine whether the same neural processes contributed to the within-category discrimination of the birds and the faces in experts and novices, we correlated the discrimination signal (1.20 Hz and harmonics) evoked by the three object categories. Previous work has showed a positive correlation between neural responses evoked by different stimuli and that are generated by the same neural processes (McGugin

et al., 2017; Peelen et al., 2009; Reeder et al., 2016). For example, in the FFA, the magnitude of the response to real faces predicts the magnitude of the response to artificial faces, as measured with fMRI (McGugin et al., 2017). Moreover, in the current study, the base signal at medial-occipital channels showed a strong correlation for faces and birds, and family- and species-birds, in both the experts and the novices that did not differ from each other (Fig. 7). This is as expected given that the base signal indexes visual responses (e.g., low-level) that are shared by all object categories (i.e., lower-level domain-general mechanisms, such as local edge detection).

In contrast to the base response, the oddball discrimination response at occipito-temporal channels between faces and birds did not correlate in the novices, despite that family- and species-level birds showed a strong correlation (Fig. 8). Thus, the lack of correlation in the novices was specific to the comparison of the face and the bird categories, consistent with the claim that face and non-face objects are processed in independent systems (e.g., Kanwisher, 2000, Schalk et al., 2017). However, this pattern was different from that of the experts, who exhibited a strong correlation between their oddball response to faces and their oddball response to family- and species-level birds. The strong correlation between the birds and the faces in the experts, but not the novices, are consistent with the predictions of the expertise account; specifically, face and expert non-face recognition are supported by overlapping neural mechanisms (Bukach et al., 2006; Tarr and Gauthier, 2000). This dissociation is unlikely to be caused by differences in selective attention between the experts and the novices for several reasons. First, the participants performed an orthogonal task that diverted attention away from the images, which have previously been shown to drastically reduce expertise effects related to selective attention (Harel et al., 2010; McGugin et al., 2014). Second, the experts and the novices did not differ in neither the overall base signal nor in the correlational patterns at the medial channels, which have been shown to be sensitive to selective attention (Morgan et al., 1996; Müller et al., 2006).

The current study contributes novel evidence to the question of whether the processes of face recognition and expert object recognition recruit dissociated or shared neural mechanisms. Previous work has shown that both face and non-face expert categories are associated with enhanced N170 and N250 ERP components. Moreover, faces and non-face expert categories evoke similar differential responses in putative face-selective areas of the VTC, such as in the OFA and the FFA (Gauthier et al., 2000a, 1999; Gauthier and Tarr, 2002; McGugin et al., 2012). Although these studies show that face and non-face expert recognition share discrimination processes at the category level, no studies to date have directly compared the neural processes involved in *within-category* discrimination of both faces and objects. The current study directly evaluated within-category discrimination by measuring the differential response generated from periodically interspersing within-category “oddball” objects in a sequence of adapting base objects. In addition, the discrimination response was disentangled from processes involved in explicit task demands, given that the participants were performing a concurrent orthogonal task (colour detection in the fixation cross). Thus, using a global neural measure, the current study adds to the existing literature by suggesting that face and non-face expert categories overlap not only in terms of category discrimination, but also in terms of within-category discrimination.

What processes could account for the patterns observed in the experts and the novices? Both face and non-face objects of expertise are recognized at specific category levels (Johnson and Mervis, 1997; Tanaka, 2001; Tanaka and Taylor, 1991), for which fine grained internal shape information plays a crucial role (Collin and McMullen, 2005; Hagen et al., 2016). It is possible that the neural processes that was shared between faces and birds in the experts, but not in the novices, contributed to efficient encoding of internal diagnostic shape information. For example, face-specific areas could contain neuronal units (i.e., columns) that are especially suited for encoding the internal

diagnostic information for recognition at specific category levels, and that learning processes incorporate these neuronal units into a stable population representation of a given category. Indeed, behavioral work has showed that both face and expert recognition of birds rely on shapes in a middle bandwidth of spatial frequencies (Costen et al., 1994; Hagen et al., 2016), providing some evidence to suggest that diagnostic shape information for both object categories are carried by the same type of shape information.

We still know little about the neural principles supporting the reorganization of putative face-specific mechanisms. On the one end of the continuum, it is possible that faces and non-face expert categories are instantiated in the same functional area but are divided into different neuronal units. This organization could give rise to the differential responses of face and non-face expert categories within the same voxel, given that a voxel measures responses that are generated by multiple units (i.e., columns). Moreover, this organization could lead to competition with faces, as has been demonstrated when faces and non-face expert domains are presented simultaneously (e.g. Gauthier et al., 2003; Rossion et al., 2004; Rossion et al., 2007), if the different neural units are connected through inhibitory lateral connections. On the other extreme, the exact same set of units could represent both face and non-face expert categories, but with differential activation across the population of units associated with the two domains. A third, and potentially more likely scenario, is that there is a partial overlap in the neuronal units recruited by face and non-face expert categories. In this view, non-face expert objects recruit a subset of the units within an area (e.g., FFA) that also support face recognition, perhaps because these units support similar recognition demands for both the faces and the non-face expert category. Thus, while face and non-face homogenous expert categories could share some face-specific units, the non-face objects should also recruit unique neuronal units spread across other cortical areas (Harel et al., 2010).

Face and object expertise differ in terms of its acquisition. Within-category discrimination of faces are enforced by the social demands to individuate faces by identity, and is potentially linked with a genetic component, as newborn infants prefer human faces over other objects (Goren et al., 1975; Johnson et al., 1991). In contrast, object expertise, such as birdwatching, train recognition, dog judging, is a specialized ability that is typically acquired through deliberate and extensive practice in early or later adulthood by a relatively small number of people in the population. Based on differences in learning procedures (implicit vs. deliberate), the age of acquisition (early development vs. adulthood), and perhaps genetic influences, it is reasonable to expect that face and object expertise are subserved by different neural mechanisms. However, face and non-face object expertise both share the need to perform fine-grained within-category discriminations, and even if evolutionary pressures due to the adaptive behavior of face identification have given rise to such fine-grained feature “detectors”, it does not exclude them from being coopted by stimuli from other categories if the recognition-demands overlap with those of faces. Thus, logically speaking, if certain cortical areas are evolved for a certain category, it should not rule out the possibility for those areas to be at least partially coopted by other categories, if the underlying recognition demands are similar.

If shared mechanisms between faces and expert domains are mainly performing “fine-grained” analysis, one could speculate that face-bird correlations in the experts would be influenced by the shape-homogeneity of the birds. Specifically, since the species-level birds are more homogenous than family-level birds in terms of their external contours, then one could hypothesize that the former would isolate this face-specific mechanism to a larger degree than latter. The more isolated the mechanism, the larger the correlations. In the current study we did not find a stronger correlation between faces and species-level birds as compared to faces and family-level birds. However, one must be careful making strong claims about this prediction in the current study since the species-level birds used in this study were selected to vary in the

external contours, so to generate discrimination signals in the novices that could be correlated with that of faces. Thus, to properly assess how shape homogeneity in expert categories influence face-overlap, future studies should carefully control for external contour homogeneity.

In summary, comparisons of the face-bird correlations in the experts and the novices revealed patterns that were consistent with the predictions of the expertise account. The current findings suggest that within-category discrimination of face and non-face expert objects rely on at least partially shared neural processes, while within-discrimination of faces and other non-face objects relies on different neural systems. Although our findings are consistent with a substantial amount of previous research on expertise, this study provided novel evidence by using an implicit discrimination task to directly measure *within-category* discrimination processes of the global recognition system. Future work should examine the shared neural processes using a method with better spatial resolution. Here, real-world expertise was used as a model to test the nature of the face specific system; however, real-world expertise can also be a useful model for understanding general principles of how cortical mechanisms reorganize to match the demands of the ever-changing environment.

CRedit authorship contribution statement

Simen Hagen: Conceptualization, Methodology, Data curation, Writing - original draft. **James W. Tanaka:** Conceptualization, Writing - review & editing, Supervision.

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