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

Simen Hagen<sup>1</sup>

James W. Tanaka<sup>2</sup>

1. Centre de Recherche en Automatique de Nancy (CRAN), Université de Lorraine
2. Department of Psychology, University of Victoria

Keywords: object recognition, face recognition, within-category discrimination, expert object  
recognition, perceptual expertise, fast periodic visual stimulation, frequency tagging, EEG

## Abstract

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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 60s 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.

51           After years of practice and experience, perceptual experts acquire the ability to quickly and  
52 accurately identify and discriminate objects in their domain of expertise. For example, an experienced  
53 bird watcher easily discriminates between different species of birds, a car aficionado quickly  
54 discriminates between car models, and a dog judge effortlessly discriminate dog breeds. In contrast,  
55 face recognition is a *naturally* occurring form of expertise where people learn, without the benefit of  
56 direct instruction or practice, to discriminate *individual* faces in a single glance (Tanaka, 2001).  
57 Although face expertise might be biologically based, as new born human infants prefer looking at  
58 human faces relative to non-face stimuli (e.g., Goren, Sarty, & Wu, 1975), it could also be influenced  
59 by the extensive within-category face experience that humans accumulate throughout the course of  
60 their life times. Thus, while non-face and face expertise differ in their developmental trajectories and  
61 learning protocols, both share the behavioral characteristics of quick and accurate within-category  
62 discrimination. However, an open question is whether within-category discrimination of faces and non-  
63 face objects of expertise rely on different or shared neural mechanisms.

64           According to the *modular account* of object recognition, face recognition is supported by a  
65 system that is exclusively dedicated to faces whereas a different and independent system supports the  
66 recognition of non-face objects, including objects from expert categories (e.g., Kanwisher, 2000). In  
67 contrast, the *expertise account* states that the putative face-specific system is domain-general by  
68 processing any object domain with a fixed set of diagnostic features (i.e., visually homogenous), for  
69 which expertise at within-category discrimination exists (e.g., Bukach, Gauthier, & Tarr, 2006; Tarr &  
70 Gauthier, 2000). Although the latter account has accumulated substantial amount of evidence over the  
71 last decade, there is still an ongoing debate as to whether face selective mechanisms can be recruited by  
72 expert non-face object domains.

73

74 *Category discrimination of faces and non-face expert objects*

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

88           However, a growing body of evidence have shown that the areas sensitive to face stimuli are  
89 also sensitive to objects from expert categories. Like faces, objects from expert categories (e.g., birds,  
90 cars, dogs) evoke an enhanced ERP response at around 170 ms in occipito-temporal channels relative  
91 to objects from non-expert categories (Busey & Vanderkolk, 2005; Rossion, Gauthier, Goffaux, Tarr,  
92 & Crommelinck, 2002; Scott, Tanaka, Sheinberg, & Curran, 2006; 2008; Tanaka & Curran, 2001).  
93 Moreover, the N170 to faces diminish in the presence of objects of expertise, relative to control  
94 categories, suggesting that face and non-face expert categories recruit related neural mechanisms  
95 (Gauthier, Curran, Curby, & Collins, 2003; Rossion, Kung, & Tarr, 2004; Rossion, Collins, Goffaux, &  
96 Curran, 2007). Studies using fMRI have shown that objects from non-face expert categories evoke a  
97 greater BOLD response in both the OFA and the FFA relative to non-face expert categories (e.g.,  
98 Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999;  
99 Gauthier & Tarr, 2002; McGugin, Gatenby, Gore, & Gauthier, 2012; McGugin, Van Gulick, Tamber-

100 Rosenau, Ross, & Gauthier, 2015; Xu, 2005). Grey matter thickness in the FFA also predicts the ability  
101 to recognize objects from expert categories, showing an effect that cannot be attributed to attention  
102 (McGugin, VanGulick & Gauthier, 2016). Consistent with the expertise account, the putative face-  
103 selective mechanisms are similarly engaged by faces and non-face expert domains (e.g., Bukach,  
104 Gauthier, & Tarr, 2006; Tarr & Gauthier, 2000).

105         Despite the growing body of evidence for the expertise account, there is disagreement as to  
106 whether these mechanisms are modular or domain-general (Gauthier, 2017). On the one hand, a few  
107 studies have failed to replicate the expertise effect, which are often cited as evidence against the  
108 expertise account (Grill-Spector, Knouf, & Kanwisher, 2004; Op de Beeck, Baker, DiCarlo, &  
109 Kanwisher, 2006; Yue, Tjan, & Biederman, 2006). For example, in an fMRI study, car experts failed to  
110 show a disproportionate response to cars in face-selective areas (Grill-Spector et al., 2004). On the  
111 other hand, all these studies have been criticized for their methodology (for a discussion, see Gauthier,  
112 2017). For example, experts with *modern* cars were tested with *antique* cars in the scanner (Grill-  
113 Spector et al., 2004). Perhaps more importantly, the rate of replication of the expertise effect is  
114 substantially higher than the rate of non-replication, and the effect has been shown using a wide range  
115 of methods. However, given the lack of agreement, the current debate could be advanced by examining  
116 a novel and important prediction by the expertise account, namely, whether the neural code of  
117 subcategories in the face and a non-face expert domain rely on shared mechanisms.

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### 119 *Within-category discrimination of faces and non-face expert objects*

120         Adaptation paradigms have played a crucial role in examining the neural mechanisms of *within-*  
121 *category* discrimination of faces. With this method, repeated presentations of the same stimulus  
122 dimension (e.g., face identity) attenuate the evoked neural response, arguably by decreasing the  
123 responsiveness in the neural units (i.e., columns) encoding that dimension. Importantly, a change in  
124 stimuli dimension (e.g., a different face identity) recovers the signal by presumably recruiting a

125 different and nonadapted neural population (Grill-Spector & Malach, 2001; Kourtzi, & Grill-Spector,  
126 2005). Adaptation studies with ERPs have shown that faces, but not cars, produce a rebound from  
127 adaption in occipito-temporal channels at about 250 ms after stimulus onset (e.g., Schweinberger,  
128 Huddy, & Burton, 2004). This indicates that cortical areas in the VTC discriminate face identities at  
129 around 250 ms. Moreover, adaptation paradigms with fMRI have revealed neural sensitivity to  
130 different face identities in both the OFA and the FFA, but not in areas that do not show face selectivity  
131 (e.g., Gauthier, Tarr, Moylan, Skudlarski, Gore, & Anderson, 2000; Loffler, Yourganov, Wilkinson, &  
132 Wilson, 2005; Natu et al., 2016). Thus, the same cortical areas are involved in category- and individual  
133 level discrimination of faces, albeit at different time scales; category discrimination occurs earlier than  
134 individual level discrimination.

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

150           The current study directly measured a within-category discrimination response to faces and a  
151 non-face expert objects, using a novel and implicit visual discrimination paradigm (FPVS: Fast  
152 Periodic Visual Stimulation) coupled with electroencephalography (EEG). Specifically, a group of  
153 expert and novice bird watchers were shown sequences of birds or faces, whereby the same object  
154 image (Figure 2: family-level birds; species-level birds; faces) were presented at a periodic rate of six  
155 images per second (i.e., 6.0 Hz), with size varying randomly at every cycle to prevent pixel-based  
156 adaptation (Liu-Shuang, Norcia, & Rossion, 2014). A different within-category “oddball” was  
157 periodically interleaved at every 5<sup>th</sup> cycle (i.e., 1.20 Hz). Thus, while the base signal (6.0 Hz and  
158 harmonics) indexed neural mechanisms that responded similarly to the base and oddball objects, the  
159 oddball signal (1.20 Hz and harmonics) indexed the mechanisms that responded differently to the base  
160 and the oddball objects. Participants were instructed to fixate a cross, centered within the objects and  
161 detect random changes in color from red to green. This task ensured that the participants maintained a  
162 constant level of attention in the center of the object, while performing a task orthogonal to the images,  
163 which have been shown to drastically reduce expertise effects related to selective attention (Harel et al.,  
164 2010; McGugin et al., 2014). This approach allowed us to obtain a behavior free (i.e., implicit) measure  
165 of within-category discrimination in *both* experts and novices that is based on the principles of neural  
166 adaptation (for review, see Norcia, Appelbaum, Ales, Cottureau, & Rossion, 2015; Rossion, 2014).

167           The claim that objects of expertise and faces partly share neural mechanisms was tested based  
168 on the assumption that neural responses that are generated within the same neural mechanisms, will  
169 correlate more than neural responses that are generated by different mechanisms (Reeder, Stein, &  
170 Peelen, 2016; McGugin, Ryan, Tamber-Rosenau, & Gauthier, 2017; Peelen, Fei-Fei, & Kastner, 2009).  
171 The bird oddballs were perceptually salient as they varied in both external contours and internal shapes,  
172 which ensured a robust discrimination signals in *both* the novices and the experts that could be



173 correlated with that of the faces<sup>1</sup>. The family- and species-level bird conditions varied in their shape  
174 homogeneity (e.g., external contour overlap), rather task demands, since there was no explicit  
175 categorization task associated with the images. The modular account, which states that two independent  
176 mechanisms are used for within-category discrimination of faces and non-face objects, predicts that for  
177 both the experts and the novices, the face and bird discrimination responses (1.20 Hz and harmonics)  
178 should not correlate, while family- and species-level birds should correlate despite differences in  
179 homogeneity and overall response magnitude (Figure 1, top row). In contrast, the expertise account,  
180 which states that expert categories share discrimination mechanisms, predicts that the discrimination  
181 response to the birds and the faces would correlate to a larger degree in the experts than in the novices,  
182 while family- and species-level birds should correlate with each other in both groups despite  
183 differences in homogeneity and overall response magnitude (Figure 1, middle row). Finally, both the  
184 modular and the expertise account predict that all object conditions (birds [family-level, species-level]  
185 and faces) in both the expert and the novices, should correlate in the base-response (6.00 Hz and  
186 harmonics), since these responses primarily originate in low-level systems that are shared by all  
187 categories (Figure 1, bottom row). Thus, a dissociation between the experts and the novices should be  
188 specific to the *discrimination* response of faces and birds.

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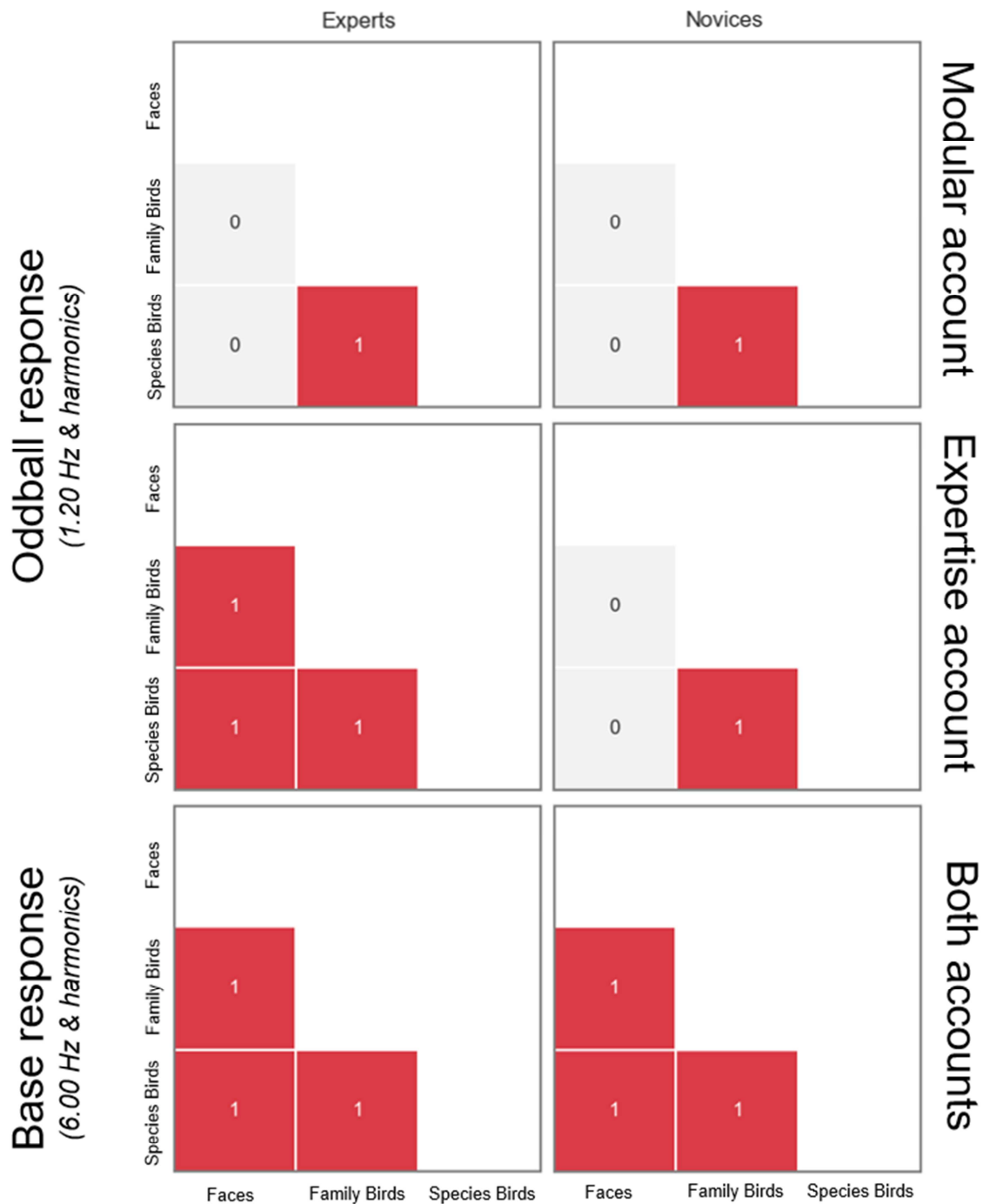
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<sup>1</sup> This approach is different than other studies using the FPVS oddball paradigm in the sense that the bird oddballs were easily perceived due to for example differences in external object contours (see video example of trial in supplemental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



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195 *Figure 1. Top row: predictions by both the modular and the expertise accounts for the base response*196 *(6.00 Hz and harmonics). Middle row: predictions by the modular account for the oddball response*197 *(1.20 Hz and harmonics). Bottom row: predictions by the expertise account for the oddball response*198 *(1.20 Hz and harmonics).*

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## Methods

### *Participants*

Sixteen expert participants, ranging in age from 20–57 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 20–70 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; Hagen et al., 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 & Curran, 2001; Tanaka & 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 ( $n = 15$ ,  $d' = 2.10$ ,  $SD=0.55$ ,  $range = 0.98-2.77$ ) compared to the novices ( $n = 15$ ,  $d' = 0.90$ ,  $SD=0.36$ ,  $range = 0.36-1.64$ ),  $t(24.14) = 7.14$ ,  $p < .001$ ). 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

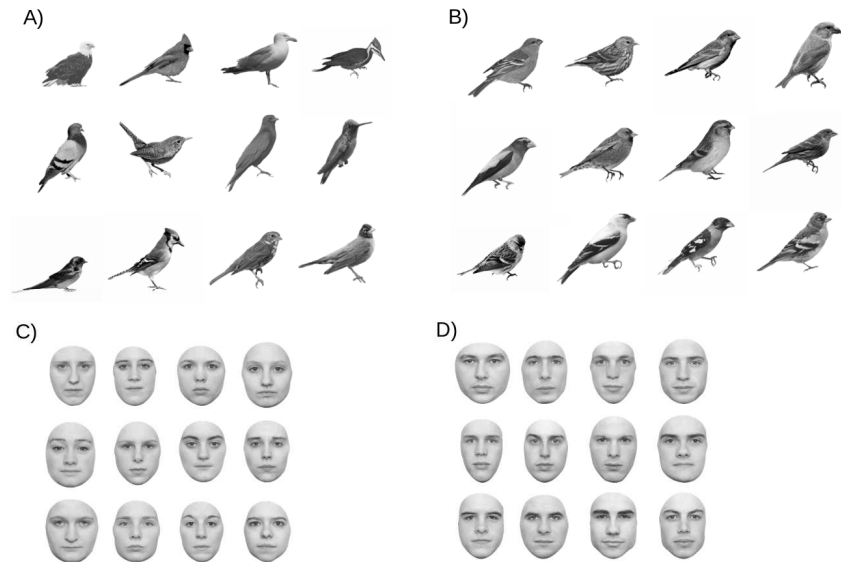
225 recruited either from the off-campus community or University of Victoria's online recruitment system  
226 for undergraduate students. Four additional novices were excluded from the data analysis because of  
227 technical issues with the EEG recording ( $n = 4$ : triggers were not recorded).

228

### 229 *Stimuli*

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

249



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

265

266

267 *Procedure.* The experiment consisted of 6 sixty-second trials during which EEG was recorded.

268 In a given trial, bird (family- or species-level) or human face (female or male) images were presented

269 at a rate of 6 cycles per second (6.00 Hz = base stimulation frequency) through sinusoidal contrast

270 modulation using a custom Matlab script (Figure 3; Liu-Shuang, et al., 2014; The Mathworks). In the

271 presentation sequence, an adapting base image of a family-level bird (e.g., Robin), a species-level bird

272 (e.g., Purple Finch) or a face (e.g., Face A) was presented repeatedly for four consecutive cycles, with

273 each cycle lasting for 167.7 ms. A different within-category “oddball” image (e.g., family-level:

274 Woodpecker; species-level: House Finch; face: Face B) was randomly selected from the remaining of

275 the 11 category images and displayed at every 5<sup>th</sup> presentation cycle ( $F/5 = 1.20$  Hz = oddball  
276 stimulation frequency). Importantly, the size of each image varied randomly between 80% and 120% in  
277 2% steps at every cycle of presentation to ensure that the low-level visual properties (e.g., retinal  
278 position of edge information) varied at every cycle (Liu-Shuang et al., 2014). Thus, the change in birds  
279 (or faces) at the oddball frequency ( $F/5 = 1.20$  Hz) should evoke a periodic oddball response in higher-  
280 level mechanisms that are invariant to the change of object size, but not in lower-level mechanisms that  
281 are not invariant to stimuli size (e.g., retinotopically organized areas).

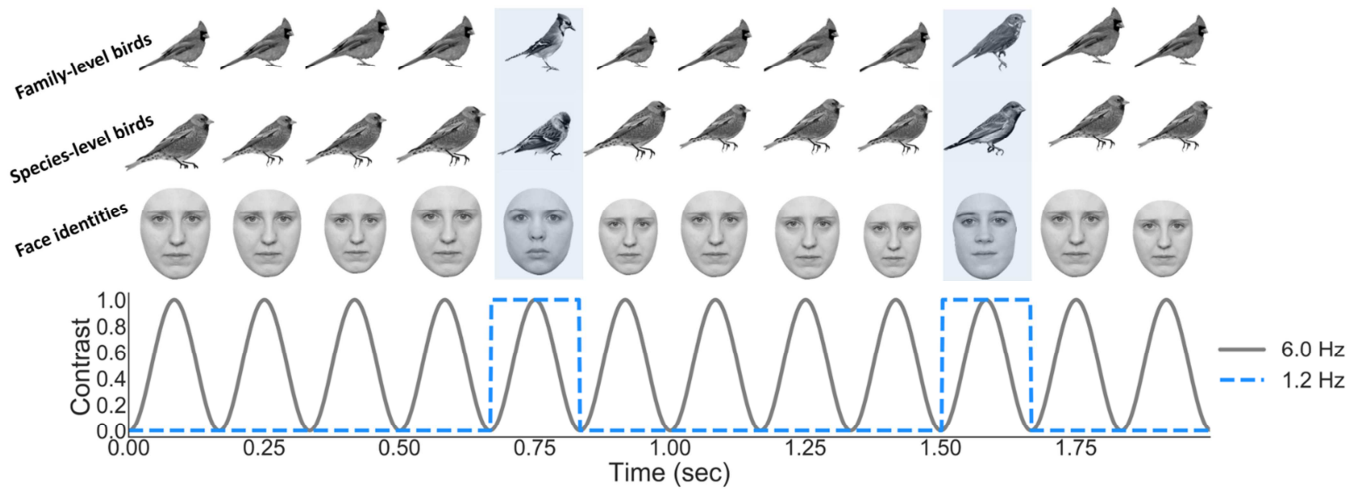
282         During the image presentation, participants were instructed to fixate a cross - centred in the  
283 birds and centered between the eyes of the faces - and press the space-bar every time it changed colour  
284 from red to green (duration of color change: 200 ms). The colour-change occurred randomly. This task  
285 ensured that every participant maintained attention in the center of the object throughout each  
286 presentation cycle, while also performing an orthogonal task to the images, which have been shown to  
287 drastically reduce expertise effects related to selective attention (Harel et al., 2010; McGugin et al.,  
288 2014).

289         Two of the six trials displayed base and oddball birds that differed at the family level (e.g., base  
290 bird: robin, oddball bird: sparrow). Two of the six trials displayed base and oddball birds that differed  
291 at the species level (e.g., base bird: Gold Finch, oddball bird: House Finch). Two of the six trials  
292 displayed images of faces whereby one trial contained base and oddball female faces (e.g., base face:  
293 female face A, oddball face: female face B) and one trial were composed of male faces (e.g., base face:  
294 male face A, oddball face: male face B). Thus, the entire experiment consisted of 240 seconds of image  
295 presentation. The order of the trials was counterbalanced across participants such that half of the  
296 participants were presented with birds followed by faces and the other half with faces followed by  
297 birds.

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

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### 315 *EEG Acquisition* □

316 The electroencephalogram (EEG) was recorded using a montage of 36 electrode sites in  
317 accordance to the extended international 10-20 system (Jasper, 1958). Signals were acquired using  
318 Ag/AgCl ring electrodes mounted in a nylon electrode cap with an abrasive, conductive gel

319 (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). Signals were amplified by low-noise electrode  
320 differential amplifiers with a frequency response of DC 0.017-67.5 Hz (90 dB--octave roll off) and  
321 digitized at a rate of 250 samples per second. Digitized signals were recorded to disk using Brain  
322 Vision Recorder software (Brain Products GmbH, Munich, Germany). The impedances were  
323 maintained below 10 k $\Omega$ . The EEG was recorded using the average reference.

324

### 325 *Data analysis*

326 Preprocessing was conducted with a customized software (Letswave 5:  
327 <http://nocions.webnode.com/letswave>) running in the Matlab environment (The Mathworks). EEG  
328 data was band-pass filtered (0.1 - 100 Hz zero-phase Butterworth filter, 24 dB/octet slope), and all  
329 channels were rereferenced to the common average reference. Filtered data was first cropped down to  
330 an integer number of 1.20 Hz that containing the start of the first presentation cycle and the end of the  
331 last presentation cycle (0 s to 60 s, 72 oddball cycles, 15000 time bins). The segmented sequences were  
332 averaged within each participant separately for each condition in the time domain to increase signal-to-  
333 noise by reducing EEG activity non-phase locked to the stimulation (e.g., Liu-Shuang, Torfs, &  
334 Rossion, 2016). To extract amplitude spectra for all channels, a Fast Fourier Transform was applied to  
335 the averaged segments (frequency resolution, 1/60, i.e., 0.017 Hz). To consider noise variations across  
336 the EEG spectrum, signal-to-noise (SNR) was computed as the ratio of the amplitude in each frequency  
337 bin to the average amplitude of the 10 surrounding frequency bins in each direction, excluding the two  
338 directly neighbouring bins. Similarly, Z-scores were computed for each bin by subtracting its  
339 amplitude by the average signal of the 20 surrounding bins (excluding the neighbours) and dividing it  
340 by the standard deviation of the 20 surrounding bins.

341 To determine the number of harmonics included in the statistical comparison between  
342 the experts and the novices in the face and bird conditions, the amplitude data from the frequency  
343 domain for each condition (group and object category) was averaged across participants and channels.



344 Next, Z-scores for the base- and oddball stimulation rate, and its 8 harmonics were extracted and  
345 analyzed until they were no longer significant (Dzhelyova & Rossion, 2014; Liu-Shuang et al., 2014).  
346 A threshold of significance was placed at a Z-score of  $z > 3.10$  ( $p < .001$ , one-tailed; i.e., signal > noise;  
347 e.g., Liu-Shuang et al., 2016, Xu, Liu-Shuang, Rossion, & Tanaka, 2017). For the base frequency, the  
348 harmonics were analyzed up to the 6<sup>th</sup> harmonic ( $6F = 36.0$  Hz). For the oddball frequency, the  
349 harmonics were analyzed up to the 7<sup>th</sup> harmonic ( $7F/5 = 8.40$  Hz). The 5<sup>th</sup> harmonic of the oddball  
350 response ( $5F/5 = 6.0$  Hz) was excluded from the oddball analysis because it overlaps with the  
351 fundamental frequency of the base response ( $F = 6.0$  Hz).

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## Results

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356 EEG data

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358 *Frequency domain analysis: group analysis*

359 Distinct peaks were observed in the frequency domain at the exact rate of visual stimulation and  
360 associated harmonics (Figure 4). Regions of interest (ROIs) for the base and oddball responses were  
361 defined based on the respective scalp topographies and by the channels with maximal response (Figure  
362 4). The maximal response of the base stimulation rate (6.0 Hz) was located at medial occipital  
363 channels (Oz, POz) for every condition. This topography is similar to previous studies using the same  
364 task with faces (e.g., Liu-Shuang et al., 2014), words (Lochy, Van Belle, & Rossion, 2015), and objects  
365 (e.g., Jacques, Retter, & Rossion, 2016), and indicate that the visual system synchronized to the visual  
366 stimulation. In contrast to the base stimulation response, the maximal response of the oddball  
367 frequency (1.20 Hz) was located at occipito-temporal channels (PO7, PO8, P7, P8) for both the birds  
368 and face conditions. This topography is consistent with previous studies using the same task with faces

369 (e.g., Liu-Shuang et al., 2014), words (Lochy et al., 2015), and objects (e.g., Jacques et al., 2016), and  
 370 corresponds with cortical areas involved in high-level visual discrimination (e.g., Scott et al., 2006;  
 371 2008).

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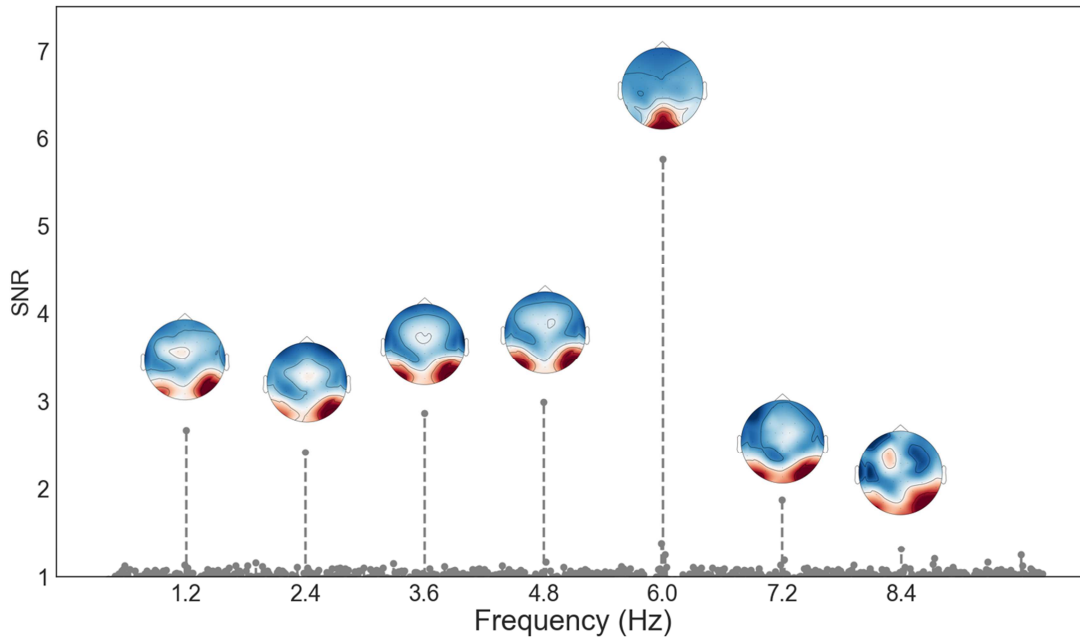
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383 *Figure 4.* EEG spectra from 0.37 to 9.83 Hz for the average across all electrodes, both groups, and  
 384 three object conditions.

385

386 *Base response (6.0 Hz and harmonics)*

387 The visual response in each participant was quantified by aggregating the signal of the 6  
 388 first harmonics averaged across channels Oz and POz. We report uncorrected p-values for the post-hoc  
 389 tests in this and subsequent analysis. Figure 5 presents the aggregate SNR for the base stimulation rate  
 390 in medial-occipital channels as a function object category and group. The SNR data for the base  
 391 response were analyzed in a mixed-design analysis of variance (ANOVA) using object category  
 392 (family-level bird, species-level bird, faces) as a within-subjects factor and group (experts, novices) as  
 393 a between-subjects factor. There was no main effect of group,  $F(1,30) = 0.22$ ,  $p = 0.646$ , *generalized*

394 *eta squared* = 0.0053. The main effect of object category was significant,  $F(2,60) = 11.21, p < 0.001,$   
395 *generalized eta squared* = 0.09. Post-hoc tests showed that Faces ( $M = 4.33; SE = 0.40$ ) evoked a larger  
396 signal than both Family-level birds ( $M = 3.38; SE = 0.27$ ) and Species-level birds ( $M = 3.60; SE = 0.33,$   
397  $ps < 0.003$ ), and that Family- and Species-level birds evoked similar responses ( $p = 0.255$ ). The two-  
398 way interaction between group and object category did not interact with object category,  $F(2,60) =$   
399  $2.24, p = 0.116, \textit{generalized eta squared} = 0.0188^2$ .

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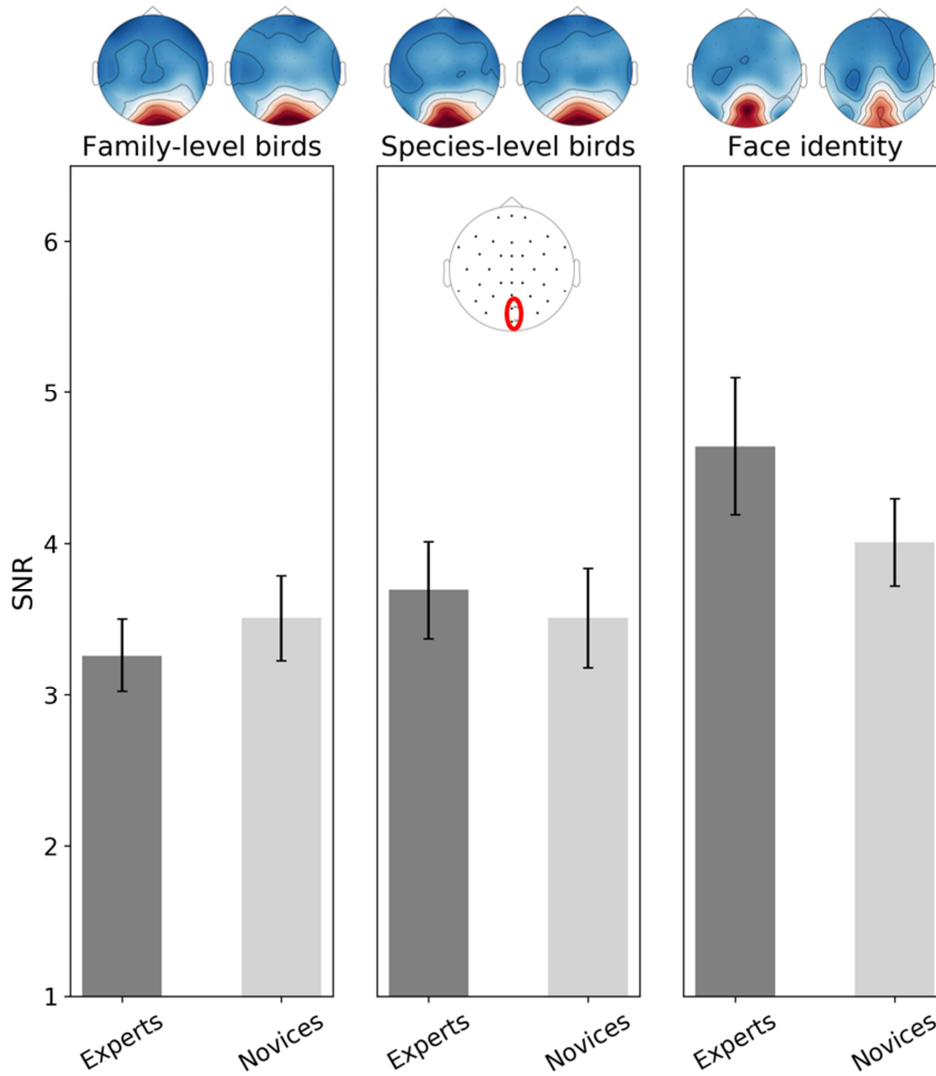
<sup>2</sup> Bayesian tests yielded a Bayes factor (BF) of 2.85 in favor of the model that only included the main effects, corresponding with the original analysis. **The small value could indicate inadequate power.**

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422 *Figure 5. SNR aggregated across the first 6 harmonics at medial-occipital channels (Oz, POz) and the*423 *associated scalp topography. Error bars represent 95% confidence intervals.*

424

425 *Oddball Discrimination Response (1.20 Hz and harmonics)*

426           The visual response in each participant was quantified by aggregating the signal of the 7 first  
427 harmonics, excluding the 5<sup>th</sup> harmonic ( $5F/F = 6.00$  Hz) averaged across channels PO7, PO8, P7, and  
428 P8. Figure 6 presents the aggregate SNR for the oddball stimulation rate in occipito-temporal channels  
429 as a function object category and group. The SNR data for the oddball response were analyzed in a  
430 mixed-design analysis of variance (ANOVA) using object category (family-level bird, species-level  
431 bird, faces) as a within-subjects factor and group (experts, novices) as a between-subjects factor. There  
432 was no main effect of group,  $F(1,30) = 0.17$ ,  $p = 0.687$ , *generalized eta squared* = 0.0037. The main  
433 effect of object category was significant,  $F(2,60) = 48.97$ ,  $p < 0.001$ , *generalized eta squared* = 0.34.  
434 Post-hoc tests showed that Family-level birds ( $M = 3.01$ ;  $SE = 0.26$ ) evoked larger signals than  
435 Species-level birds ( $M = 2.41$ ;  $SE = 0.19$ ,  $p < 0.001$ ) and that both Family- and Species-level birds  
436 evoked larger signal than Faces ( $M = 1.66$ ,  $SE = 0.11$ ,  $ps < 0.001$ ). The two-way interaction between  
437 group and object category was not significant,  $F(2,60) = 2.52$ ,  $p = 0.089$ , *generalized eta squared* =  
438 0.026<sup>3</sup>.

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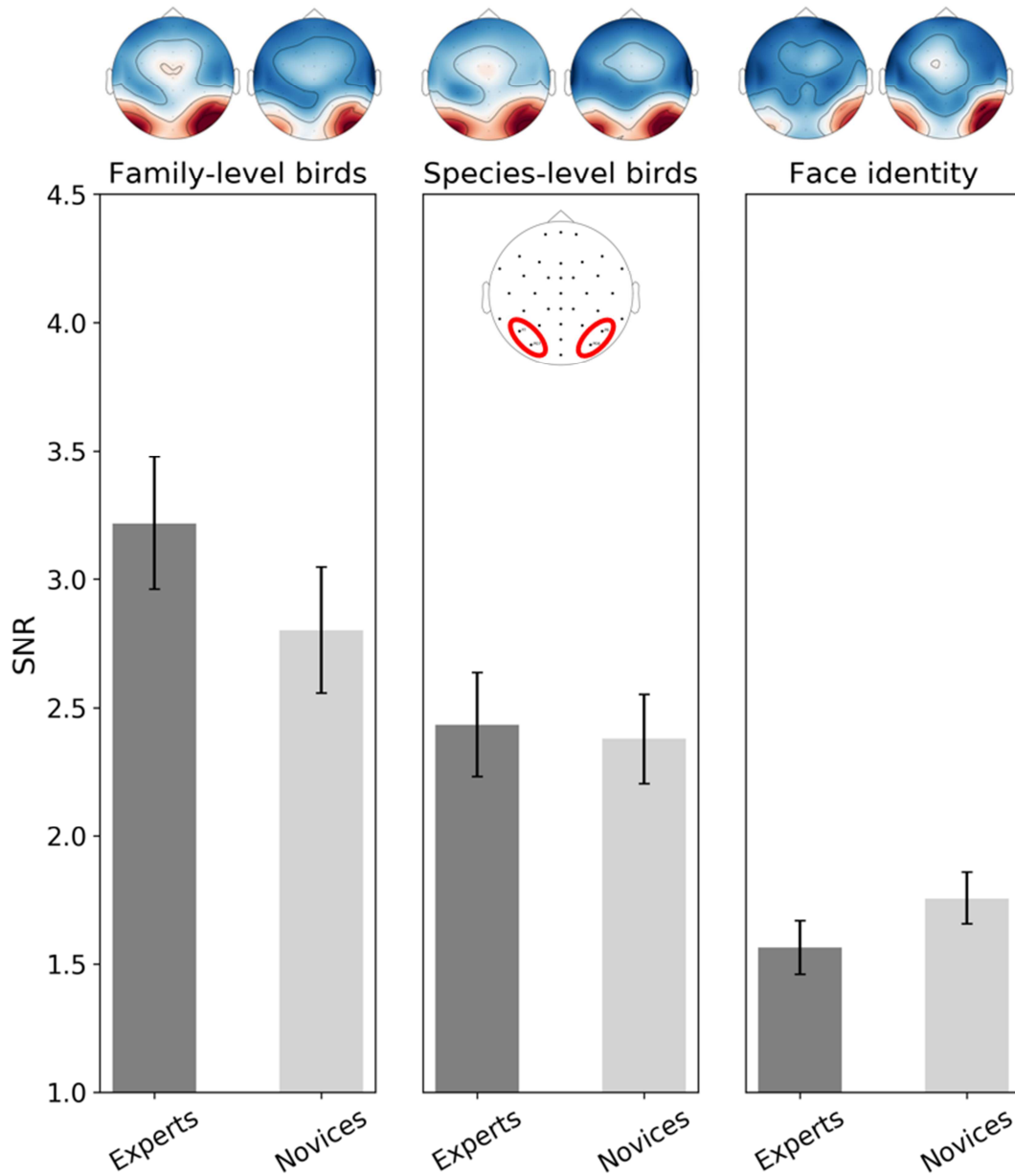
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<sup>3</sup> Bayesian tests yielded a Bayes factor (BF) of 1.89 in favor of the model that only included the main effects, corresponding with the original analysis. The small value could indicate inadequate power.

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452 *Figure 6.* SNR aggregated across the first 7 harmonics, excluding the 5<sup>th</sup> harmonic ( $5F/F = 6.00$  Hz) at

453 occipito-temporal channels (PO7, P7, PO8, P8) and the associated scalp topography. Error bars

454 represent 95% confidence intervals.

455

456 *Correlation of the EEG response of each object category*

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

462 For the base response (6.00 Hz and harmonics) at medial-occipital channels, a significant  
463 correlation was found across all object categories for both the experts ( $r_{fb\&f} = 0.59$ ,  $p_{fb\&f} = 0.016$ , 95%  
464  $CI_{fb\&f} [0.14, 0.84]$ ;  $r_{sb\&f} = 0.72$ ,  $p_{sb\&f} = 0.002$ , 95%  $CI_{sb\&f} [0.35, 0.90]$ ;  $r_{sb\&fb} = 0.82$ ,  $p_{sb\&fb} < 0.001$ , 95%  
465  $CI_{sb\&fb} [0.54, 0.94]$ ) and for the novices ( $r_{fb\&f} = 0.62$ ,  $p_{fb\&f} = 0.011$ , 95%  $CI_{fb\&f} [0.17, 0.85]$ ;  $r_{sb\&f} = 0.53$ ,  
466  $p_{sb\&f} = 0.033$ , 95%  $CI_{sb\&f} [0.05, 0.81]$ ;  $r_{sb\&fb} = 0.64$ ,  $p_{sb\&fb} = 0.007$ , 95%  $CI_{sb\&fb} [0.22, 0.86]$ ), and there  
467 was no difference between the two groups ( $p_{fb\&f} = 0.462$ , one-tailed;  $p_{sb\&f} = 0.209$ , one-tailed;  $p_{sb\&fb} =$   
468  $0.321$ , two-tailed) (Figure 7). Thus, irrespective of the group, the responsiveness (6.00 Hz and  
469 harmonics) to one object category predicted the responsiveness to another category at the medial-  
470 occipital channels.

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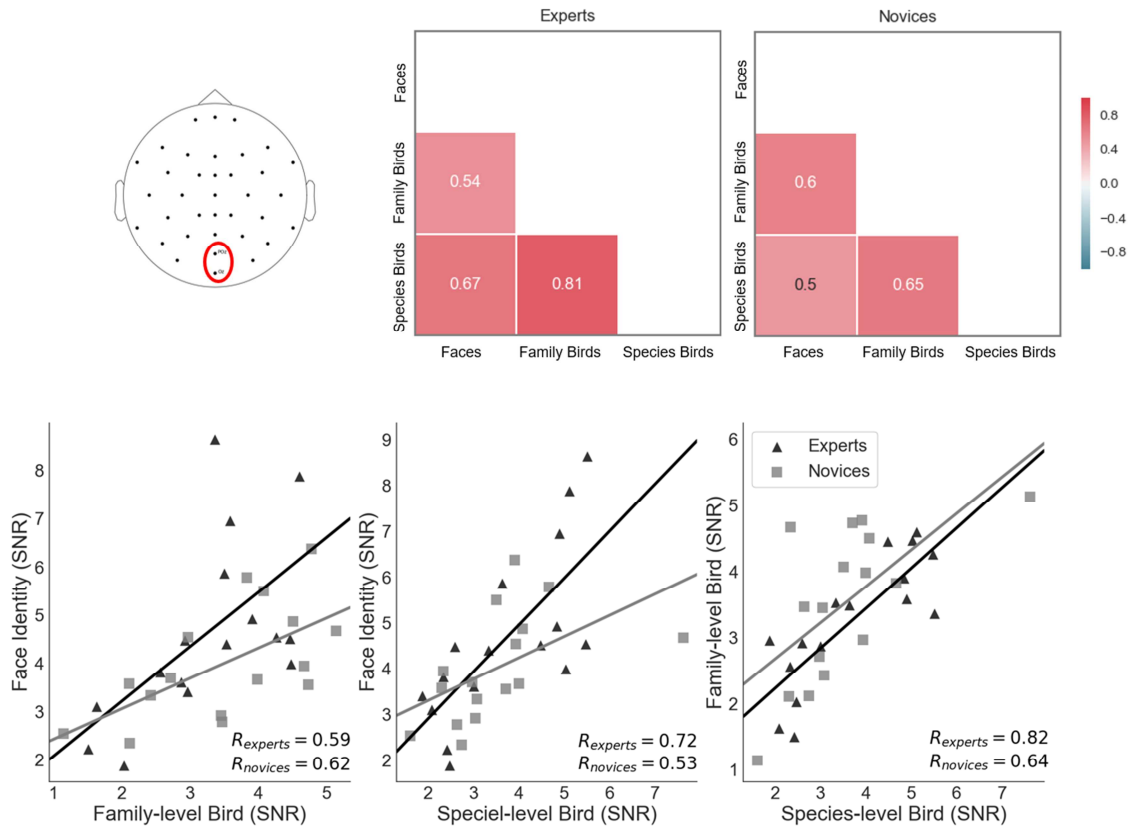
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489 *Figure 7.* Correlations of the base response (SNR) at medial-occipital channels to Face identity and

490 Family-level birds, Face identity and Species-level birds, and Family-level birds and Species-level

491 birds.

492

493 In contrast to the base response at medial-occipital channels, the oddball response (1.20 Hz and

494 harmonics) at the more anterior occipito-temporal channels to Family-level birds correlated with Faces

495 in the experts ( $r = 0.76$ ,  $p < 0.001$ , 95% CI [0.42, 0.91]), but not in the novices ( $r = 0.10$ ,  $p = 0.706$ ,



496 95% CI [-0.42, 0.57]), and importantly, the difference between the correlations was significant ( $p =$   
497 0.012, one-tailed) (Figure 8). Similarly, the oddball discrimination response at occipito-temporal  
498 channels to Species-level birds correlated with Faces in the experts ( $r = 0.69$ ,  $p = 0.003$ , 95% CI [0.29,  
499 0.88]), but not in the novices ( $r = 0.13$ ,  $p = 0.638$ , 95% CI [-0.39, 0.59]), and the difference between  
500 the correlations was significant ( $p = 0.034$ , one-tailed). In contrast, the oddball discrimination response  
501 at occipito-temporal channels to Family- and Species- level birds was significant in both the experts ( $r$   
502  $= 0.76$ ,  $p < 0.001$ , 95% CI [0.42, 0.91]) and the novices ( $r = 0.82$ ,  $p < 0.001$ , 95% CI [0.54, 0.93]), and  
503 there was no difference between the correlations in the two groups ( $p = 0.708$ , two-tailed). Thus, in the  
504 experts, the neural mechanism that discriminated different birds responded in a consistent manner with  
505 the neural mechanism that discriminated faces, while in the novices, the mechanism that discriminated  
506 different birds responded in a way that was not consistent with the mechanism that discriminated  
507 different faces.

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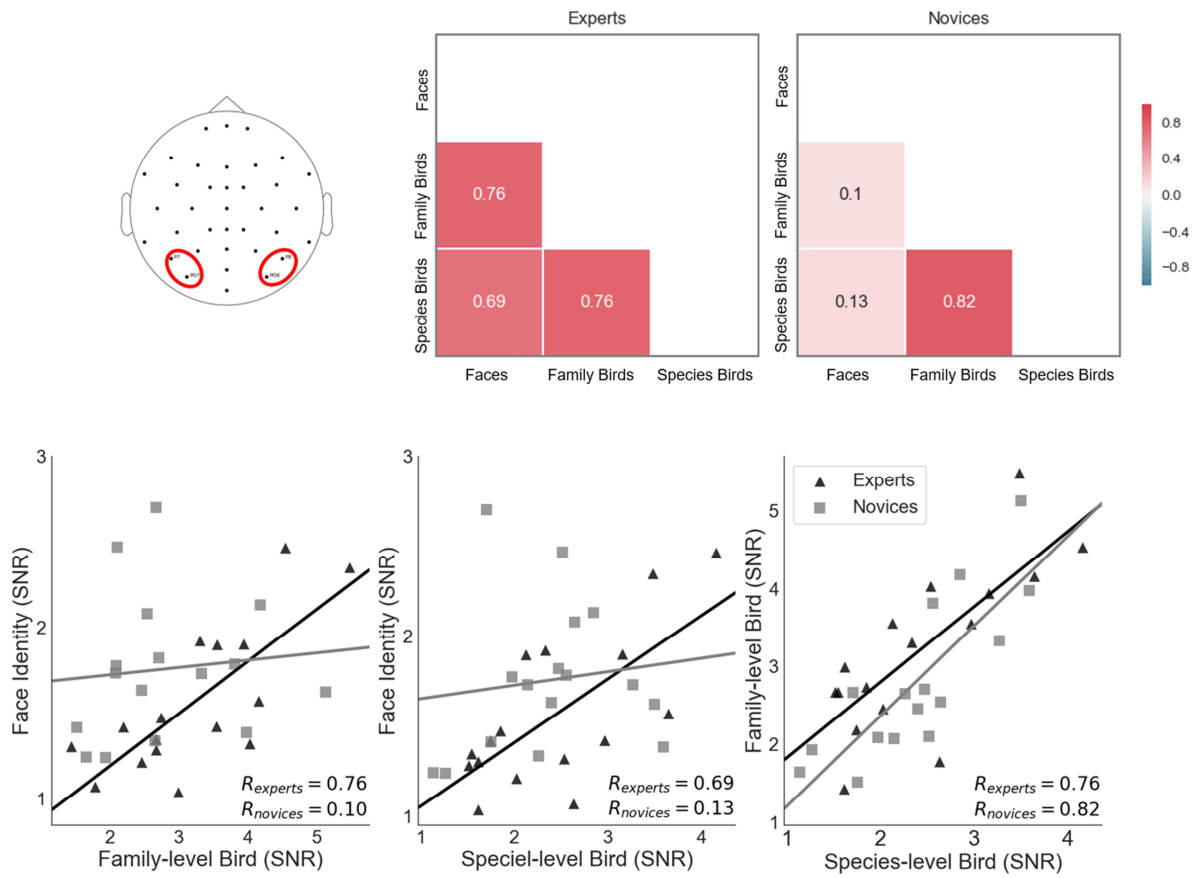
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530 *Figure 8.* Correlations of the discrimination response (SNR) at occipito-temporal channels to Faces and  
 531 Family-level birds, Faces and Species-level birds, and Family-level birds and Species-level birds.

532

533           The main findings were that the experts and novices showed similar overall base (6.00 Hz and  
534 harmonics) and oddball (1.20 Hz and harmonics) responses to birds (family- and species-levels) and  
535 faces. Moreover, for the base response, there was a strong positive correlation between all object  
536 categories (birds [family- and species-levels] and faces), which did not differ between the experts and  
537 the novices. However, for the base signal one should note the low precision as indicated by the large  
538 CIs. In contrast, for the oddball discrimination response, the experts showed a strong positive  
539 correlation across all object categories, while novices showed a strong correlation between the birds  
540 (family-level vs species-level), but no correlation between birds and faces. The dissociation between  
541 experts and novices that was specific to the discrimination response for faces and birds is consistent  
542 with the claim of the expertise account that proposes a shared neural mechanism for faces and objects  
543 of expertise.

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## Discussion

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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 (Figure 4). Faces evoked a larger base response at the medial-occipital channels than did the birds (family- and

558 species- levels; Figure 5). This difference could be caused by the larger visual angle of the faces than  
559 of the bird by evoking a larger retinotopic neural population response, or the faces could have attracted  
560 more attention than did the birds, as it has been shown that the responses at medial channels are  
561 influenced by selective attention (e.g., Morgan, Hansen, & Hillyard, 1996; Müller et al., 2006).  
562 Importantly, the experts and the novices did not differ in their base response to the birds or to the faces,  
563 suggesting that the experts did not allocate more selective attention to the birds than did the novices  
564 (Figure 5). The medial-occipital topography for the base response is consistent with previous studies  
565 examining face, non-face, and letter recognition, and the claim that it indexes neural processes shared  
566 by all object categories (e.g., low-level processes; Liu-Shuang et al., 2014; Lochy et al., 2015; Jacques  
567 et al., 2016).

568         Distinct signal peaks were also observed at the exact rate of within-category oddball stimulation  
569 (1.20 Hz and harmonics) in the family- and species-level bird and face categories (Figure 4). However,  
570 unlike the base response, the oddball response was maximal at the occipito-temporal channels and was  
571 larger for the birds than the faces (Figure 6). The larger response to the birds as compared to the faces  
572 is likely explained by the larger difference in external contour and internal features in the former as  
573 compared to the latter (Figure 2). The discrimination responses to birds or faces did not differ in the  
574 expert and novices indicating that the face and bird oddballs were discriminated with equal ease by  
575 both groups. The same scalp topography has previously been reported in studies of face, non-face, and  
576 word recognition (Liu-Shuang et al., 2014; Lochy et al., 2015; Jacques et al., 2016), and is consistent  
577 with the claim that the oddball response is reflecting higher-level visual discrimination responses  
578 located in VTC.

579         To examine whether the same neural processes contributed to the within-category  
580 discrimination of the birds and the faces in experts and novices, we correlated the discrimination signal  
581 (1.20 Hz and harmonics) evoked by the three object categories. Previous work has showed a positive  
582 correlation between neural responses evoked by different stimuli and that are generated by the same

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

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

606 The current study contributes novel evidence to the question of whether the processes of face  
607 recognition and expert object recognition recruit dissociated or shared neural mechanisms. Previous

608 work has shown that both face and non-face expert *categories* are associated with enhanced N170 and  
609 N250 ERP components. Moreover, faces and non-face expert categories evoke similar differential  
610 responses in putative face-selective areas of the VTC, such as in the OFA and the FFA (Gauthier et al.,  
611 2000; Gauthier et al., 1999; Gauthier & Tarr, 2002; McGugin et al., 2012). Although these studies  
612 show that face and non-face expert recognition share discrimination processes at the *category* level, no  
613 studies to date have directly compared the neural processes involved in *within-category* discrimination  
614 of both faces and objects. The current study directly evaluated within-category discrimination by  
615 measuring the differential response generated from periodically interspersing within-category  
616 “oddball” objects in a sequence of adapting base objects. In addition, the discrimination response was  
617 disentangled from processes involved in explicit task demands, given that the participants were  
618 performing a concurrent orthogonal task (colour detection in the fixation cross). Thus, using a global  
619 neural measure, the current study adds to the existing literature by suggesting that face and non-face  
620 expert categories overlap not only in terms of category discrimination, but also in terms of within-  
621 category discrimination.

622         What processes could account for the patterns observed in the experts and the novices? Both  
623 face and non-face objects of expertise are recognized at specific category levels (Johnson & Mervis,  
624 1997; Tanaka, 2001; Tanaka & Taylor, 1991), for which fine grained internal shape information plays a  
625 crucial role (Collin & McMullen, 2005; Hagen et al., 2016). It is possible that the neural processes that  
626 was shared between faces and birds in the experts, but not in the novices, contributed to efficient  
627 encoding of internal diagnostic shape information. For example, face-specific areas could contain  
628 neuronal units (i.e., columns) that are especially suited for encoding the internal diagnostic information  
629 for recognition at specific category levels, and that learning processes incorporate these neuronal units  
630 into a stable population representation of a given category. Indeed, behavioral work has showed that  
631 both face and expert recognition of birds rely on shapes in a middle bandwidth of spatial frequencies  
632 (Costen, Parker, & Craw, 1994; Hagen et al., 2016), providing some evidence to suggest that

633 diagnostic shape information for both object categories are carried by the same type of shape  
634 information.

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

652         Face and object expertise differ in terms of its acquisition. Within-category discrimination of  
653 faces are enforced by the social demands to individuate faces by identity, and is potentially linked with  
654 a genetic component, as newborn infants prefer human faces over other objects (Goren, Sarty, & Wu,  
655 1975; Johnson, Dziurawiec, Ellis, Morton, 1991). In contrast, object expertise, such as birdwatching,  
656 train recognition, dog judging, is a specialized ability that is typically acquired through deliberate and  
657 extensive practice in early or later adulthood by a relatively small number of people in the population.

658 Based on differences in learning procedures (implicit vs. deliberate), the age of acquisition (early  
659 development vs. adulthood), and perhaps genetic influences, it is reasonable to expect that face and  
660 object expertise are subserved by different neural mechanisms. However, face and non-face object  
661 expertise both share the need to perform fine-grained within-category discriminations, and even if  
662 evolutionary pressures due to the adaptive behavior of face identification have given rise to such fine-  
663 grained feature “detectors”, it does not exclude them from being coopted by stimuli from other  
664 categories if the recognition-demands overlap with those of faces. Thus, logically speaking, if certain  
665 cortical areas are evolved for a certain category, it should not rule out the possibility for those areas to  
666 be at least partially coopted by other categories, if the underlying recognition demands are similar.

667         If shared mechanisms between faces and expert domains are mainly performing “fine-grained”  
668 analysis, one could speculate that face-bird correlations in the experts would be influenced by the  
669 shape-homogeneity of the birds. Specifically, since the species-level birds are more homogenous than  
670 family-level birds in terms of their external contours, then one could hypothesize that the former would  
671 isolate this face-specific mechanism to a larger degree than latter. The more isolated the mechanism,  
672 the larger the correlations. In the current study we did not find a stronger correlation between faces and  
673 species-level birds as compared to faces and family-level birds. However, one must be careful making  
674 strong claims about this prediction in the current study since the species-level birds used in this study  
675 were selected to vary in the external contours, so to generate discrimination signals in the novices that  
676 could be correlated with that of faces. Thus, to properly assess how shape homogeneity in expert  
677 categories influence face-overlap, future studies should carefully control for external contour  
678 homogeneity.

679         In summary, comparisons of the face-bird correlations in the experts and the novices revealed  
680 patterns that were consistent with the predictions of the expertise account. The current findings suggest  
681 that within-category discrimination of face and non-face expert objects rely on at least partially shared  
682 neural processes, while within-discrimination of faces and other non-face objects relies on different



683 neural systems. Although our findings are consistent with a substantial amount of previous research on  
684 expertise, this study provided novel evidence by using an implicit discrimination task to directly  
685 measure *within-category* discrimination processes of the global recognition system. Future work should  
686 examine the shared neural processes using a method with better spatial resolution. Here, real-world  
687 expertise was used as a model to test the nature of the face specific system; however, real-world  
688 expertise can also be a useful model for understanding general principles of how cortical mechanisms  
689 reorganize to match the demands of the ever-changing environment.

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Department of the Army position, policy, or decision.

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