Behavioral and neural correlates of domain-general object recognition ability

By

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To my parents, thank you for everything

ACKNOWLEDGMENTS

Kao and I once joked during a dinner with prospective graduate students that when describing what it's like to work with Isabel we sounded as though we were in some sort of fan club. I'd be more than happy to join that fan club, as would anyone who works with Isabel. It only took a semester or so for me to realize that Isabel was a great PhD advisor, but it took me a few years to appreciate how amazing of a mentor she is. She has taught me countless things, some small (there's no "h" after the "C" in "Cronbach"), and some large (like to celebrate accomplishments when you can). But, more than that, she somehow knows exactly how you're feeling about a paper, presentation, or situation and will tell you what you need to hear before you even ask for it. Simply put, she is kind, tenacious, patient, empathetic, humble, creative and honest and she inspires me every single day. So thank you to Isabel, for never trying to make it look easy, but always making it look fun.

To my parents, though it will never be enough, I hope I have thanked you for the relentless support and love. What I may not have thanked you for are the myriad of other things you have taught me. To my father, you've shown me what passion truly looks like. That if you're passionate about something, like coaching, then dragging a dozen teenagers around the state and even the country to races is actually something you want to do. To my mother, you've shown me the incredible power of humor. That finding the humor in things can make tough situations better and that humor can help you reach out to reluctant students or get an audience on your side (or just entertain yourself). And from both of my parents I've learned what sacrifice is. Whether it was during my childhood by reading aloud *Lord of the Rings* to me every night after teaching all day or financially supporting my college adventures to Greece or India or New Zealand, my parents have never missed a chance to put my needs ahead of theirs. I don't have any hope of being able to pay it back, but I will certainly try to pay it forward. It

took passion, sacrifice and lots of humor to get to this point in graduate school, so I would not be where I am today without them.

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Chapter I

Introduction

We intuitively understand that humans vary in many aspects. Some people are taller

than others, some smarter than others and some more extraverted. These cases exemplify

more apparent aspects of variability, but other areas of variability may be harder to detect. One

such area of variability is that of individual differences in high-level vision, meaning how people

vary in aspects of complex visual processing (e.g. recognizing birds or global processing style, as

opposed to low-level variability in acuity or color perception). Efforts to better understand

individual differences in visual processing can lead to insights into underlying mechanisms

(Mollon, Bosten, Peterzell, & Webster, 2017; Wilmer, 2008), have clinical (Reavis et al., 2017;

Sunday, Donnelly, & Gauthier, 2017; Trueblood et al., 2017) and professional applications

(Biggs, Cain, Clark, Darling, & Mitroff, 2013; Davis, Lander, Evans, & Jansari, 2016), and can shed

light on differences for which we have poor intuitions (as demonstrated by poor correlations

between self-reported visual abilities and performance on visual tasks; Barton, Hanif, & Ashraf,

2009; McGugin, Richler, Herzmann, Speegle, & Gauthier, 2012; Palermo et al., 2017; Richler,

Wilmer, & Gauthier, 2017).

Most initial efforts to measure and study individual differences in high-level visual

processing focused on separating individuals with face recognition deficits from those with

normal face recognition abilities (Benton, Hamsher, Varney, & Spreen, 1983; Duchaine &

Nakayama, 2006; Warrington, 1984). These studies demonstrated that variability in visual

abilities (skills that cannot be directly observed) could be measured with specific behavioral tasks. This opened the door for more studies investigating, among other things, how face recognition ability relates to object recognition ability (Gauthier et al., 2014; Gauthier, Behrmann, & Tarr, 1999; Kanwisher, 2000) and holistic processing (DeGutis, Wilmer, Mercado, & Cohan, 2013; Konar, Bennett, & Sekuler, 2010; Richler, Cheung, & Gauthier, 2011; Richler, Floyd, & Gauthier, 2015). More recently, McGugin and coauthors developed a test battery aimed at capturing variation between individuals in the recognition of several object categories (McGugin, Richler, et al., 2012). These tests, called the Vanderbilt Expertise Tests or VETs, used a learning exemplars paradigm similar to what has been successfully used to measure face recognition ability (Duchaine & Nakayama, 2006). Critically, these tests produced reliable scores (Cronbach α's > .7), demonstrating that there is measurable variability in object recognition between individuals and that these tests have the psychometric properties necessary to capture this variability (McGugin, Richler, et al., 2012).

Performance on the VET (or any object recognition measure) can be influenced both by domain-specific experience and domain-general ability. There is evidence that domain-specific experience with real-world categories (indexed, for instance, by hometown population or self-reported experience) relates to recognition performance (Balas & Saville, 2015, 2017; Barton et al., 2009; Ryan & Gauthier, 2016; Sunday, Donnelly, & Gauthier, 2018; Van Gulick, McGugin, & Gauthier, 2016). To better characterize how experience relates to object recognition performance, Van Gulick and coauthors related VET scores to a measure of domain-specific semantic knowledge, the Semantic Vanderbilt Expertise Test or SVET (Van Gulick et al., 2016). SVETs and VETs showed domain-specific correlations (e.g. VET-Car with SVET-Car) and, for all

categories except birds, these domain-specific correlations were stronger than domain-general correlations (VET-Car with averaged VET from seven other categories), supporting the VET's validity as measures of recognition ability in a given category. The overlap between VET and SVET performance within categories was largely accounted for by self-reported experience, further supporting the idea that experience plays a role in familiar object recognition (Van Gulick et al., 2016).

As more measures of visual abilities are developed it becomes easier to study not only how task- or domain-specific abilities relate to one another, but also how performance for multiple tasks and categories inter-relate. For instance, when analyzing car recognition ability within a set of several familiar object categories, it becomes apparent across several studies that car recognition ability is strikingly less correlated with other categories as compared with how those other categories correlate with one another (Ćepulić, Wilhelm, Sommer, & Hildebrandt, 2018; Richler et al., 2017; Sunday, Dodd, Tomarken, & Gauthier, 2018). More generally, when examining correlations between performance on several different familiar object recognition tests (from a VET battery), it is clear that these tests share common variance (on average, ~9%; McGugin, Richler, Herzmann, Speegle, & Gauthier, 2012; Van Gulick, McGugin, & Gauthier, 2016). Moreover, this shared variance exists despite variability in experience across familiar categories and the presence of measurement error in these zero-order correlations. This hints at an underlying construct responsible for the common variance across object categories.

Evidence for a domain-general object recognition ability

To formally investigate the possibility of a domain-general object recognition construct, Richler and colleagues measured recognition abilities using five novel object categories (to control for experience levels) and three different tasks (Richler et al., 2019). They found evidence of a latent visual factor accounting for a large portion of the variance shared between categories and tasks, which they called "*o*" (Figure 1). Indeed, *o* was able to account for approximately 89% of the variance between the lower-order factors for each novel object category.
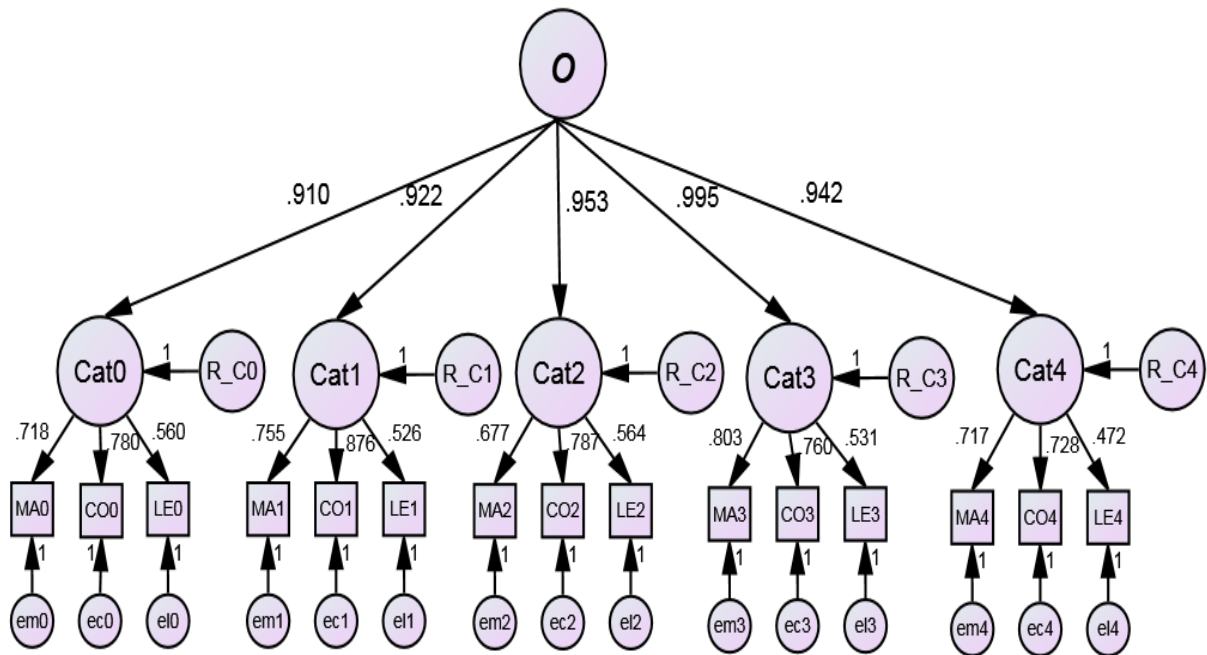
Figure 1. Standardized solution of the Confirmatory Factor Analysis performed in Richler et al., (2019), showing strong evidence of a 2nd-order factor, *o*. Here, tasks load onto each novel object category, which then load onto *o* (MA = Matching task, CO = Composite task, LE = Learning Exemplar task).

Though the latent variable model provided strong evidence for a higher-order factor accounting for much of the variability in recognition performance, this did not necessarily imply that this latent factor tapped into a new construct distinct from any that have been previously identified. An important question was whether this observed shared variance was driven by extant constructs like fluid intelligence, working memory capacity or even conscientiousness (i.e. some individuals will be self-motivated to diligently perform all tasks as compared with others). A follow-up to the initial Richler et al. work aimed at dissociating domain-general novel object recognition from several such constructs (Richler et al., 2019). To do this, subjects completed versions of the three tests used in the original study for two novel object categories and measures of constructs like fluid intelligence, perceptual style and visual short-term memory. The correlation between average performance with the two novel object categories (r_{52} = 0.71, p < .001) was significantly higher than the correlation between either novel object category and performance on any other test (e.g. average performance with one novel category and fluid intelligence; Richler et al., 2019). More importantly, there was little difference between the zero-order correlations between average performance with the novel categories and partial correlations between average performance with the novel categories after controlling for any given discriminating test. These results, along with work showing that none of the shared variance between novel object recognition tasks was accounted for by intelligence measures (Richler et al., 2017), provide evidence that o is distinct from several existing cognitive constructs.

While there is evidence that *o* diverges from individual differences in complex cognitive skills like intelligence, it remains to be determined whether *o* relates to individual differences in low-level visual perception. There is evidence that variability in low-level visual perception exists. For example, in 1999, Halpern and coauthors reported that performance on low-level visual tasks covaried across individuals (within an admittedly small sample of 20; Halpern, Andrews, & Purves, 1999). More recently, Ward and coauthors found that performance on seven low-level visual tasks (e.g. motion coherence and contrast sensitivity) loaded onto two latent factors, which mirrored a high- and low-spatial frequency distinction (Ward, Rothen, Chang, & Kanai, 2016). Notably, they also found that two indices (peak gain in contrast sensitivity and temporal order discrimination) loaded equally onto both latent factors, providing some evidence of a more general visual construct (Ward et al., 2016). Future studies will need to determine if this general visual construct found in low-level visual tasks relates to *o*.

Generally, these findings suggest the existence of a domain-general, experience-independent visual ability ripe for exploration. To help guide work on individual differences in any given trait, the prolific intelligence researcher Ian Deary listed three goals: "to describe them accurately, to discover the real-life impact of trait differences and to discover the aetiologies of trait differences, including their biological bases" (Deary, Penke, & Johnson, 2010). The behavioral work presented in Chapter II speaks to the first goal. Recent work, discussed in Chapter IV, analyzing how novel object recognition relates to radiological abnormality detection skills indicates that *o* may manifest in real-world situations (Sunday, Donnelly, et al., 2017). The neuroimaging work presented in Chapter III speaks to the last goal

of searching for *o*'s biological bases by relating MRI measures to behaviorally measured

domain-general object recognition.

Chapter II

Behavioral Study

The work reviewed above suggesting the existence of a domain-general object

recognition construct used novel object categories as stimuli. Though this choice ensures that

the measured construct is independent from experience, it does raise the question of how this

domain-general object recognition construct operates in familiar categories. One possibility is

that o is predictive of performance in both novel and familiar object recognition tasks (i.e. that

novel and familiar object recognition abilities relate). Such a finding would have several

implications. First, this would provide evidence that o can be measured equally well using either

novel or familiar stimuli, suggesting o would have "indifference to the indicator" (Spearman,

1904). Second, finding that novel and familiar object recognition abilities relate would suggest a

common mechanism underlying both, which could inform potential studies into neural

correlates (for example, see Chapter III). Third, a strong correlation between novel and familiar

object recognition abilities would imply a large portion of shared variance between experienced

and un-experienced (novel) categories. This would suggest that variability in familiar object

recognition is not completely due to variability in experience. While we would refrain from

over-interpreting such a finding, given in the present study we only used a small subset of

familiar objects, this could lend some insight into the limitations of experience's influence on

familiar object recognition performance.

Another possibility is that novel and familiar object recognition abilities do not relate. This would imply that something about the familiar domains causes recognition of these objects to rely on different abilities from those used to recognize novel objects. This could be simply due to some inherent properties of familiar objects that are not present in the novel objects. However, if the categories are diverse enough, it seems unlikely that some emergent visual property only present in real-world categories would exist (e.g. some visual property common across birds, planes and transformer toys but not common with novel objects). Rather, it seems more likely that if novel and familiar object recognition abilities do not relate, this would stem from the fact that our subjects will have some degree, however small, of experience with familiar categories that they will not have with novel categories. This domain-specific experience could confer knowledge (perceptual or otherwise) that would recruit different mechanisms or processing strategies from those used with novel objects. For example, behavioral performance can be influenced by the acquisition of domain-specific semantic knowledge (Gilbert, Regier, Kay, & Ivry, 2006; Lupyan, 2008; Richler, Gauthier, & Palmeri, 2011; Roberson & Davidoff, 2000), or knowledge of how to manipulate objects (Chua, Bub, Masson, & Gauthier, 2017; Herbort & Butz, 2011; Jax & Buxbaum, 2010; Yoon, Heinke, & Humphreys, 2002). In addition, learning semantic associations for objects can also change the viewpoint-dependency of the processing of those objects (Collins & Curby, 2013) as well as the relative contribution of each hemisphere to perceptual judgments (Curby, Hayward, & Gauthier, 2004). Moreover, with individuation training, individuals sometimes show a unique style of perceptual processing known as holistic processing (often characterized as a failure of selective attention) for objects from the trained category (Busey & Vanderkolk, 2005; Gauthier, Curran, Curby, &

Collins, 2003; Gauthier & Tarr, 2002; A. Wong, Palmeri, & Gauthier, 2009), though this relation is complex and can vary with task context (Hsiao & Cottrell, 2009; Robbins & McKone, 2007; Y. Wong & Gauthier, 2010, see Richler, Wong, & Gauthier, 2011 for a discussion). It is possible that when holistic processing arises with experience, this could further dissociate performance on familiar object recognition measures from novel object recognition measures.

Richler and colleagues suggested that *o* relates to familiar object recognition, evidenced by the significant correlations between performance on several VET tests and a measure of face recognition ability with *o* (rs ranging from .27-.60). However, in this case, familiar object recognition ability for each category was indexed by a single task, meaning domain-specific variance and measurement error influenced these correlations. In the present study, both novel object recognition ability and familiar object recognition ability were analyzed using a latent variable framework, which allowed the relation between these two constructs to be estimated free from measurement error and domain-specific variance. Moreover, using a latent variable framework (specifically, confirmatory factor analysis) also allowed for the estimation of model-fit parameters and proportion of variance explained by higher-order factors, which provided further insight into the relation between novel and familiar object recognition.

The Richler et al. study found that the novel categories for which subjects completed an exposure component did not show any evidence of loading onto *o* differently from the non-exposed categories, suggesting that exposure to a category does not inherently lessen how that category loads onto *o*. The exposure in this previous work was accomplished with an at-home training game, which took approximately 90 minutes to complete, so while the results suggest that domain-specific experience may not impact how domain-specific recognition relates to *o*, it

is entirely possible that more exposure of a differing nature (i.e. more realistic exposure that would occur for real-world categories) may impact how familiar object recognition relates to o. Given this, in the present study, none of the novel objects were accompanied by a training component; this manipulation is expected to further sharpen the potential distinction between novel and familiar objects (i.e. if experience influences how domain-specific recognition relates to o, then excluding any training component should cause the novel and familiar latent factors to dissociate). Furthermore, to quantitatively assess how experience impacts the relation between novel and familiar object recognition, the present study included an objective experience index for each familiar object category (the Semantic Vanderbilt Expertise Test).

The broad goal of this study was to better characterize the domain-general ability initially reported by Richler and coauthors by evaluating the extent to which it generalizes to familiar object recognition. Several studies have investigated experience-dependent and experience-independent influences on face and object recognition (Anastasi & Rhodes, 2005; Balas & Saville, 2015, 2017; Barton et al., 2009; De Heering, De Liedekerke, Deboni, & Rossion, 2010; Gauthier et al., 2014; Picci & Scherf, 2016; Ryan & Gauthier, 2016; Sangrigoli, Pallier, Argenti, Ventureyra, & De Schonen, 2005; Shakeshaft & Plomin, 2015; Short, Balas, & Wilson, 2017; Sunday, Dodd, et al., 2018; Sunday, Donnelly, et al., 2018; Van Gulick et al., 2016; Wilmer et al., 2010). The present study extends this line of research by assessing how the proposed experience-independent o relates to experience-dependent recognition abilities.

Methods

Subjects

Subjects were recruited through the Vanderbilt SONA subject pool as well as through flyers posted throughout Vanderbilt campus. Two-hundred-and-ninety-four Vanderbilt University community members were recruited (100 male, 194 female; mean age = 22.6, SD age = 6.5, age range = 18-63, 259 right-handed). Subjects were compensated with either course credit or pay ($15/hour).

Behavioral task overview

To measure both novel and familiar object recognition ability, subjects completed multiple tests in multiple domains. The previous study finding strong evidence for a domain-general recognition ability used two similar matching tasks (Richler et al., 2019), suggesting that more variable tasks may increase the construct coverage of the latent variable derived from these tasks (the more different the tasks, the more general the construct). Thus, in the present study, subjects completed three tasks with differing requirements, for each of the six categories (Table 1). The first task, which was also used in the Richler et al study, was a learning exemplar (LE) task. This task employs a similar paradigm to several face and object recognition tests (Dennett et al., 2012; Duchaine & Nakayama, 2006; McGugin, Richler, et al., 2012; Richler et al., 2017) and included a learning component (learning six exemplars which are then repeatedly tested) unique to this task. The second task was a classic matching (MA) task also used in the Richler et al study. The last task was an ensemble perception (EP) task modeled after previous work investigating individual differences in varying visual domains (Haberman, Brady, &

Alvarez, 2015). This task was chosen because its requirements (to estimate an average from a group) differ from those of the other two tasks (which both rely more on single object identification), thereby increasing the task-generality of any resulting latent construct. Moreover, preliminary work suggested this task strongly correlates with learning exemplars task performance from the same domain.

Task	Description	Trial Requirements	Response Options	Study time	Used in Richler et al, 2019 paper
LE	Study 6 exemplars that are repeatedly tested in subsequent trials	Choose studied exemplar from 2 distractors	3 AFC	unlimited	Yes
MA	Determine if pairs of exemplars are the same or different	Respond same or different to probe stimuli within 3000 ms	2 AFC	300 ms or 150 ms	Yes
EP	Estimate average of 4 exemplars	Choose option closest to estimated average	6 AFC	1000 ms	No
SVET	Recognize object labels of familiar exemplars	Identify real exemplar label from distractor labels	3 AFC	-	No

Table 1. Task details of the four tasks used in the present study. LE = Learning Exemplar, MA = Matching, EP = Ensemble Perception, SV = Semantic Vanderbilt Expertise Test, AFC = Alternative Forced-Choice

To index experience with familiar object categories, subjects also completed the Semantic Vanderbilt Expertise Test or SVET (Van Gulick et al., 2016) for each familiar category. Over two two-hour sessions, subjects completed twenty-one tests. The tests were randomized first, and then each subject completed the tests in the same order; Session 1: EP-Greeble, LE-

Bird, MA-Transformer, EP-Plane, LE-Sheinbug, MA-Bird, SVET-Plane, MA-Greeble, EP-Ziggerin,

EP-Transformer; Session 2: MA-Ziggerin, LE-Transformer; EP-Sheinbug, MA-Sheinbug, LE-Plane,

SVET-Transformer, MA-Plane, EP-Bird (Figure 2). All tests were administered using Matlab and

Psychtoolbox-3 software (Brainard, 1997; Matlab, 2016).
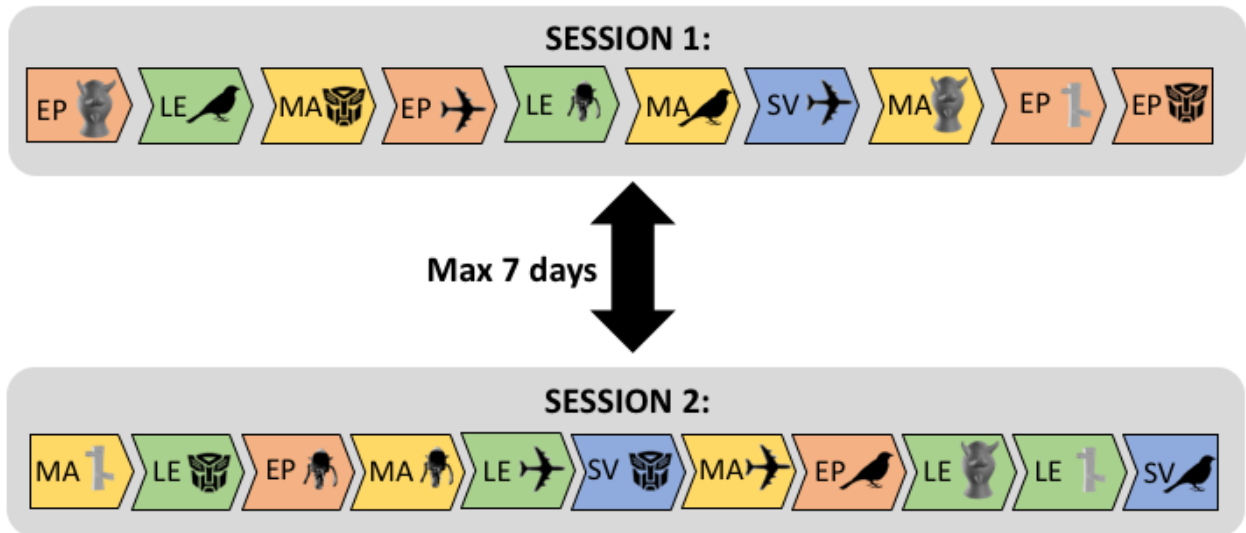
Figure 2. Schematic of the study design and test orders. Session 1 tests are shown in the top box
and Session 2 tests in the bottom box. Ensemble Perception = EP (orange), Learning Exemplar = LE
(green), Matching = MA (yellow) and SVET = SV (blue). Categories are represented by silhouette
figures (e.g. Greebles, Birds, Transformers, Planes, Sheinbugs and Ziggerins).

Behavioral stimuli

The intraclass correlations of previous data revealed diminishing returns in the

estimated reliability of averaged standardized scores after three categories (Richler et al.,

2019). Based on this, the present study used three novel and three familiar object categories.

For novel object categories, we chose vertical Ziggerins (A. Wong, Palmeri, & Gauthier, 2009)

and symmetrical Greebles (Gauthier & Tarr, 1997) because of their high reliabilities in previous data (learning exemplar task Cronbach α's of .84 and .89 respectively as compared with α = .74 for asymmetric Greebles and .74 for horizontal Ziggerins; Richler et al., 2019). For the third novel object category, we chose Sheinbugs because of their visual distinctness from the other two categories.

We selected familiar categories according to four criteria:

1) Avoiding categories for which recognition performance appears to be "special", in that it systematically fails to correlate with recognition performance for most other categories, such as faces or cars (see Ćepulić et al., 2018; Hendel et al., 2019; McGugin, Richler, et al., 2012; Sunday, Dodd, et al., 2018; Van Gulick et al., 2016)

2) Choosing categories in which domain-specific experience is not strongly correlated, as this would make it more difficult to disentangle ability from experience

3) Choosing categories that, everything being equal, represent a variety of different familiar categories (e.g., not all animals, or all large objects)

4) Choosing categories with high naturally-occurring variability in experience in the population, as this has been the main explanation for the limited correlations among performance with different familiar categories

To address the first criterion, an examination of previous data relating performance on VETs for several categories (Van Gulick et al., 2016) found that recognition performance for birds, planes, leaves, dinosaurs, mushrooms and transformers showed relatively high correlations with each other, as compared with categories like cars and shoes, which correlated to a lesser extent with other categories (Figure 3, left). To address the second criterion, we

considered correlations between both self-reported experience with categories and performance on a domain-specific semantic knowledge measure (Van Gulick et al., 2016). For both of these measures, birds, planes, transformers and mushrooms showed relatively low average correlations with other categories (Figure 3, right). We chose transformers because they met criteria one and two, and because the variability in experience with transformers also meets criterion four. To include the most variable categories possible (criterion three), we then chose birds (living, physically small) and planes (non-living, physically large) for the additional categories in the present study. Though this choice reflects compromises and accessibility of prior results, if o is truly domain-general, the choice of familiar object category should be relatively arbitrary. All familiar object images were obtained from the Internet and include the exemplar object and background (except on the ensemble perception task, in which the background was removed, Figure 4). Bird images include passerine bird species common to North America (Figure 5), transformer images include images of transformer figures, and plane images include a range of commercial and military plane models.

Learning exemplars (LE) task

This task required subjects to learn and subsequently recognize six exemplars from a given category. The paradigm was modeled after paradigms used in the Cambridge Face Memory Test (Duchaine & Nakayama, 2006), Vanderbilt Expertise Tests (McGugin, Richler, et al., 2012) and the Novel Object Memory Tests (Richler et al., 2017). The novel category tasks used here were identical to those used in Richler et al., 2019. The task began with subjects studying six exemplars from a given category for as long as they liked. Next, subjects completed

two 24-trial blocks (48 trials total) in which they made an unspeeded choice as to which of

three objects presented together were one of the six studied exemplars (Figure 4). Subjects

were allowed to review the target exemplars after trials 6 and 24 and instructed after trial 24
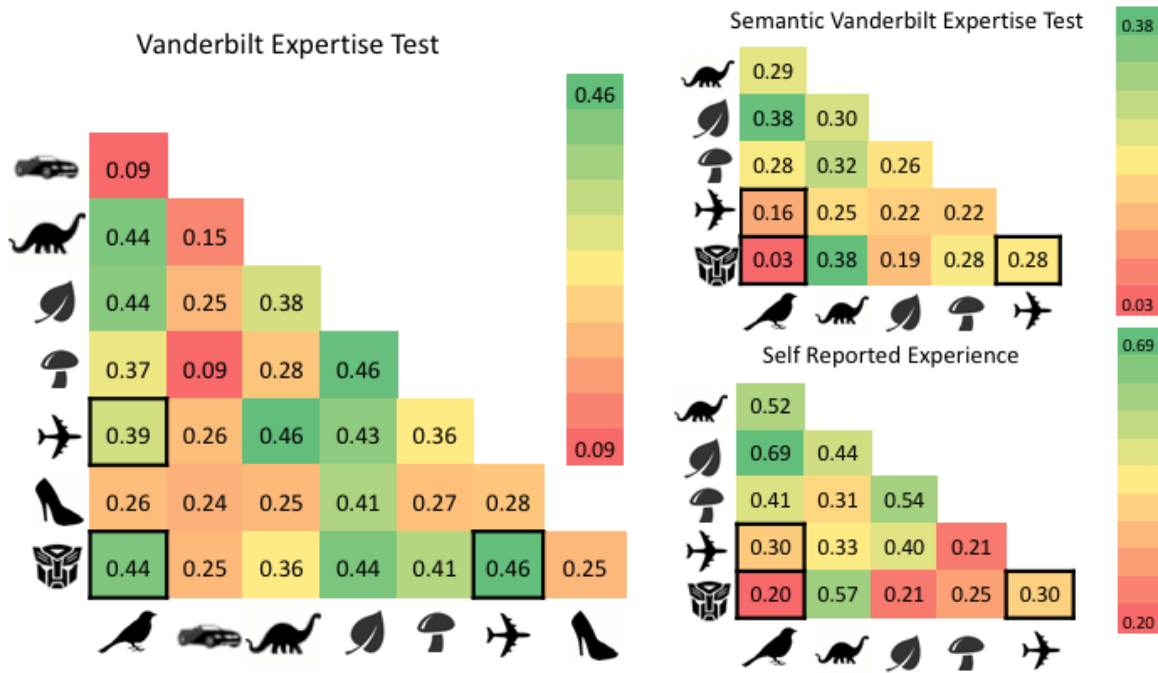
Figure 3. Correlations between VET performance (left), SVET performance (right top) and self-reported experience (right bottom) from Van Gulick et al., 2016 (N = 213). Green indicates higher correlations and red indicates lower correlations. Categories are represented by silhouette figures (VET: cars, dinosaurs, leaves, mushrooms, planes, shoes transformers, owls; SVET and Self-report: dinosaurs, leaves, mushrooms, planes, transformers and owls). Cars and shoes are not shown in right two images because they did not meet Criterion 1 (instead showing relatively low correlations in comparison to other

that the subsequent targets would differ in viewpoint. Thirty-six total objects from each

category were used, 6 as targets and 30 as distractors. In the first block, targets were an

identical image to the studied image. In the second block the targets were shown from a

different viewpoint than that of the studied image. Targets were never consecutively repeated

across trials. Performance was indexed by percent accuracy. This task took approximately eight minutes to complete for each category.

The familiar object learning exemplars tasks were the VET-Bird, VET-Transformer and VET-Plane used in Van Gulick et al. (2016), hereafter referred to as LE-Bird, LE-Transformer, and LE-Plane, respectively. These tasks were identical to the novel object learning exemplars measures with some exceptions. Subjects were allowed to review the target exemplars after trials 6 and 12 and received feedback on the first 12 trials, on which the target was identical to the studied image. On the transformers test, 48 total objects were used, 6 as targets and 42 as distractors (including 6 catch distractors meant to ensure subjects fully understood task instructions and were paying attention). On the bird task, 36 total objects were used, 6 as targets and 30 as distractors (including 6 catch distractors) and on the plane test 45 total objects were used, 6 as targets and 39 as distractors (including 6 catch distractors). The three catch trials from the original familiar category tests (which were added in prior work to evaluate compliance with instructions during online data collection) were also included for a total of 51 trials.

Matching (MA) task

This task required subjects to determine, on each trial, if a single probe object matched the identity of a single studied object, when presented sequentially. Each trial began with an object presented for 300 ms in the first block and 150 ms in the second block. This object was followed by a domain-specific scrambled mask for 500 ms, followed by a probe object and a 500 ms fixation inter-stimulus interval (Figure 4). Subjects determined if the probe object was

the same or different identity from the studied object (regardless of viewpoint), within a maximum of 3000 ms to respond. There were 360 total trials and subjects were given a break every 90 trials. There were equal numbers of same and different trials. Fifty total objects were used, each in two different viewpoints of the objects rotated around a vertical axis (i.e. rotated out of the screen, see Figure 4, left trial). For the novel categories, the probe image size also varied randomly across trials, where half the trials presented the probe image in the same size as the study image (125x125 pixels) and half in a slightly smaller size (95x95 pixels). Objects repeated between the matching and learning exemplar task (70 objects for Ziggerins, 68 for Greebles, 72 for Sheinbugs).
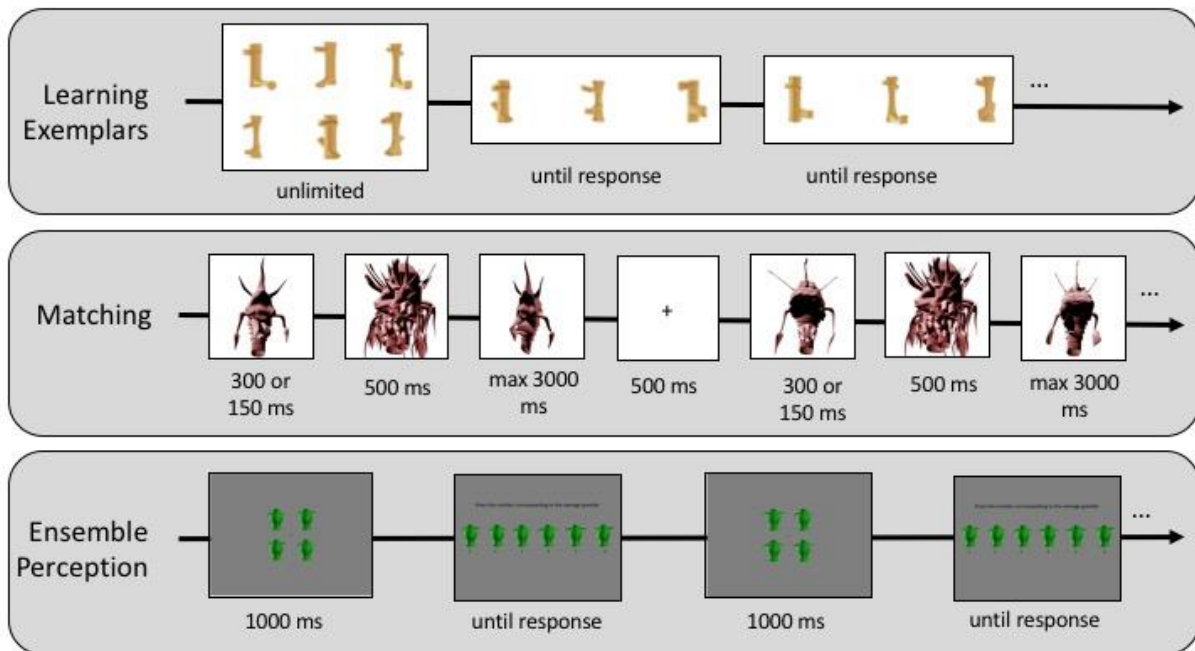
Figure 4. Schematics for the three behavioral tasks and three novel categories: learning exemplars with Ziggerins (top), matching with Sheinbugs (middle) and ensemble perception with Greebles (bottom).

The matching task for the familiar objects was identical to the task with novel objects

with the exception of the stimuli. For each familiar category, 2 views of 80 exemplars from each

category were used. Some of the exemplars were also used in the learning exemplars task. Half

of the trials in which the correct response was "same" showed one view of the exemplar at

study and a different view at test. For the other half of the "same" trials, the study and test

exemplars were the same image. On these trials, to make visual information in the background

less diagnostic, the backgrounds in both of these images (study and test images on these

"same" trials) were slightly modified using Adobe Photoshop to create two new versions of the

image (Figure 5). This task took approximately 20 minutes to complete for each category.

Performance on this task was indexed by calculating d' scores.

Ensemble perception (EP) task

This task required subjects to decide which of six objects most closely matches the

average identity of four objects presented simultaneously. In this task, three objects from a

given category were morphed together using MorphAge software (Creaceed SPRL, 2008) to

produce all six possible 25%/75% and 75%/25% morphs. Each trial began with subjects studying

a 2x2 array of four morphs for 1000 ms. Next, subjects were presented with an unspeeded six-

alternative forced choice in which they chose which of the six options was closest to the

average of the studied array (Figure 4). The answer choices were always presented in the same

order, though the leftmost choice varied across trials (e.g. choices could be 1, 2, 3, 4, 5, 6 or 3,

4, 5, 6, 1, 2) There were 70 trials and none of the three original objects that were morphed

were one of the six studied exemplars from the LE task. Each response was scored as the

absolute value of the difference between the response and the correct answer (e.g. if the

correct answer was 3 and the subject responded 2, then response accuracy was scored as a 1).

Summed scores were used as an index of performance, with higher scores indicating poorer

performance. The task took approximately seven minutes per category to complete.
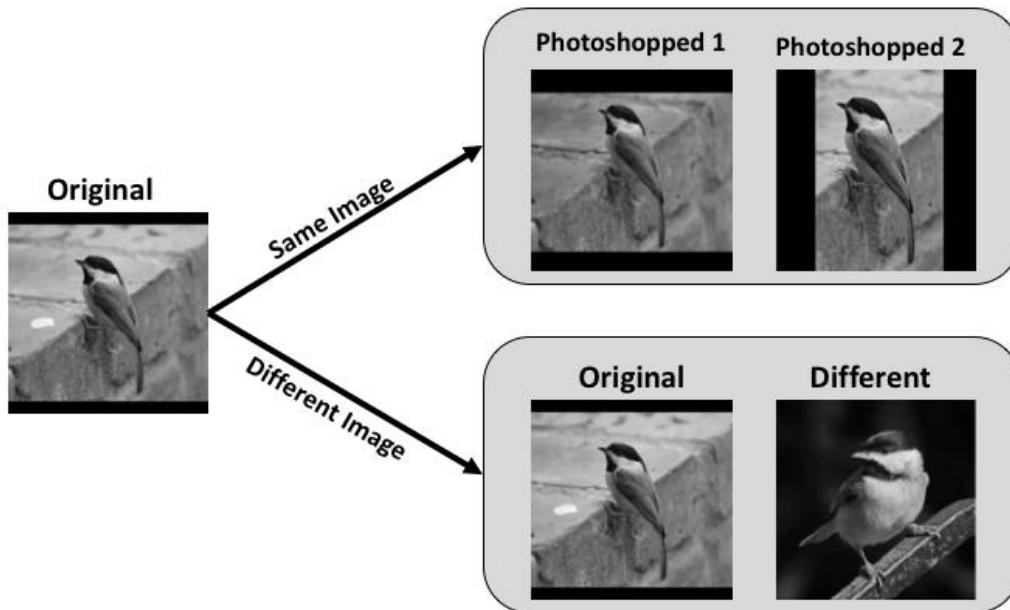
Figure 5. Examples of stimuli used on the familiar domain matching task same trials. All
images shown here are of a Carolina chickadee (*Poecile carolinensis*), thus correct responses
for both trials is "same". The original image (left) was photoshopped to create two new
versions with differing backgrounds (top row, "Same Image"). Bottom row shows a trial in
which the original image was shown with a different image of the same species ("Different
Image").

Semantic vanderbilt expertise (SV) task

In this task, subjects used their prior semantic knowledge of a given object category to

identify the real subordinate-level object label from two plausible-sounding distractors across

51 total trials. For example, on one trial of the SVET-Transformers, subjects should have

correctly identified "Megatron" and not "Uppercut" or "Outlook" as the correct transformer

label. The SVET consisted of 48 trials plus three catch trials in which the two distractors were

not plausible object labels (e.g. "JC Penny" or "Oatmeal Raisin"). The task took approximately

five minutes per category *(*birds, planes, transformers) to complete.

Results

All data from 12 subjects were excluded for having more than six tests on which the

subject had either below chance accuracy (50% for matching, 33.33% for VET, -1.5 for ensemble

perception), reaction times quicker than 2 standard deviations below the mean reaction time

for each task and category, or more than 20 timed-out trials on the matching tests.

Additionally, one subject chose to leave the study during the first test of the first session and so

was excluded from analysis. Thus, data from 281 subjects (96% of sample; 94 male; mean age =

22.7, age range = 18-63, 249 right-handed) were included in the analyses. Some tests were not

administered (47 tests from 28 subjects, 0.8% of total data), either due to computer errors

causing the test to be skipped entirely, or computer error occurring during the test so that only

a few trials were completed. On matching tests in which subjects timed out (responded later

than 3000 ms) on more than 20 trials, the data for that matching test only was omitted (86

tests from 45 subjects, 5.1% of matching data). Additionally, one subject was accidentally run

through session 2 twice, so only the first session 2 data was included. Fourteen subjects did not

return for the second session. There were no significant differences between scores on the

session 1 tests (MA-Greeble, MA-bird, MA-transformer, EP-Plane, EP-Transformer, EP-Greeble,

EP-Ziggerin, LE-Sheinbug, LE-Bird, SVET-Plane) for the fourteen subjects who did not return for

Session 2 and the 268 non-excluded subjects who did both sessions (all ps > .30 except, VET-Sheinbugs p = .06 on which the subjects who did not return for Session 2 had a higher average performance).

Descriptive statistics for each test are reported in Table 2. Mean performances on matching and learning exemplars tasks for novel categories were similar to previous work (Richler et al., 2019) and SVET mean performances were similar to previous work (Van Gulick et al., 2016). Cronbach α's provided evidence of acceptable internal consistency, except for SVETs. Though most SVETs have produced measurements with good reliability in prior work (Sunday, McGugin, & Gauthier, 2017; Van Gulick et al., 2016), their reliabilities were low here (α's $\leq$ .5). This low reliability has been reported previously for the SVET-Bird (α = .50; Sunday, Dodd, et al., 2018), but we are unsure of why the SVETs here produced lower reliabilities than previous reports. Skewness and kurtosis indicated significant non-normality for several tests, most often on matching tests (Table 2). This is similar to the previous study using only novel objects, which also found evidence of non-normality for several tests (Richler et al., 2019). Skew and kurtosis values and qq-plots revealed non-normality was not severe for all tests except MA-Transformers.

Task	N	Mean (SD)	Range	Skew	Kurtosis	Cronbach's α
EP-Z	278	0.98 (0.23)	1.27	-0.59***	0.17	0.86
EP-G	278	0.94 (0.20)	1.09	-0.58***	0.14	0.79
EP-S	265	1.00 (0.25)	1.30	-0.23	-0.39	0.85
EP-B	265	0.94 (0.27)	1.30	-0.58***	-0.22	0.89
EP-P	278	1.10 (0.23)	1.21	-0.33*	-0.33	0.81
EP-T	278	0.85 (0.25)	1.30	-0.64***	0.08	0.88
MA-Z	253	1.42 (0.44)	3.00	-0.65***	0.90*	0.96
MA-G	265	1.22 (0.53)	2.48	0.03	-0.55*	0.95
MA-S	248	0.70 (0.34)	2.05	0.08	0.24	0.92
MA-B	264	1.95 (0.40)	2.60	-0.82***	1.38*	0.96
MA-P	252	1.88 (0.49)	3.39	-0.89***	1.62***	0.97
MA-T	256	1.91 (0.51)	4.52	-1.63***	8.14***	0.98
LE-Z	264	0.61 (0.15)	0.67	-0.07	-0.64**	0.83
LE-G	266	0.60 (0.17)	0.77	0.04	-0.77***	0.86
LE-S	273	0.51 (0.12)	0.63	0.02	-0.12	0.69
LE-B	277	0.69 (0.15)	0.67	-0.16	-0.84***	0.87
LE-P	266	0.68 (0.12)	0.65	-0.30*	0.25	0.78
LE-T	267	0.76 (0.12)	0.58	-0.39*	-0.46	0.83
SV-B	266	0.46 (0.08)	0.65	0.89***	3.10***	0.41
SV-P	278	0.44 (0.08)	0.42	0.38**	-0.21	0.44
SV-T	265	0.40 (0.09)	0.56	0.30*	0.25	0.50

Table 2. Descriptive statistics for each behavioral test. EP = Ensemble Perception, MA = Matching, LE = Learning Exemplar, SV= Semantic Vanderbilt Expertise Test. Categories: Z = Ziggerins, G = Greebles, S = Sheinbugs, B = birds, P = planes, T = transformers. D'Agostino test of normality for skewness and Anscombe-Glynn tests of normality for kurtosis significance levels are reported, *p < .05, ** p <.01, *** p <.001

First-order correlations are reported in Figure 6.
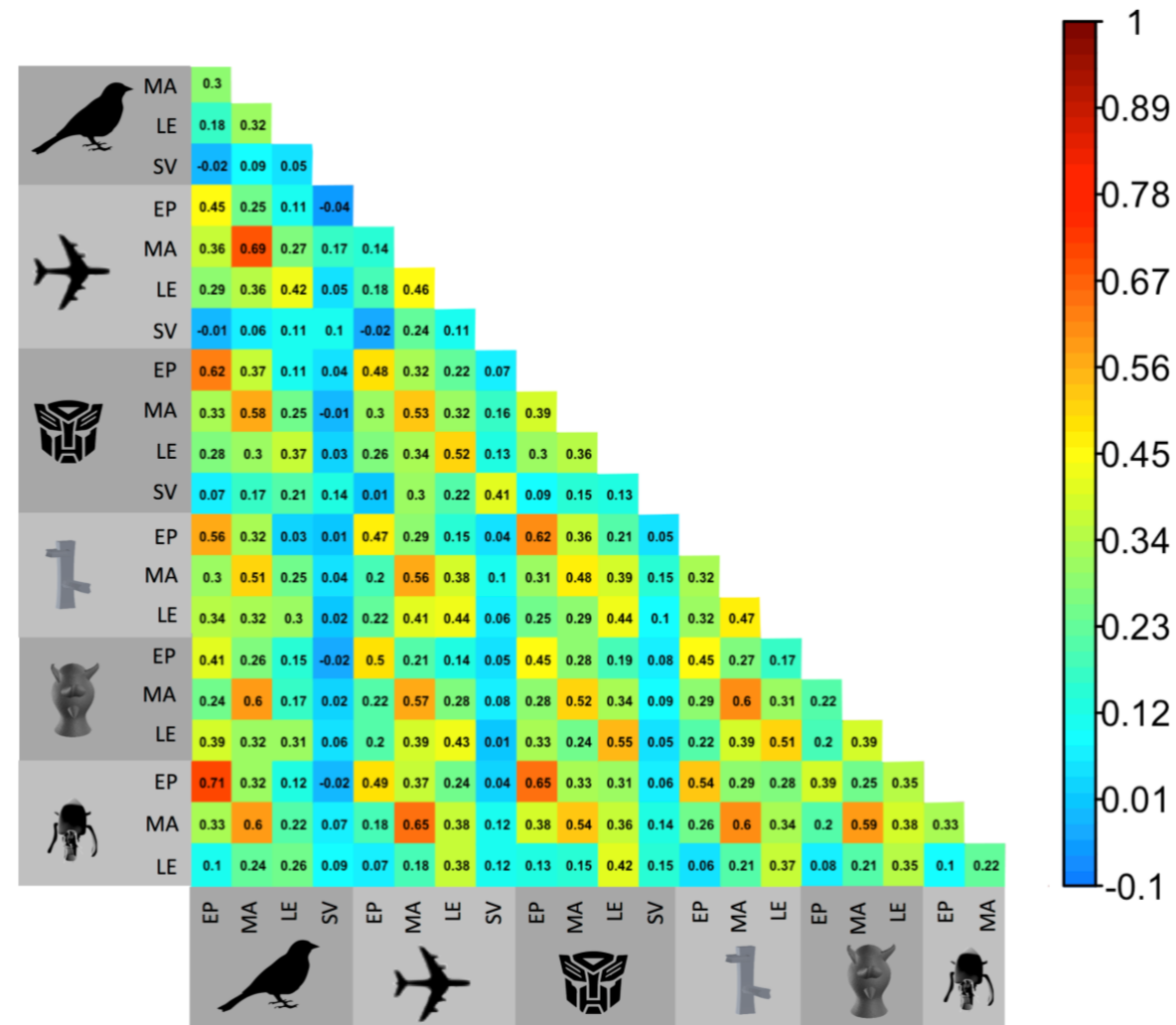
Figure 6. Heatmap of correlations between all tests with correlation coefficients. Categories are represented by silhouette figures. EP = Ensemble Perception, MA = Matching, LE = Learning Exemplar, SV= Semantic Vanderbilt Expertise Test. $p < .05$ if $r > .11$ (except MA-Sheinbug with SV-Plane, where p = .07); $p < .01$ if $r > .15$; $p < .001$ if $r > .20$ (except LE-Greeble with EP-Plane, p < .001 and LE-Sheinbug with MA-Ziggerin, p = .001)

To compare the correlations between familiar and novel categories, we examined the

strengths of these relations within each task (Table 3). Previous work has shown that, generally,

novel categories tend to correlate to a greater extent than familiar categories (McGugin,

Richler, et al., 2012; Richler, Cheung, et al., 2011; Richler et al., 2017; Van Gulick et al., 2016),

presumably because variability in experience with familiar categories attenuates correlations

between these categories (i.e. if you have differing levels of experience with different

categories, this drives the recognition abilities of these categories to diverge). However, as can

be seen in Table 3, this is not the case in the present study: familiar categories and novel

categories intercorrelate to a similar extent in each task.

	Familiar				Novel		
	Birds	Planes	Mean		Greebles	Ziggerins	Mean
MA			.60				.60
Planes	0.69			Ziggerins	0.60		
Trans	0.58	0.53		Sheinbugs	0.60	0.59	
LE			.43				.41
Planes	0.42			Ziggerins	0.51		
Trans	0.34	0.52		Sheinbugs	0.37	0.35	
EP			.52				.46
Planes	0.45			Ziggerins	0.45		
Trans	0.62	0.48		Sheinbugs	0.54	0.39	

Table 3. Correlations between all tests grouped by task. N's for each correlation range
from 234-276 and all correlations are significant (all *p*s < .001). The average correlation
for each task is shown in shaded columns (correlations were Fisher-transformed before
averaging). EP = Ensemble Perception, MA = Matching, LE = Learning Exemplar

In fact, not only do familiar categories intercorrelate just as strongly as novel categories, but the variability in performance on each task with familiar and novel categories are similar (coefficient of variation ranges: MA-Familiar = 0.21-0.27; MA-Novel = 0.31-0.49; EP-Familiar = 0.21-0.29; EP-Novel = 0.21-0.25; LE-Familiar = 0.16-0.22; LE-Novel = 0.24-0.28, see Figure 7 for distributions). As can be seen in Figure 7, in the ensemble perception tests, the distributions of performance are less similar (i.e. overlap less) for familiar categories as compared with novel categories. However, in the matching tests, distributions of performance with the novel categories are less similar than with familiar categories. Thus, it is not always the case that across-category distributions are more similar in novel categories for which there is no variability in experience.

Do latent factors account for performance across recognition tests?

By examining the zero-order correlations, we see that the tests correlate with one-another both across-tasks and across-categories. However, these correlations reflect the relation between the observed tests with both measurement error and category-specific variance present (both of which could attenuate correlations, Gauthier, 2018; Nunnally, 1970). Moreover, examining zero-order correlations only allows a comparison of two observed tests but here we are interested in the existence and relation between higher-order factors. Thus, the data were submitted to a 2nd-order structural equation model (SEM) using MPlus 8.2 software (Muthén & Muthén, 1998). Given the non-normality of several tests, the MLR estimator was used in Mplus. The MLR estimator uses the expectation-maximization (EM) algorithm and numerical integration and provide standard errors using the Huber-White

sandwich estimator robust against nonnormality. For each category, one of the three tests' loading was constrained to 1 and the variance of the 2nd-order factors were set to 1. Similar to Richler et al., (2019), a series of models was fit for both 2nd-order factors (*n* and *f*). In the first
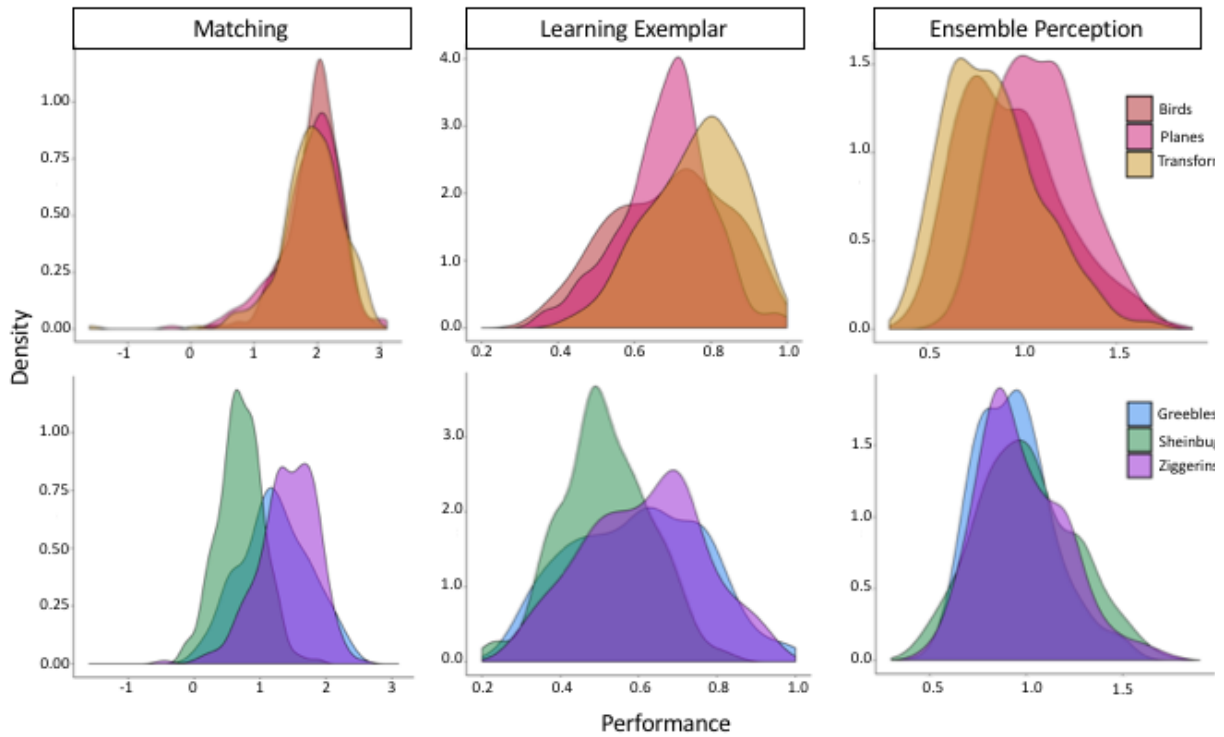
Figure 7. Density plots for subjects' performances on each task separated in novel categories (bottom row) and familiar categories (top row). N's for each distribution range from 234-276. Birds = red, Planes = pink, Transformers = Yellow, Greebles = Blue, Sheinbugs = Green, Ziggerins = Purple

model (1n and 1f, Table 4), observed tests (MA, LE and EP, denoted by squares in Figure 8), loaded onto category-specific factors (e.g. Greeble factor). The second model (2n and 2f) added in correlated error terms within task to allow for method effects, which may occur because the same tasks were used across several categories (e.g. some of the variance shared between MA-

Bird and MA-Plane may result from the matching task itself). The third model (3n and 3f) required the factor loadings of the three tasks to be invariant across categories (i.e. equal) meaning that, for example, each of the three EP loadings were constrained to be equal. The last model (4n and 4f) added a higher-order factor of either general novel object recognition (*n*) or general familiar object recognition ability (*f*)

Model	Description	df	χ^2	RMSEA (90% CI)	CFI	SRMR	AIC	BIC	SABIC
1n	Correlated novel categories	24	176.954, $p = 0.00$	0.151 (0.130, 0.172)	0.754	0.082	558.977	449.826	544.955
2n	1n + errors across tasks	15	17.007, $p = 0.32$	0.022 (0.000, 0.062)	0.997	0.024	698.834	556.938	680.605
3n	2n + within-tasks invariant loadings on category factors	19	49.049, $p = 0.00$	0.075 (0.049, 0.101)	0.952	0.083	674.417	547.075	658.059
4n	3n + 2nd-order category factors	20	49.048 $p = 0.00$	0.072 (0.047, 0.098)	0.953	0.083	676.379	552.675	660.487
1f	Correlated familiar categories	51	318.124, $p = 0.00$	0.137 (0.122, 0.151)	0.642	0.110	2263.425	2121.529	2245.197
2f	1f + errors across tasks	42	141.361 $p = 0.00$	0.92 (0.075, 0.109)	0.867	0.089	2426.018	2251.377	2403.583
3f	2f + within-tasks invariant loadings on category factors	48	159.682, $p = 0.00$	0.091 (0.076, 0.107)	0.850	0.099	2418.628	2265.817	2398.997
4f	3f + 2nd-order category factors	46	113.532, $p = 0.00$	0.072 (0.056, 0.089)	0.909	0.086	2464.627	2304.539	2444.061

Table 4. Model fit indices for both novel (*n*) and familiar (*f*) 2nd-order factors. χ^2 = Satorra-Bentler χ^2 test of model fit, RMSEA = root mean square error of approximation, CFI = comparative fit index, SRMR = standardized root mean square residual, AIC = Akaike Information Criteria, BIC = Bayesian Information Criteria, SABIC = sample-size adjusted BIC

Both models 1n and 1f showed evidence of poor fit (e.g. high RMSEA, low CFI), similar to what was found in the previous Richler et al. study. The fit improved in models 2n, 3n, 2f and

3f. Model 4f, which adds a 2nd-order factor to model 3f, has a lower RMSEA and SRMR and higher CFI than model 3f (3f: RMSEA = .091, SRMR = 0.099, CFIs = 0.850; 4f: RMSEA = .072, SRMR = 0.086, CFIs = 0.909). Similarly, model 4n has lower RMSEA, equal SRMR and higher CFI than model 3n (3n: RMSEA = .075, SRMR = 0.083, CFIs = 0.952; 4n: RMSEA = .072, SRMR = 0.083, CFIs = 0.953). These differences in model fit between models 3f and 4f, and 3n and 4n, are not large; this suggests adequate fit for all models. Since the final models with 2nd-order factors (4n and 4f) showed evidence of good fit (RMSEAs < .08, CFIs > 0.9, SRMR < .09) and allow for a correlation to be estimated between a general novel object recognition factor and a general familiar object recognition factor, we proceeded with these models in the subsequent analyses.

Does experience explain some of the variability in recognition abilities?

In the present study, we used both novel and familiar categories to test how experience influences recognition ability. As an indirect measure of experience, we included a measure of semantic knowledge about each familiar category (SVETs), and were interested in whether these tests could account for some of the variability in familiar object recognition performance. To test this, we fit model 4f both with and without SVETs included. SVETs were included as latent variables (with no error variance) because of their relatively low reliabilities (see Table 2). The SVETs showed little evidence of having an effect on the model. No category resulted in a significant parameter estimate (Bird: estimate = 0.05, *SE* = 0.22, *p* = 0.84; Plane: estimate = 0.59, *SE* = 0.34, *p* = 0.08; Transformer: estimate = 0.13, *SE* = 0.50, *p* = 0.62). Additionally, adding SVETs did not result in a significant improvement in the R-squared values (SVETs included: Bird

$R^2 = 1.00$, Plane $R^2 = 1.00$, Transformer $R^2 = 0.88$; SVETs not included: Bird $R^2 = 1.00$, Plane $R^2 = 1.00$, Transformer $R^2 = 0.90$; Bird R^2 percent increase = 0.02, Plane R^2 percent increase = 0.00, Transformer R^2 percent increase = 0.00).

Do novel and familiar object recognition rely on the same underlying ability (o) or does acquiring domain-specific experience led to the recruitment of differing abilities during recognition?

Our main question was to what extent (if any) novel and familiar object recognition abilities relate to one another. To determine the extent to which *n* and *f* relate, a full model was fit in which *n* and *f* were allowed to correlate (joining models 4n and 4f from Table 4, with factor invariance and errors across tasks, Figure 8). SVETs were included in the model, but not allowed to correlate with *n* or *f*. The model showed evidence of good fit ($df = 143$, $\chi^2 = 230.14$, $p = 0.00$, RMSEA= 0.047, RMSEA 90% CI = (0.035,0.057), CFI = 0.957, SRMR = 0.092). Parameter estimates of this model are shown in Figure 8. To have a model with admissible correlations (i.e. the correlation between *n* and *f* between -1 and 1), it was necessary to constrain MA-Bird errors to correlate with EP-Bird errors. Without this constraint the correlation between *n* and *f* exceeded 1, thus a constraint was clearly necessary. Loadings of observed tests onto category-specific factors were moderately high and significant (all *ps* < .01 except SVETs, for which only SVET-Plane was significant with *p* = .02). MA generally showed the highest loading (range = .73-.88), followed by LE (range = .38-.52), then EP with the lowest loadings (range = .21- .40). Category-specific factor loadings onto the 2nd-order factors were high (range = .87-.98, all *ps* < .001). Both 2nd-order factors showed evidence of good reliability (reliability of *f* = 0.84, CI = [0.77, 0.93]; reliability of *n* = 0.80, CI = [0.72, 0.88], Raykov, Goldammer, Marcoulides, Li, &

Menold, 2018), with reliability here meaning the proportion of true scores in the total score variance of the indicators (MA, LE and EP for either the familiar or novel domains for *f* and *n* respectively). The correlation between the 2nd-order *n* and *f* factors was extremely high at 1.00, suggesting these 2nd-order factors were strongly, if not perfectly, related.
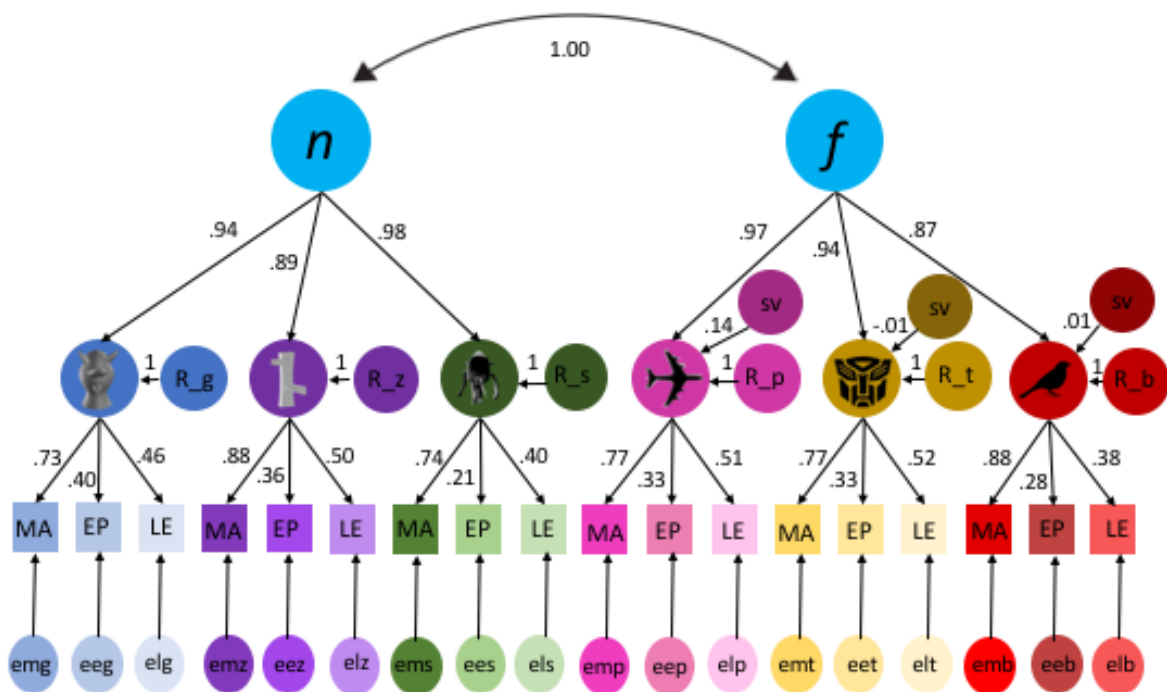
Figure 8. Full SEM model standardized solution (both observed tests and factors are standardized). Categories are represented by silhouette figures. EP = Ensemble Perception, MA = Matching, LE = Learning Exemplar, SV= Semantic Vanderbilt Expertise Test.

Discussion

The primary goal of the present study was to investigate how domain-specific experience influences recognition ability. Specifically, we were interested in determining the

role *o*, the recently-discovered domain-general object recognition ability, plays in recognition of categories for which we have variable real-world experience. Using a latent variable framework, we found strong evidence that novel and familiar object recognition factors are related. In fact, given the correlation between these two factors was perfect, the evidence suggested these factors are actually indistinguishable, meaning that knowing how well an individual performs on several novel object recognition tests allowed for a perfect prediction of that individual's general familiar object recognition factor.

The final SEM model (Figure 8), replicated the Richler et al., previous finding that first-level domain-specific factors strongly load onto higher-order domain-general factors (here, loadings ranged from .87- .98), with these higher-order factors accounting for a large portion of the shared variance. We found this to be true not only for novel object categories, but familiar object categories as well. Because we used more variable tasks than in the initial Richler et al. work (by including the ensemble perception task instead of the part-matching composite task used in Richler et al.), our findings showed that strong factor-loadings onto *o* can still be found with a wider range of object recognition tasks. This result extends the task-generality of *o*.

Given that novel categories are inherently equated for experience (i.e. no experience), one might expect novel categories to correlate more strongly with one another than familiar categories in which experience varies. Previous work supports this prediction, reporting average correlations around 0.30 for familiar categories (McGugin, Richler, et al., 2012; McGugin, Van Gulick, Tamber-Rosenau, Ross, & Gauthier, 2015) and average correlations around 0.50 for novel categories (Richler et al., 2019). However, this does not seem to be the case in the present study (average MA correlation: novel: 0.60, familiar: 0.60; average LE

correlation: novel: 0.41, familiar: 0.43; average EP correlation: novel: 0.46, familiar: 0.52, Table

3); though it should be noted that these categories were partially chosen because they have

previously demonstrated relatively strong correlations with other categories (Criterion 1). The

results here suggested that the variability in experience present in familiar but not novel object

categories does not limit how performance with these categories correlate, at least for cases

where categories like faces or cars are avoided. Thus, it is possible that with the familiar

categories chosen here, our three tasks are not influenced by experience as much as we might

have expected based on previous work (Barton et al., 2009; Van Gulick et al., 2016).

Our findings demonstrated the utility of latent variable approaches for investigating

how familiar and novel object recognition relate; using latent variable models of familiar object

recognition allowed for more insight into this relation than in the Richler et al. work (in which

familiar object recognition was measured with only single domain-specific tests). This previous

work found significant correlations between *o* and familiar object learning exemplar tests (*r*s =

.26-.54), suggesting a moderate relation between novel and familiar object recognition. More

specific to the present study, the pairwise correlations between *o* and birds and *o* and planes

were much lower than the correlation reported here between *n* and *f* (birds: *r* = 0.39; planes: *r*

= 0.46; Richler et al., 2019). The latent variable framework, which allowed for correlations

between factors to be estimated free from attenuations due to measurement error and

domain-specific variance, enabled us to further probe the strength of this relation. We found

that *o* can be measured equally well using either novel or familiar object categories.

We also found that including measures of domain-specific semantic knowledge did not

result in significant improvement in model fit, providing little evidence for an influence of

semantic knowledge on the relation between familiar and novel object recognition abilities. It is

possible that measuring semantic knowledge was not the best measure of domain-specific

experience pertinent to recognition performance (i.e. some other aspect of experience could be

more relevant to how well an individual can recognize objects from a given domain). However,

these measures have been found to correlate with single recognition measures and self-

reported experience measures (Van Gulick et al., 2016). To be clear, we do not interpret our

results as suggesting that experience has no impact on object perception. Indeed, there is

ample evidence that domain-specific experience affects the processing of objects from that

domain. For example, experts often exhibit evidence of holistically processing exemplars for

their domain of expertise (Busey & Vanderkolk, 2005; Gauthier et al., 2003; Gauthier & Tarr,

2002; A. Wong, Palmeri, & Gauthier, 2009; Y. Wong & Gauthier, 2010) and improvements in

performance resulting from perceptual training can transfer to objects from the trained domain

that were not used during training (Scott, Tanaka, Sheinberg, & Curran, 2006; Tanaka, Curran, &

Sheinberg, 2005; Tanaka & Pierce, 2009; B. Xu, Rourke, Robinson, & Tanaka, 2016). This does

not contradict our findings here as it is entirely possible for o to be predictive of an individual's

recognition performance in two domains even if the individual processes the domains

differently. This is congruent with Richler et al.'s finding that the domain that subjects were

exposed to showed increased holistic processing but correlated equally well with the un-

exposed categories (Richler et al., 2019). Taken together, these results suggest that experience

with domains can affect perceptual processing in measurable, quantitative ways. With regard

to variability in recognition performance across individuals, however, the processing differences

do not result in differences in the recruitment of the underlying skill that drives performance, o.

As a comparison, work in artificial intelligence has shown that it is possible for different visual strategies to produce similar performance on the Raven's Progressive Matrices test (Kunda, Mcgreggor, & Goel, 2011), which could suggest that individuals with the same level of fluid intelligence can engage in different processing strategies. In a similar way, experience could modulate the processing of objects from various domains, but the underlying skill driving the manifest observations remains the same regardless of changes in processing.

Though we specifically chose our familiar object categories to maximize how representative they were of a typical familiar object category, it of course remains possible that the results might differ if other categories were chosen. Future replications could test new sets of familiar categories, like mushrooms, shoes or leaves. Critically, the familiar categories we used had to result, relative to novel objects, in higher basic-level familiarity and some variability in subordinate-level familiarity in our subjects. That is, our subjects had knowledge regarding what a plane or a bird is, which they could not have had for a Greeble or a Ziggerin. Furthermore, some of them likely also had knowledge about individual exemplars in a way they could not have had for novel objects. Our results therefore clearly demonstrate that o can be measured equally well under these conditions. However, this may not apply to all familiar categories equally. For instance, faces and cars often dissociate from other familiar object categories (Ćepulić et al., 2018; Hendel et al., 2019; McGugin, Richler, et al., 2012; Sunday, Dodd, et al., 2018; Van Gulick et al., 2016), and future work could address how face and car recognition relate to novel object recognition within a latent variable framework. Especially given that several studies have found evidence that experience can influence face recognition (e.g. the other-race effect Brigham & Malpass, 1985; Sangrigoli, Pallier, Argenti, Ventureyra, &

De Schonen, 2005; Tanaka, Kiefer, & Bukach, 2004; or the hometown effect Balas & Saville, 2015, 2017; Sunday et al., 2018), determining if or why *o* diverges from face or car recognition may yield insight into theories about how experience and *o* interact.

Given the present findings, we might speculate that as a domain-general ability, *o* could be considered analogous to fluid intelligence. Similar to fluid intelligence, *o* does not require any previous experience to be relevant but is still pertinent in tasks that involve familiar stimuli. Recognition ability in domains with which we have substantial experience (for example faces and cars), may rely more on a type of crystallized, experience-dependent ability. To continue with this analogy, using novel objects to measure *o* would be similar to measuring fluid intelligence using novel stimuli like the abstract matrices used in the Raven's Progressive Matrices test (Raven, 2000). Using familiar objects that meet the criteria outlined here (specifically that they aren't too "special") is like measuring fluid intelligence with IQ measures like the Wechsler Adult Intelligence Scale (Wechsler, 1955), which uses letter and numbers with which adults are certainly familiar. Lastly, measures of domain-specific face or car recognition would be similar to measures of crystallized abilities, for example a baseball trivia quiz where performance mostly reflects specific experience with baseball. In both of these last instances, we would not expect such crystallized measures to strongly relate to their fluid counterparts. In this vein, previous work has reported distinct face, car and general object recognition factors (Ćepulić et al., 2018). Future work could more explicitly test this theory using a large battery of multiple tasks (note that Ćepulić et al, 2018 used only one task) and multiple novel, familiar and "special" categories like faces or cars.

Overall, this work further characterizes the newly proposed domain-general object recognition ability, *o*. At this point, *o* has been shown to account for a large portion of shared variance between novel object categories, to dissociate from other constructs like fluid intelligence, and to relate to domain-general familiar object recognition. These promising findings generate an exciting new line of research exploring, for example, if *o* extends into other perceptual modalities or if *o* has useful applications in various perception-heavy professions (e.g. radiology or security screening). In Chapter III, we pursue another research avenue by exploring potential neural correlates of *o*.

Chapter III

Neuroimaging Study

Several studies have looked for correlations between neural activity (or activity

patterns) and domain-specific recognition abilities (Bilalic, Grottenthaler, Nagele, & Lindig,

2016; Bilalić, Langner, Ulrich, & Grodd, 2011; Gauthier, Skudlarski, Gore, & Anderson, 2000;

Martens, Bulthé, van Vliet, & Op de Beeck, 2018; McGugin, Newton, Gore, & Gauthier, 2014; Y.

Xu, 2005), though no work to date has investigated neural correlates of a domain-general

object recognition ability. In the present study we attempted to localize the neural correlates of

o using functional magnetic resonance imaging (fMRI). In doing so, we hope to begin research

into the neural underpinnings of individual differences in domain-general object recognition. Is

there measurable variability in individuals' neural structures or functions that corresponds with

variability in domain-general object recognition? If such neural underpinnings exist, localizing

them could inform theories about the mechanisms responsible for variability in object

recognition abilities.

When considering what brain regions may support domain-general object recognition

ability, we first considered neuroimaging work localizing domain-specific recognition abilities.

Many studies report correlations between cortical activation and behavioral object recognition

measures for domains like cars (Gauthier, Skudlarski, et al., 2000; McGugin, Gauthier, Gatenby,

& Gore, 2012; McGugin et al., 2014; Y. Xu, 2005), faces (Furl, Garrido, Dolan, Driver, &

Duchaine, 2011; Huang et al., 2014) and birds (Gauthier, Skudlarski, et al., 2000; Y. Xu, 2005).

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Most of these studies focus on perceptual expertise effects in the fusiform face area (FFA), a

cortical region in the ventral temporal cortex that responds preferentially to faces (Kanwisher,

McDermott, & Chun, 1997) and objects of expertise (Bilalic et al., 2016; Bilalić et al., 2011;

Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; McGugin et al., 2014). Anatomical and

functional studies have shown that this FFA region is composed of two distinct clusters (one

posterior and one more anterior), which have been named FFA1 and FFA2 respectively (Pinsk et

al., 2008; Weiner, Sayres, Vinberg, & Grill-Spector, 2010). There is recent evidence that FFA2s

tend to more strongly relate to behavioral object recognition measures than FFA1s (McGugin,

Ryan, Tamber-Rosenau, & Gauthier, 2017; McGugin, Van Gulick, Tamber-Rosenau, et al., 2015),

supporting the utility in analyzing these regions separately when relating neural signals to

behavioral performance. Given the work focusing on correlates of perceptual expertise in the

fusiform gyrus, this region was also examined in a region-of-interest (ROI) analysis in the

present study. Indeed, functionally defining and analyzing ROIs (like the FFA and other object-

selective regions discussed below) will help to increase power and is necessary to account for

variability in the location of these functional regions (since the exact coordinates of FFA1s and

FFA2s differ between individuals so anatomical landmarks are less helpful). Critically, all of the

previous work has related behavioral measures of familiar object recognition to neural activity.

Thus, because those behavioral measures included variability due to experience, the results

then localized correlates of recognition abilities potentially influenced by experience. Indeed,

recent work has found that the relation between behavioral face recognition measures and FFA

activation can be amplified by manipulating experience with faces (McGugin et al., 2017),

specifically within the right FFA2. However, given the goal of the present work is to find

correlates of domain-general object recognition ability, independent of experience, there is no reason to limit our search to just the regions that relate to domain-specific recognition abilities. Thus, in addition to exploring potential correlates in ROIs, we also analyzed data from the entire cortex so that possible correlates outside the ROIs could be localized.

In designing the present study, we considered both where to search for correlates (discussed above) and what neural indices to use for our search. Should we use univariate activation differences, or would it be more informative to use more complex indices? Here, we chose to use a functional adaptation paradigm (a-fMRI) to index neural sensitivity. We chose to measure neural sensitivity because it reflects not only responsiveness to objects but also neural capability to perform functions critical to object recognition (like detecting subtle visual information) that could be diagnostic of object identities. This paradigm is based on the phenomenon (also called repetition suppression) that neural responses are reduced with the repetition of stimuli (Grill-Spector & Malach, 2001), which has been measured in object-selective regions across species (De Baene & Vogels, 2010; Li, Miller, & Desimone, 1993; Sawamura, Georgieva, Vogels, Vanduffel, & Orban, 2005; Verhoef, Kayaert, Franko, Vangeneugden, & Vogels, 2008) and using several methods, like single-cell recordings (De Baene & Vogels, 2010; McMahon & Olson, 2007; Verhoef et al., 2008), local field potentials (De Baene & Vogels, 2010), and MR spectroscopy (Apšvalka, Gadie, Clemence, & Mullins, 2015). Notably, using an adaptation paradigm also allows us to measure overall activity, so we can explore both how neural sensitivity and general responsiveness relate to *o*.

Our study follows a long line of work using a-fMRI paradigms to probe neural representations of varying object properties (Grill-Spector et al., 1999; Kourtzi & Kanwisher,

2000; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003; Vuilleumier, Henson, Driver, &

Dolan, 2002), including representations within the fusiform gyrus (Gauthier, Tarr, et al., 2000;

Grill-Spector et al., 1999; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston, 2004). The

underlying concept behind these adaptation studies is that if a cortical region is sensitive to a

given property (size, viewpoint, identity, etc.), then it should show more release from

adaptation to an object set with more variation in this property (i.e. less repetition of the

property). Conversely, a cortical region insensitive to a given property should show release

from adaptation of equal magnitude since that region has no means of representing the

differences between stimuli. Though the precise mechanisms underlying this reduction are still

unclear and could include firing-rate adaptation, synaptic and long-term depression, and

potentiation (Grill-Spector, Henson, & Martin, 2006), a-fMRI has proven to be a useful tool to

probe neural representations (for reviews, see Barron, Garvert, & Behrens, 2016; Larsson,

Solomon, & Kohn, 2016).

Most a-fMRI studies have examined neural sensitivity at the group level, but some have

looked for correlations between adaptation indices and individual behavioral measures (similar

to the present study). Epstein and co-authors found a correlation between navigational ability

and adaptation magnitude to scene stimuli in the parahippocampal place area (Epstein, Higgins,

& Thompson-Schill, 2005). Natu and co-authors found a relation between the slope of a

subject's adaptation function and an index of that subject's perceptual face discrimination

ability (Natu et al., 2016). These studies demonstrate how a-fMRI can provide insight into

neural correlates of individual differences that might not be evident with univariate methods.

The present study used a similar individual differences approach, because the goal is not to

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localize regions that are sensitive to object identity but rather to localize regions where sensitivity to object identity is related to an individual's domain-general object recognition ability. Regions that, on average, show adaptation effects to object identity are not of interest here, unless they also correlate with behavioral ability. We would, however, expect to see average adaptation effects in object-selective regions, since our stimuli are objects (similar to other studies using novel objects; Kourtzi, Erb, Grodd, & Bülthoff, 2003; Kourtzi & Kanwisher, 2000; Vuilleumier et al., 2002). Along these lines, because we would not expect face-selective regions to be particularly selective to novel objects on average, we would expect less average adaptation to occur in these regions than in object-selective regions.

In summary, based on previous neuroimaging work investigating neural correlates of domain-specific recognition abilities, the present study uses an a-fMRI paradigm to search for neural correlates of *o* in both ROI and whole brain analyses. Importantly, no study to date has specifically searched for neural correlates of individual differences in experience-independent object recognition, making the present study inherently exploratory. Drawing from the previous work finding experience-dependent correlates in FFA2s (McGugin et al., 2017; McGugin, Van Gulick, Tamber-Rosenau, et al., 2015), we can make one of two predictions. The first is that we find neural correlates with *o* only in FFA2s (which show strong relations with experience-dependent object recognition measures), which would suggest that these regions relate to recognition ability both when variability in domain-specific experience is present and when it is absent. The second prediction is that we find correlates outside FFA2s, which would suggest that regions correlating with experience and domain-general ability form parts of a network involved in object learning and recognition. We would expect these correlates of *o* outside of

FFA2s to be found in regions associated with high-level visual processing, but it is of course

possible that these correlates could be found elsewhere (for example, we might find correlates

in frontal regions if o derives from top-down feedback from areas responsible for executive

functioning, or correlates in early visual areas like V1 if o relates to bottom-up modulations

arising early in visual processing). Importantly, as compared with areas like V4 and MT,

adaptation effects in high-level visual regions seem to be more intrinsic as opposed to inherited

from top-down or bottom-up effects (De Baene & Vogels, 2010; McMahon & Olson, 2007, see

Barron et al., 2016), thus the possibility of our results stemming for inherited effects would be

minimal if we only find correlates within high-level visual regions. If we find evidence for this

second prediction (correlates of o outside FFA2s), this could indicate that FFA2s correlate with

experience either because they have a propensity for plasticity or because they code for

features that are well-suited for individuating objects. If the first hypothesis is true, with FFA2s

being particularly plastic, this would imply that various regions in the ventral visual stream

represent objects, but only specific regions (like the FFA2s) are capable of the plasticity that

supports learning to individuate objects. Thus, the high-level object recognition system may be

both capable of becoming specialized and maintaining flexibility (i.e. we can become experts at

discriminating between cars, while not losing the ability to tell apart objects we have never

encountered before). If the second hypothesis, that FFA2s code for features useful in object

individuation, is true, this would imply that (1) FFA2s contains neuronal populations capable of

representing object features complex enough for within-domain individuation (e.g.

distinguishing a Toyota Camry from a Honda Accord) and general enough to transfer to new

exemplars from experienced domains (e.g. distinguishing new car models from one another)

and (2) the other high-level visual regions, like the lateral occipital complex (Malach et al., 1995), contain neuronal populations capable of encoding more general features better suited for distinguishing between any two objects from any domain.

Methods

Subjects

Subjects were recruited from a previous behavioral study (Chapter II), attempting to sample a range of object recognition abilities. Thirty-seven subjects were scanned roughly 1-9 months after completing the behavioral study, though scanner malfunction lead to functional data collection for only thirty-six subjects (19 female, mean age = 21.5, SD = 3.9). A power analysis using G*Power software (Faul, Erdfelder, Lang, & Buchner, 2007) based on the correlation reported in Natu et al. revealed that to detect a similar correlation with 80% power required a sample size of 30 subjects (correlation between neural sensitivity and face perceptual discriminability in inferior occipital gyrus r = 0.47, see Figure 9 of Natu et al., 2016).

Functional localizer

To localize face and object-selective regions using independent data, subjects completed one localizer run. It is important to define face- and object-selective regions with data independent from the subsequent analyses, to avoid invalidating statistical inferences by using the same data to select regions for analysis and test for effects (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). During the localizer run, subjects were presented with 21 16-second

blocks of faces, body parts (with no faces), household objects and scrambled images. Each block

consisted of 16 trials in which a stimulus is presented for 900 ms followed by a 100 ms fixation.

Stimuli were greyscaled images of 35 faces, 35 objects, 37 scrambled images and 54 body parts

shown on a white background. A specific image repeated 1-2 times per block and subjects were

tasked with indicating these repeats with a button press. Stimuli were also presented randomly

in three different sizes, which never repeated in immediate succession. Variations of this

localizer have been used in prior work to localize medial and posterior FFA peaks (McGugin et

al., 2017; McGugin, Van Gulick, & Gauthier, 2015; McGugin, Van Gulick, Tamber-Rosenau, et al.,

2015). Total, this run lasted 5.6 minutes and stimuli were presented using Matlab and

Psychtoolbox-3 software (Brainard, 1997; Matlab, 2016).

Functional adaptation

    Stimuli

Because our goal was to correlate neural sensitivity with domain-general object

recognition ability, we used a wide range of novel object domains as stimuli during the

adaptation runs. De Baene and Vogels (2010) showed that similarity between objects drives

adaptation effects in inferior temporal regions of rhesus monkeys (a homologue to the lateral

occipital complex or LOC in humans, Denys et al., 2004; Sawamura et al., 2005), thus we would

expect that a range of novel object similarities should result in variable levels of adaptation,

hopefully helping us to discriminate among individuals whose neural activity show variable

levels of adaptation. If *o* is truly domain-general, then measuring neural sensitivity with many

novel object domains should afford more construct coverage than selecting only a few

domains. Moreover, the range of novel object domains used here will vary in attributes that have been shown to engage differing neural substrates, like animacy (e.g. Noppeney, Price, Penny, & Friston, 2006; Wiggett, Pritchard, & Downing, 2009), surface texture (Echavarria, Nasr, & Tootell, 2016) and curvilinearity/rectilinearity (Nasr, Echavarria, & Tootell, 2014; Yue, Pourladian, Tootell, & Ungerleider, 2014). Any region showing evidence of sensitivity to object identity in a set of novel domains with varying levels of these attributes is more likely to reflect attribute-general (and thus domain-general) neural correlates. Many of these domain choices were relatively subjective, but pilot data suggested these domains varied in their similarity and produced variable levels of adaptation.

A set of novel objects was collected from several sources and include 17 computer-generated novel object domains (Biederman et al., 2014; Horst & Hout, 2016; Leek et al., 2012; Op de Beeck, Torfs, & Wagemans, 2008; Watson, Voloh, Naghizadeh, & Womelsdorf, 2017; A. C.-N. Wong & Hayward, 2005; stimuli adapted by Erez Freud from Farley Norman, Norman et al., 2016; stimuli downloaded from http://wiki.cnbc.cmu.edu/Novel_Objects, see Figure 8). Additional stimuli were gathered from the Internet, including images of abstract three-dimensional sculptures, three-dimensional printed abstract chess pieces and dog toys (Figure 8). None of the three novel domains used in the behavioral study (vertical Ziggerins, Sheinbugs and symmetric Greebles, Chapter II) were used during scanning. All images were transformed to greyscale and equated for low-level images properties using the Matlab SHINE toolbox (Willenbockel et al., 2010).
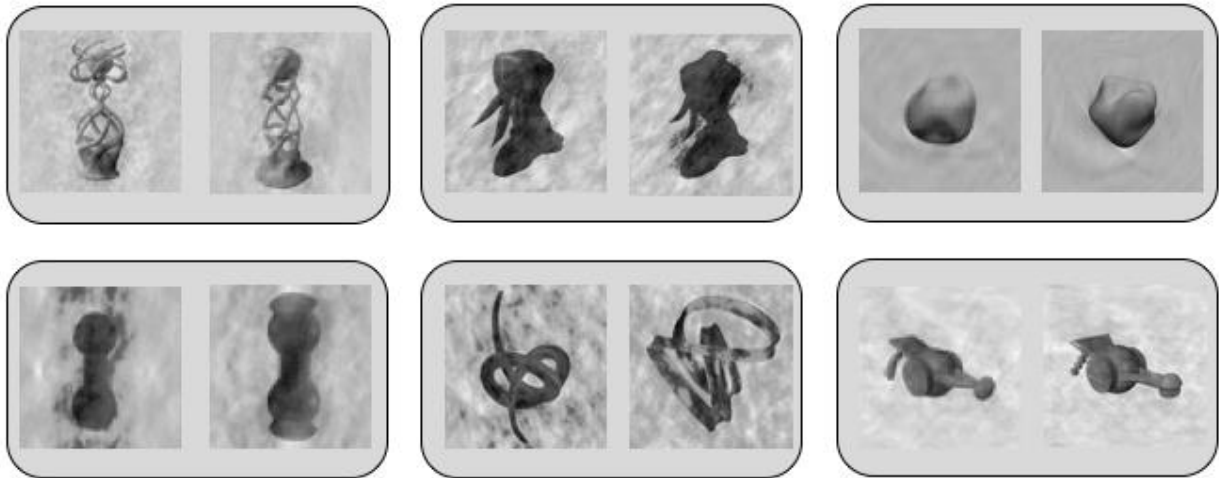
Figure 9. Example SHINED functional adaptation novel object stimuli. Top row, left to right: 3D printed abstract chess pieces, YUFOs from http://wiki.cnbc.cmu.edu/Novel_Objects, blobs used with permission from Erez Freud. Bottom row, left to right: dog toys, abstract sculpture, Fribbles from http://wiki.cnbc.cmu.edu/Novel_Objects

From each novel domain, three exemplars were chosen. For each set of three exemplars, there were three possible pairs. Our goal in selecting novel object pairs was to maximize the range of similarities between novel pairs (i.e. have some very similar pairs, some very dissimilar pairs, and pairs in between). Having a range of similarities between object pairs allows us to discriminate along the entire continuum of neural sensitivity to novel objects. In comparison, using, for example, one level of pair similarity would only allow us to group the responses across subjects in a given brain region into two groups (similar to how a test of intelligence should have questions varying in difficulty rather than only very easy and very hard questions). To get similarity ratings for each of these object pairs, each pair was presented in a matching task conducted online. In this task, subjects studied one object for 800 ms followed by

a mask for 500 ms, and then another probe object. Subjects decided whether the probe object was the same or different identity as the studied object. On trials in which the correct response was same, the studied object was rotated 15 degrees in-plane clockwise so that the images did not match exactly. There were 87 trials in which the correct response was different (the 3 possible pairs for 29 domains), and 87 trials in which the correct response was same (one trial for each object). The order of the 174 trials was randomized. Subjects completed three practice trials with feedback and were given feedback on the first three experimental trials. Data from 45 subjects were collected via Amazon Mechanical Turk. Five subjects were excluded for clicking through the study periods, leaving 40 subjects for analysis (29 male, mean age = 36.2 years). For each object pair, average accuracy and the correlation between subjects' average accuracy and item response were calculated (Table 5). In addition, hit rates were calculated for each "same" trial and false alarm rates were calculated for each "different" trial. Then the difference between hit and false alarm rates were calculated for each object pair. We chose which two object pairs to use in the adaptation runs based on these values. Importantly, our decisions of which of the three object pairs to exclude was relatively ambiguous for some object pairs for which all the behaviorally measured values were similar (for example, 3DPrintedAbstract domain). For other domains, the choice of which object pair to exclude was more obvious (for example object pair round_5050/round5000). Additionally, to shorten the length of the scans and reduce redundancy, we excluded three sub-domains taken from a broader domain that showed low accuracies and item-total correlation (Op De Beeck's rect_d2, spiky objects and FribblesC).

Study	test	HIT-FA rate	Acc	Correl
1A1B7_Art_F21.jpg	1A3B2_Art_F21.jpg	-0.15	0.08	-0.08
1A3B2_Art_F21.jpg	1A4B6_Art_F21.jpg	-0.30	0.05	0.06
1A4B6_Art_F21.jpg	*1A1B7_Art_F21.jpg*	*-0.20*	*0.03*	*-0.24*
1tool1v1.jpg	1tool3v1.jpg	-0.13	0.08	0.04
1tool3v1.jpg	*1tool6v1.jpg*	*0.00*	*0.08*	*-0.13*
1tool6v1.jpg	1tool1v1.jpg	0.15	0.20	0.22
3DPrintedAbstract1.jpg	*3DPrintedAbstract2.jpg*	*0.68*	*0.88*	*0.31*
3DPrintedAbstract2.jpg	3DPrintedAbstract4.jpg	0.68	0.78	0.45
3DPrintedAbstract4.jpg	3DPrintedAbstract1.jpg	0.78	0.80	0.46
chesspiece1.jpg	chesspiece2.jpg	-0.20	0.53	0.31
chesspiece2.jpg	*chesspiece3.jpg*	*0.63*	*0.93*	*0.16*
chesspiece3.jpg	chesspiece1.jpg	0.53	0.75	0.30
dogtoy2.jpg	dogtoy5.jpg	0.35	0.40	0.29
dogtoy5.jpg	*dogtoy6.jpg*	*0.65*	*0.73*	*0.27*
dogtoy6.jpg	dogtoy2.jpg	0.68	0.73	0.32
EdittDavidovici1.jpg	EdittDavidovici2.jpg	0.75	0.93	0.31
EdittDavidovici2.jpg	*EdittDavidovici3.jpg*	*0.93*	*1.00*	*NA*
EdittDavidovici3.jpg	EdittDavidovici1.jpg	0.63	0.93	0.31
F1FAPOS3.jpg	F1FFPOS3.jpg	0.10	0.20	0.38
F1FFPOS3.jpg	F1MEPOS3.jpg	0.10	0.30	0.47
F1MEPOS3.jpg	*F1FAPOS3.jpg*	*0.18*	*0.35*	*0.22*
Fa1_1111.jpg	*Fa1_2222.jpg*	*0.50*	*0.65*	*0.28*
Fa1_2222.jpg	Fa1_3333.jpg	0.88	0.95	0.33
Fa1_3333.jpg	Fa1_1111.jpg	0.68	0.80	0.56
Fb4_1111.jpg	Fb4_2222.jpg	0.48	0.68	0.47
Fb4_2222.jpg	Fb4_3333.jpg	0.58	0.75	0.41
Fb4_3333.jpg	*Fb4_1111.jpg*	*0.63*	*0.70*	*0.39*
Fc2_1111.jpg	*Fc2_2222.jpg*	*0.23*	*0.33*	*0.25*
Fc2_2222.jpg	*Fc2_3333.jpg*	*0.10*	*0.18*	*0.17*
Fc2_3333.jpg	*Fc2_1111.jpg*	*0.28*	*0.43*	*0.42*
G3_240.jpg	*GP1_240.jpg*	*0.63*	*0.75*	*0.23*
GO10_150.jpg	GO5_90.jpg	0.50	0.70	0.55
GO5_90.jpg	*GO7_60.jpg*	*0.78*	*0.93*	*0.26*
GO7_60.jpg	GO10_150.jpg	0.73	0.78	0.28
GP1_240.jpg	GP3_240.jpg	0.83	0.88	0.26
GP3_240.jpg	G3_240.jpg	0.53	0.60	0.24
KarsMarshall1.jpg	KarsMarshall2.jpg	0.80	0.93	0.36
KarsMarshall2.jpg	KarsMarshall3.jpg	0.95	0.95	0.39
KarsMarshall3.jpg	*KarsMarshall1.jpg*	*0.88*	*1.00*	*NA*
LenaAriceLucas1.jpg	LenaAriceLucas2.jpg	0.83	0.90	0.04
LenaAriceLucas2.jpg	LenaAriceLucas3.jpg	0.78	0.85	0.30
LenaAriceLucas3.jpg	*LenaAriceLucas1.jpg*	*0.75*	*0.90*	*0.24*
nam1_0.jpg	*nam2_0.jpg*	*0.48*	*0.53*	*0.33*
nam2_0.jpg	nam3_0.jpg	0.38	0.48	0.62
nam3_0.jpg	nam1_0.jpg	0.10	0.23	0.43

ng1-f-7-a.jpg	ng1-m-13-a.jpg	0.05	0.30	0.46
ng1-m-13-a.jpg	*ng1-m-25-a.jpg*	*0.00*	*0.25*	*0.29*
ng1-m-25-a.jpg	ng1-f-7-a.jpg	0.05	0.35	0.31
nre12_1.jpg	*nre8_1.jpg*	*0.18*	*0.48*	*0.30*
nre8_1.jpg	nre9_1.jpg	0.15	0.43	0.62
nre9_1.jpg	nre12_1.jpg	0.18	0.45	0.63
nz2_31_a.jpg	*nz2_41_b.jpg*	*0.43*	*0.63*	*0.32*
nz2_41_b.jpg	nz2_78_b.jpg	0.40	0.63	0.62
nz2_78_b.jpg	nz2_31_a.jpg	0.65	0.73	0.41
ob1-50.jpg	ob3-40.jpg	0.30	0.93	0.19
ob3-40.jpg	ob5-40.jpg	0.35	0.80	0.14
ob5-40.jpg	*ob1-50.jpg*	*0.68*	*0.93*	*0.07*
offset5Object11.jpg	offset5Object16.jpg	0.25	0.55	0.58
offset5Object16.jpg	*offset5Object7.jpg*	*0.55*	*0.73*	*0.26*
offset5Object7.jpg	offset5Object11.jpg	0.15	0.48	0.45
quaddle1.jpg	quaddle2.jpg	0.40	0.63	0.41
quaddle2.jpg	quaddle3.jpg	0.50	0.55	0.52
quaddle3.jpg	*quaddle1.jpg*	*0.63*	*0.83*	*0.34*
rect_0000.jpg	*rect_0005.jpg*	*0.20*	*0.35*	*0.24*
rect_0005.jpg	rect_0055.jpg	0.33	0.38	0.27
rect_0055.jpg	rect_0000.jpg	0.50	0.53	0.29
rect_d2_0500.jpg	*rect_d2_0505.jpg*	*-0.20*	*0.10*	*0.14*
rect_d2_0505.jpg	*rect_d2_0550.jpg*	*0.20*	*0.25*	*0.39*
rect_d2_0550.jpg	*rect_d2_0500.jpg*	*0.20*	*0.23*	*0.39*
round_5000.jpg	round_5005.jpg	0.10	0.18	0.31
round_5005.jpg	round_5050.jpg	0.15	0.23	0.27
round_5050.jpg	*round_5000.jpg*	*-0.18*	*0.08*	*-0.30*
S1_SD.jpg	*S1_SS.jpg*	*0.65*	*0.73*	*0.19*
S1_SS.jpg	S2_SS.jpg	0.78	0.98	0.24
S2_SS.jpg	S1_SD.jpg	0.90	0.95	0.23
SeymourMeyer1.jpg	*SeymourMeyer2.jpg*	*0.80*	*0.90*	*0.11*
SeymourMeyer2.jpg	SeymourMeyer3.jpg	0.40	0.93	0.34
SeymourMeyer3.jpg	SeymourMeyer1.jpg	0.65	0.85	0.43
spiky_5500.jpg	*spiky_5505.jpg*	*0.08*	*0.08*	*0.34*
spiky_5505.jpg	*spiky_5550.jpg*	*0.13*	*0.18*	*0.42*
spiky_5550.jpg	*spiky_5500.jpg*	*-0.08*	*0.05*	*0.41*
string1.jpg	string2.jpg	0.45	0.63	0.33
string2.jpg	*string3.jpg*	*0.38*	*0.38*	*0.12*
string3.jpg	string1.jpg	0.58	0.68	0.39
TrevorAskin1.jpg	TrevorAskin2.jpg	0.65	0.88	0.48
TrevorAskin2.jpg	TrevorAskin3.jpg	0.80	0.98	0.15
TrevorAskin3.jpg	*TrevorAskin1.jpg*	*0.70*	*0.83*	*0.15*

Table 5. Results from novel domain pair piloting on Amazon Mechanical Turk. Italicized rows are the excluded object pairs.

Stimulus presentation

A total of 52 object pairs were selected, using 26 novel object domains (2 object pairs per domain). The reliability of the measurements gathered online for this subset of trials was 0.91 (Cronbach α), suggesting these object pairs will tap into a sufficient range of visual ability and, by extension, the neural correlates of the mechanisms that support this ability.

In the scanner, each pair was presented once in a repeating block and once in an alternating block. To minimize adaptation across the entire scan (e.g. to avoid showing a repeating and an alternating block from the same domain in immediate succession), all 26 objects pairs were shown once (domains 1 to 26 across runs 1 and 2) and then shown again in the same order (1 to 26 again across runs 3 and 4). In this way, 25 object pairs were shown between each presentation of one domain. Based on previous work (Grill-Spector & Malach, 2001), this should have allowed enough time to minimize any domain-specific adaptation. Repeating and alternating blocks were interleaved. Fourteen fixation blocks of 6000 ms were randomly inserted in each run. During these blocks, a red fixation cross was presented in the center of the screen on a grey background. Though other studies separate each adaptation block with a fixation block (Andrews, Baseler, Jenkins, Burton, & Young, 2016; Davies-Thompson, Newling, & Andrews, 2013; Harris, Young, & Andrews, 2012), our stimuli were more variable and thus adaptation across blocks was not as much of a concern.

Adaptation effects can be measured with both event-related (e.g. Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003) and block designs (e.g. Gauthier, Tarr, et al., 2000). Here,

we chose a block design (1) to ensure that the hemodynamic response for each domain was as strong as possible with as little noise as possible (Grill-Spector et al., 2006) and, (2) because use of blocked designs has resulted in adaptation effects for objects in prior work (Gauthier, Tarr, et al., 2000; Natu et al., 2016). Each block included the presentation of eight images. On repeating blocks, the same object was shown on each trial (though the image did increase in size once per block, see below). On alternating blocks, an object pair was shown in an ABABABAB format (Figure 10). Previous work has used similar numbers of repetitions (Andrews et al., 2016; Natu et al., 2016) and both single-cell recordings and fMRI responses often plateau after approximately eight repetitions (Grill-Spector et al., 2006). For repeating blocks, every other image was rotated 15-degrees clockwise so that while the same exact object was shown on subsequent trials, the same exact image (in the same orientation) was not (Figure 10). Previous work has found that in-plane rotations of 2D objects did not cause a reduction in adaptation effects in the LOC (Kourtzi, Erb, et al., 2003). Moreover, pilot data indicated that this rotation did not cause release from adaptation during these blocks. Each 1000 ms trial consisted of a 900 ms stimuli presentation followed by a 100 ms inter-stimulus interval. Several studies using block-designs to find adaptation effects within the FFA have used similar stimulus presentation and inter-stimulus interval timing (Andrews et al., 2016; Davies-Thompson et al., 2013; Harris et al., 2012).

Task

Subjects performed a size-detection task in which they pressed a response button when the stimulus size increased (425x425 to 500x500 for 7 subjects, 525x525 to 600x600 for the

remaining subjects for which stimuli were presented using a different computer). The FFA has

shown invariance to size changes of up to three-fold increases (Andrews & Ewbank, 2004), and

anterior LOC regions have invariance to size changes from 7x7 images to 22x22 (Grill-Spector et

al., 1999). Thus, this size change should not be large enough by itself to cause a release from
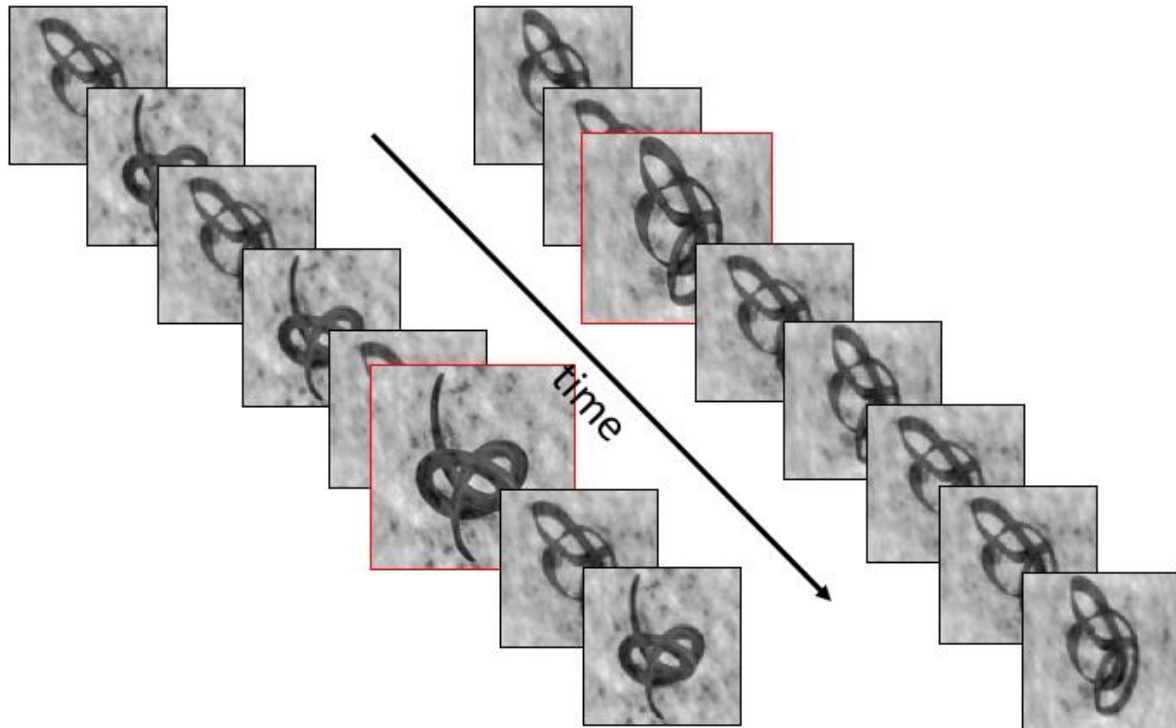
Figure 10. Schematic of alternating (left) and repeating (right) blocks used in adaptation
runs. Each stimulus was presented for 900 ms with a 100 ms inter-stimulus interval between
each presentation. Red outlined image represents the change in size that occurred once per
block, and the size change is exaggerated for illustrative purposes.

adaptation in high-level visual processing regions. A size increase occurred once per block and

never occurred on the first stimuli presentation. This task ensured that subjects attended to the

stimuli without requiring attention to object identity, keeping subjects visually engaged but

lessening the likelihood that activation differences would be driven by modulations of attention

to object identity. Moreover, the size detection task encouraged subjects to maintain central

fixation throughout the scans as, regardless of size, the stimuli were always centered on the

screen.

Scanning parameters

Subjects were scanned on a Philips 7-Tesla (7T) Achieva human magnetic resonance scanner

with a 32-channel parallel receive array coil (Nova). A 3D TFE (Turbo Field Echo) acquisition

sequence with sensitivity encoding (TR = 4.3 ms, TE = 1.90 ms (minimum), flip angle = 7°,

sagittal plane acquisition, for 7 subjects: FOV = 256 mm x 256 mm, matrix size = 224 x 224, 170

slices, slice gap = 0 mm, for 30 subjects: FOV = 256 mm x 256 mm, matrix size = 224 x 224, 200

slices, slice gap = 0 mm, for an isometric voxel size of 1 mm^3) was used to acquire high-

resolution T1-weighted anatomical volumes. All functional scans were acquired using standard

gradient-echo echoplanar T2*-weighted imaging (TR = 2000 ms, TE = 25 ms, flip angle = 65°,

axial plane acquisition, FOV = 240 mm x 240 mm, matrix size = 80 x 79, slice gap = 0 mm, for an

isometric 3 x 3 x 3 mm voxel). Following 5 dummy scans, for 31 subjects, 40 ascending

interleaved slices were acquired (for 1 subject: 42 slices, for 4 subjects: 45 slices). Subjects were

scanned in the following order: anatomical, functional localizer, adaptation runs (4 runs),

diffusion, resting-state, diffusion. The total scan time was approximately 1 hour and 15

minutes. For some scans in which the subject appeared to move during the scan (6 structural

scans) or subjects either fell asleep or a scanner error occurred (2 functional scans), these scans

were redone within the same session. Technical scanner issues resulted in poor or no

acquisition of structural, diffusion or resting states scans for several subjects. Thus 16 subjects

returned for a second session to complete the scan series.

Preprocessing

All MRI data were processed using SPM12 and in-house matlab (Matlab, 2016) scripts.

Functional data were first realigned and then slice-time corrected. Next, the functional images

were co-registered to the structural image using a skull-stripped structural image as a source

image. Both structural and functional images were then transformed into the standard

Montreal Neurological Institute (MNI) space. No spatial smoothing was applied.

ROI identification

For each subject, a linear model was fit to the localizer run with a regressor for each

domain (face, object, body part, scrambled images) as well as six movement parameters (x-

translation, y-translation, z-translation, pitch, roll, yaw). The linear model was then convolved

with the standard HRF function and a high-pass temporal filter of 128 seconds was applied. A

contrast of face>object was used to define face-selective areas in the fusiform gyrus and an

object>face contrast was used to define object-selective areas in the lateral occipital complex

(LOC) and parahippocampal (PHG) regions (using the Marsbar toolbox, Brett, Anton,

Valabregue, & Poline, 2002). For each identified ROI, an in-house matlab script selected the

peak functional voxel (27 mm^3). Given previous research has found maximal reliability of

individual differences in face selectivity in the center of face-selective ROIs, without an

advantage (and sometimes a decrease in reliability) of larger ROIs (McGugin & Gauthier, 2016),

this peak voxel was used for all subsequent analyses. A summary of the ROI coordinates is

reported in Table 6 and Figure 11 provides a schematic of ROI locations.

ROI	Mean X	Mean Y	Mean Z	t-value	p-value	N
lFFA1	-36.6 (7.1)	-68.9 (5.8)	-16.6 (4.0)	6.2	0.0	33
lFFA2	-38.9 (5.1)	-52.2 (6.1)	-19.5 (4.2)	6.3	0.0	37
lLOC	-43.7 (5.3)	-70.6 (6.3)	-5.5 (5.9)	7.0	0.0	37
lPHG1	-26.7 (4.0)	-65.9 (5.8)	-12.6 (5.8)	7.8	0.0	35
lPHG2	-27.5 (4.1)	-49.2 (4.7)	-15.3 (5.3)	7.4	0.0	37
rFFA1	36.2 (6.7)	-66.0 (5.9)	-15.8 (5.1)	6.5	0.0	30
rFFA2	37.5 (5.3)	-49.8 (5.3)	-18.6 (4.0)	6.2	0.0	34
rLOC	44.9 (6.6)	-69.1 (8.5)	-5.2 (5.1)	5.6	0.0	34
rPHG1	27.3 (4.5)	-64.2 (5.4)	-10.6 (5.0)	7.5	0.0	36
rPHG2	29.6 (4.6)	-47.2 (5.8)	-13.3 (5.7)	7.1	0.0	35

Table 6. Average (and standard deviations) MNI coordinates of independently localized ROIs, along with average t-values and p-values. N is the number of subjects in whom we localized each ROI.
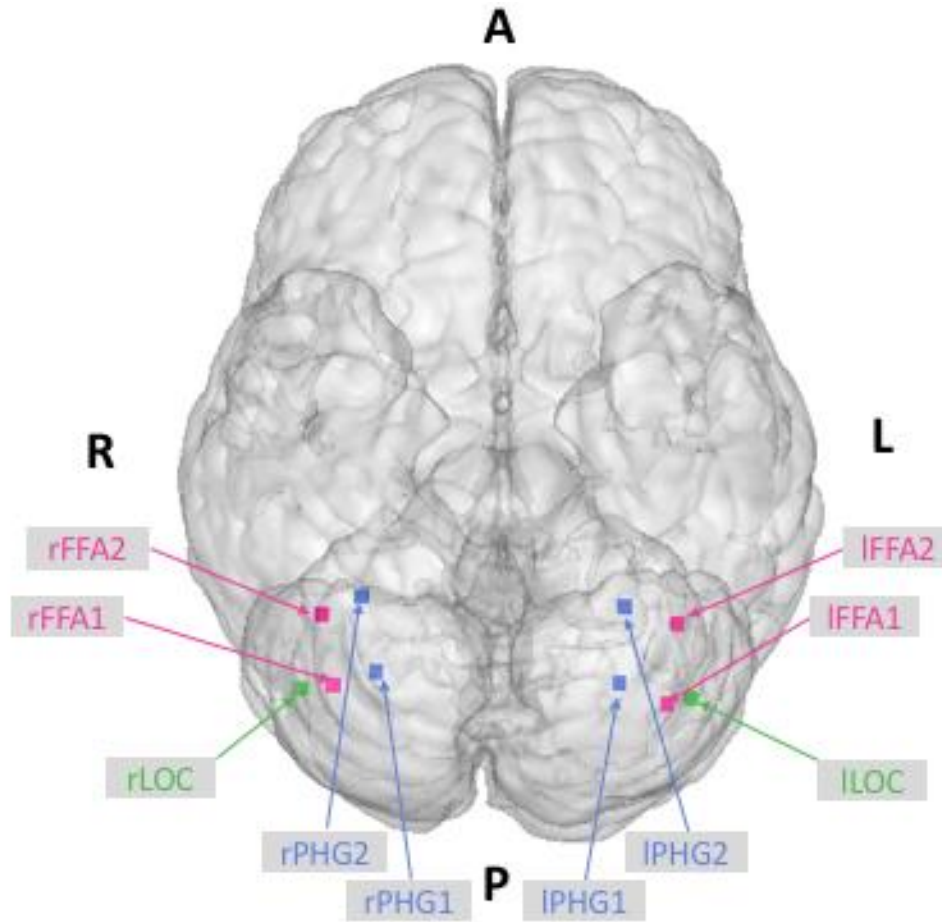
Figure 11. Schematic showing the approximate average location of ROIs used in the ROI analysis overlaid onto a MNI glass brain template shown in a ventral view. R = Right, L = Left, P = Posterior, A = Anterior. ROIs are shown in each hemisphere with green representing LOCs, pink representing FFAs and blue representing PHGs.

Results

Behavioral measure of domain-general object recognition

Factor scores were extracted for every subject using Mplus software (Muthén & Muthén, 1998). Because of the perfect correlation between *n* and *f* factor scores (R = 1.00, see

Figure 8), *n* factor scores (hereafter referred to as *o*-factors) were used as indices of domain-general object recognition ability for all following analyses. Scanned subjects showed a range of *o*-factors (range = -2.97-1.74, Figure 12).
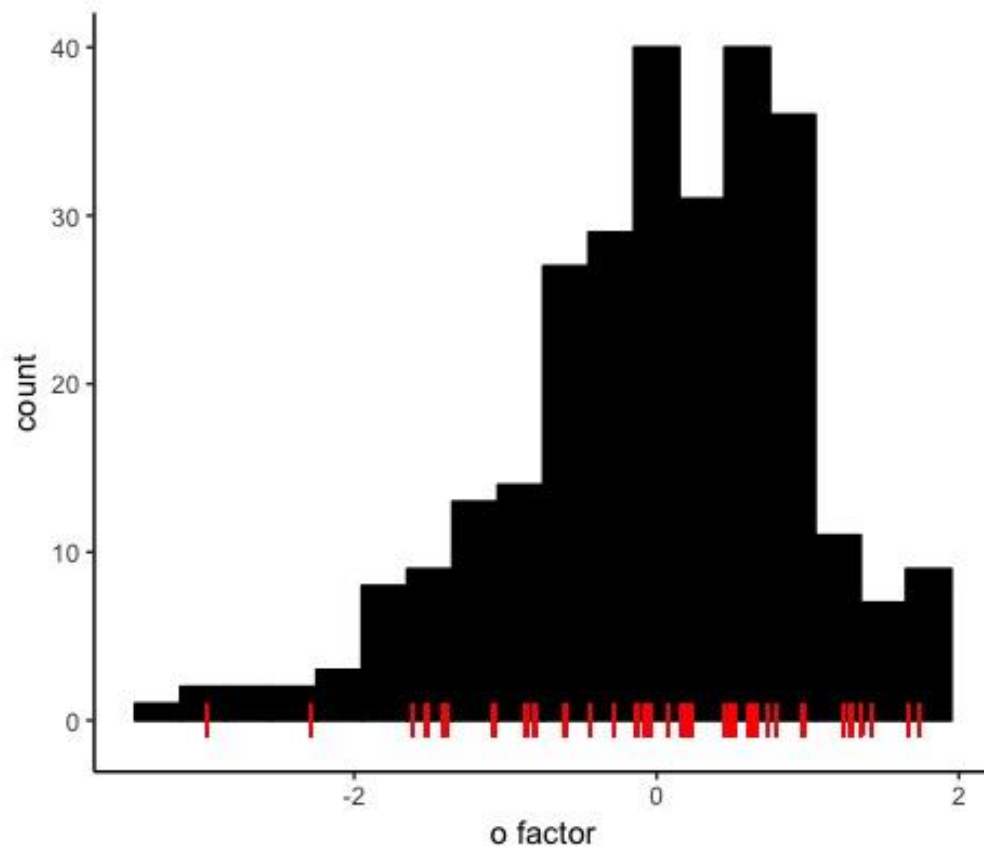
Figure 12. Histogram of *o*-factors for the 282 subjects from the behavioral study in Chapter II (+ 2 additional subjects). Scanned subjects' *o*-factors are indicated with red tick marks.

Factor score reliability was indexed by internal consistency coefficients calculated from standard errors of the factor scores using the following formula:

$$r = \frac{\frac{1}{J-1}\Sigma_{j=1}^{J}(\hat{\theta}_{j} - \bar{\theta})^{2} - MSE}{\frac{1}{J-1}\Sigma_{j=1}^{J}(\hat{\theta}_{j} - \bar{\theta})^{2}}$$

where J is the number of subjects (36), MSE is the mean error variance across subjects, $\hat{\theta}$ is the factor score and $\bar{\theta}$ is the mean of the factor scores across subjects. The reliabilitys across all 36 subjects was r = 0.78, showing acceptable reliability.

Behavioral scanning task

Average performance on the 1-back localizer task was 90% (SD = 13%) and average performance on the size-detection task for the adaptation runs was 62% (SD = 23%). Subjects' average accuracies on the adaptation runs did not correlate with o-factors (r_{34} = 0.29, p = .09).

Adaptation results

ROI analysis

For all ROIs, the raw signal for each adaptation run was extracted. For every data point, a pre-period signal was calculated by averaging the signal at the timepoints two seconds before the onset of every block and the timepoints at the onset of every block. This pre-period signal was calculated separately for alternating and repeating conditions and for each run, resulting in eight pre-period signal averages (e.g. Run 1 alternating or Run 3 repeating). Every data point was then normalized using the respective average pre-period signal, producing percent signal changes (PSC) from this baseline for every datapoint ((signal - pre-period/pre-period)*100). Figure 13 shows the PSC for each of the 10 ROIs.
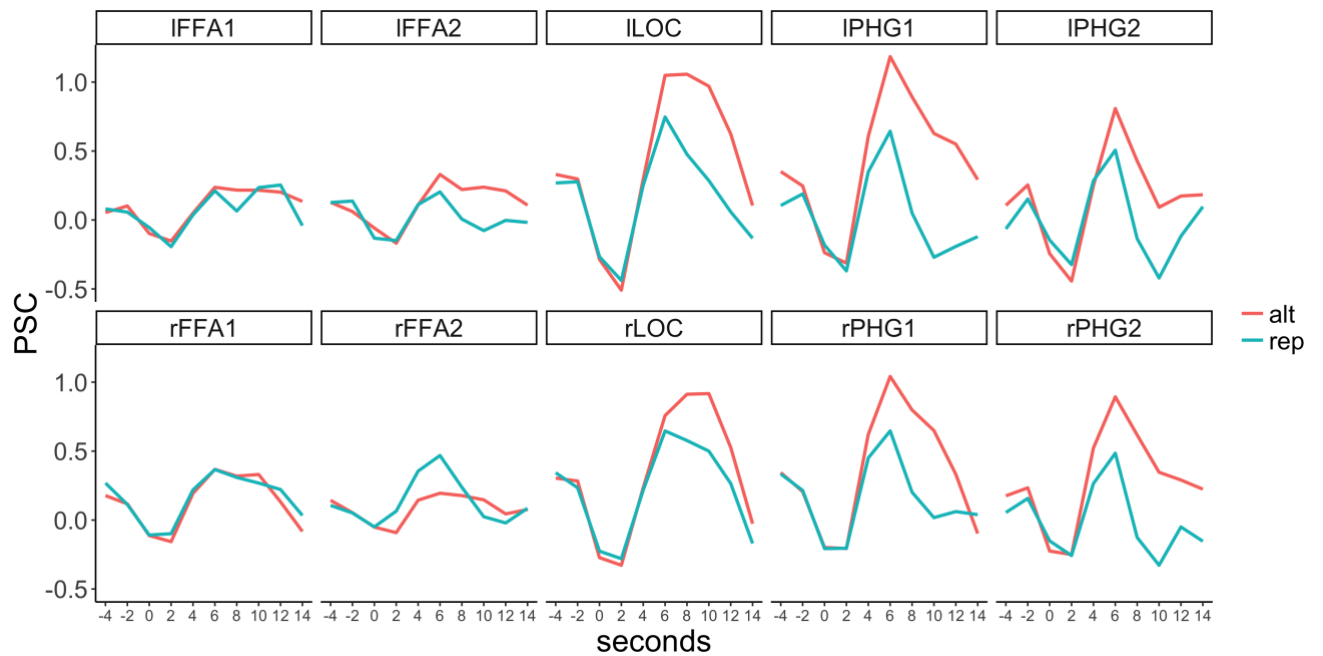
Figure 13. Percent signal changes for each ROI (top row: left hemisphere, bottom row: right hemisphere), averaged across runs and subjects. The PSC timecourse is shown from 4 seconds before each block to 6 seconds after the block end, for a total of 14 seconds. Alternating PSC is shown in pink and repeating PSC in blue.

To quantify the maximum response for each block, the PSCs for each block (from 6-12 seconds after block-onset) were averaged together. The average responses for alternating and repeating conditions are shown in Figure 14. On average, responses during alternating blocks were significantly larger than during repeating blocks in all object-selective ROIs (lPHG1, lPHG2, lLOC, rPHG1, rPHG2, rLOC, ps < .01), but were not significant in face-selective ROIs.
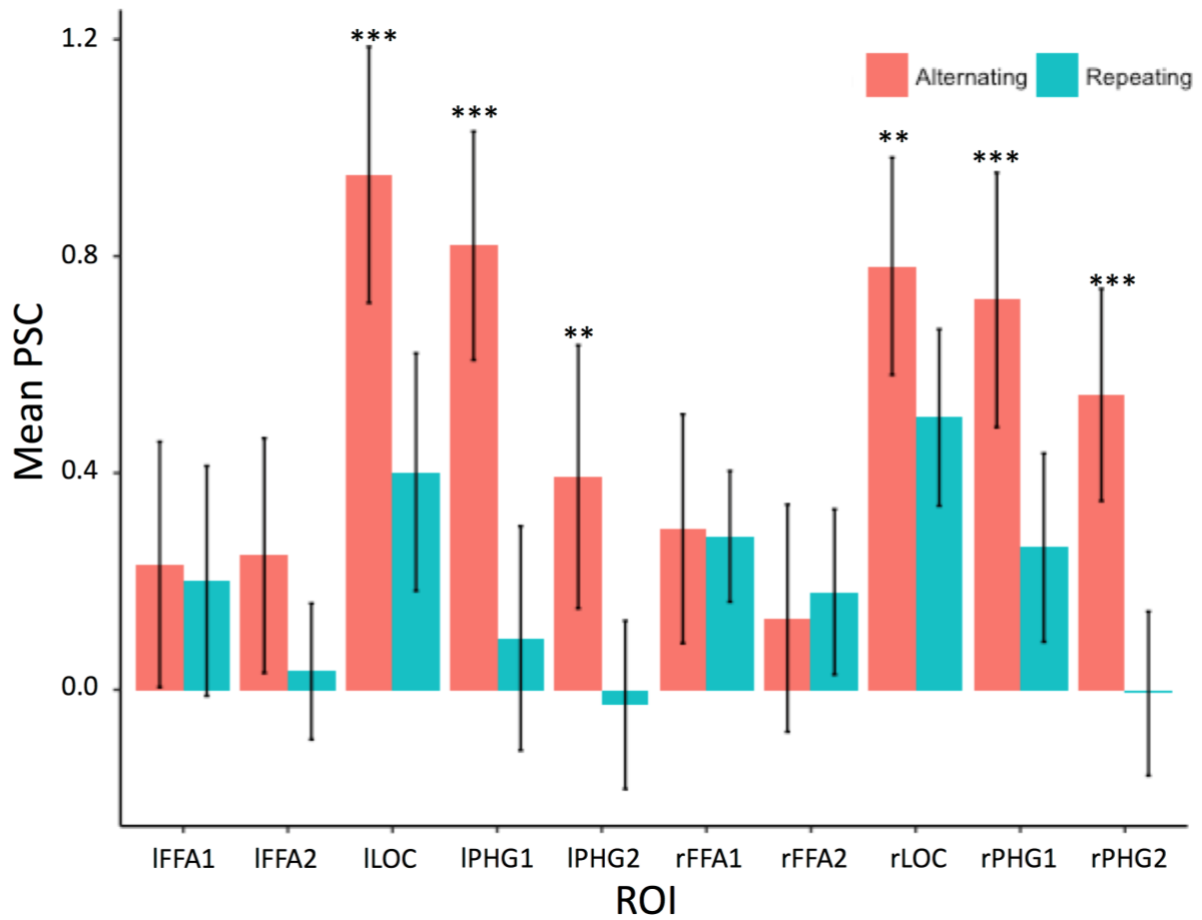
Figure 14. Average PSC for each ROI, with 95% confidence interval error bars. Alternating PSC is shown in pink and repeating PSC in blue. ** p <.01, *** p <.001

To index sensitivity to object identity, each subject's PSCs for repeating blocks were regressed out of the respective alternating blocks and these alternating residuals were used for all subsequent correlations. Reliabilities for these residuals, in each ROI, were calculated using the following formula (Rogosa, Brandt, & Zimowski, 1982):

$$\rho(U) = \frac{\rho(X_1) + \rho(X_2)\rho_{x1x2}^2 - 2\rho_{x1x2}^2}{1 - \rho_{x1x2}^2}$$

Where ρ_{x1x2} is the correlation between the two measures, $\rho(X_1)$ is the Guttman's $\lambda2$

for the alternating condition and $\rho(X_2)$ is the Guttman's $\lambda2$ for the repeating condition.

Reliabilities for each condition and associated residuals are reported in Table 7.

ROI	Alt Guttman's λ2	Rep Guttman's λ2	Residual reliability
lFFA1	0.57	0.52	0.56
lFFA2	0.70	0.14	0.61
lLOC	0.77	0.74	0.37
lPHG1	0.50	0.48	0.48
lPHG2	0.73	0.34	0.69
rFFA1	0.74	0.24	0.68
rFFA2	0.66	0.43	0.53
rLOC	0.79	0.67	0.60
rPHG1	0.71	0.52	0.66
rPHG2	0.62	0.37	0.61

Table 7. Guttman's λ2 for alternating and repeating conditions, and the reliabilities of the alternating residuals for each ROI.

Before examining the relation between neural sensitivity and *o*, we first explored

whether general activity in any ROI was related to *o*. To do this, we examined the correlations

between average alternating, average repeating and overall (average alternating and repeating)

PSCs with *o*-factors (Table 8). Average alternating PSC significantly correlated with *o*-factors in

lPHG2, rFFA1 and rPHG1 (lPHG2: $r_{34} = 0.49$, 95% CI [.20, .71], $r^2 = 0.24$ $p = .002$, rFFA1: $r_{27} = $

0.42, 95% CI [.07, .68], $r^2 = 0.18$ $p = .02$, rPHG1: $r_{33} = 0.54$, 95% CI [.25, .74], $r^2 = 0.29$, $p < .001$).

Average repeating PSC did not significantly correlate with *o*-factors in any ROIs. The average

overall signal significantly correlated with *o*-factors in lPHG2 and rPGH1 (lPHG2: r_{34} = 0.46, 95%

CI [.15, .68], r^2 = 0.21 p = .005, rPHG1: r_{33} = 0.39, 95% CI [.07, .64], r^2 = 0.15, p = .021).

	lFFA1	lFFA2	rFFA1	rFFA2	lPHG1	lPHG2	rPHG1	rPHG2	lLOC	rLOC
Alternating	-0.06	0.05	**0.42**	0.26	0.12	**0.49**	**0.54**	0.19	0.24	0.12
Repeating	0.18	0.14	-0.20	-0.17	-0.13	0.15	0.00	0.18	-0.12	-0.12
Overall	0.08	0.13	0.24	0.13	-0.01	**0.46**	**0.39**	0.27	0.07	0.01

Table 8. Correlations between alternating PSC, repeating PSC, and overall activity with *o*-factors across ROIs. Correlations > 0.38 have *p*-values < .05 and are bolded, correlations > 0.45 have *p*-values < .01, correlations > 0.53 have *p*-values < .001

Our main analysis aimed to localize cortical regions in which variability in neural

sensitivity to object identity relates to variability in domain-general object recognition. To this

end, we examined the correlations between alternating residuals across ROIs and *o*-factors,

(reported in Table 9 and illustrated in Figure 15). rFFA1, lPHG2, rPHG1 and lLOC significantly

correlated with *o*-factors (rFFA1: r_{27} = 0.49, 95% CI [.14, .72], r^2 = 0.24 p = .008, lPHG2: r_{34} =

0.47, 95% CI [.17, .69], r^2 = 0.22 p = .004, rPHG1: r_{33} = 0.55, 95% CI [.27, .75], r^2 = 0.30, p < .001,

lLOC: r_{34} = 0.43, 95% CI [.11, .66], r^2 = 0.18, p < .001).

	lFFA1	lFFA2	rFFA1	rFFA2	lPHG1	lPHG2	rPHG1	rPHG2	lLOC	rLOC
lFFA2	0.21									
rFFA1	-0.07	0.22								
rFFA2	0.21	-0.03	**0.66**							
lPHG1	0.15	0.18	0.23	0.11						
lPHG2	0.23	0.11	**0.43**	0.28	0.03					
rPHG1	0.07	0.23	**0.42**	**0.37**	-0.11	**0.51**				
rPHG2	**0.38**	**0.36**	0.36	0.27	0.04	**0.47**	0.30			
lLOC	-0.03	**0.44**	**0.37**	0.11	0.17	**0.34**	**0.41**	0.21		
rLOC	**0.37**	0.11	0.20	0.30	-0.08	**0.37**	**0.47**	0.28	**0.37**	
o	-0.04	0.09	**0.49**	0.21	0.14	**0.47**	**0.55**	0.20	**0.43**	0.21

Table 9. Correlations between alternating residuals across ROIs and *o*-factors. Correlations > .36 have *p*-values < .05 and are bolded, in addition to lLOC with lPHG2 (*p* = .04) and rPHG2 with lFFA2 (*p* = .04). Correlations > .42 have *p*-values < .01 except lPHG2 with rFFA1 (*p* = .02) and correlations > .54 have *p*-values < .001.
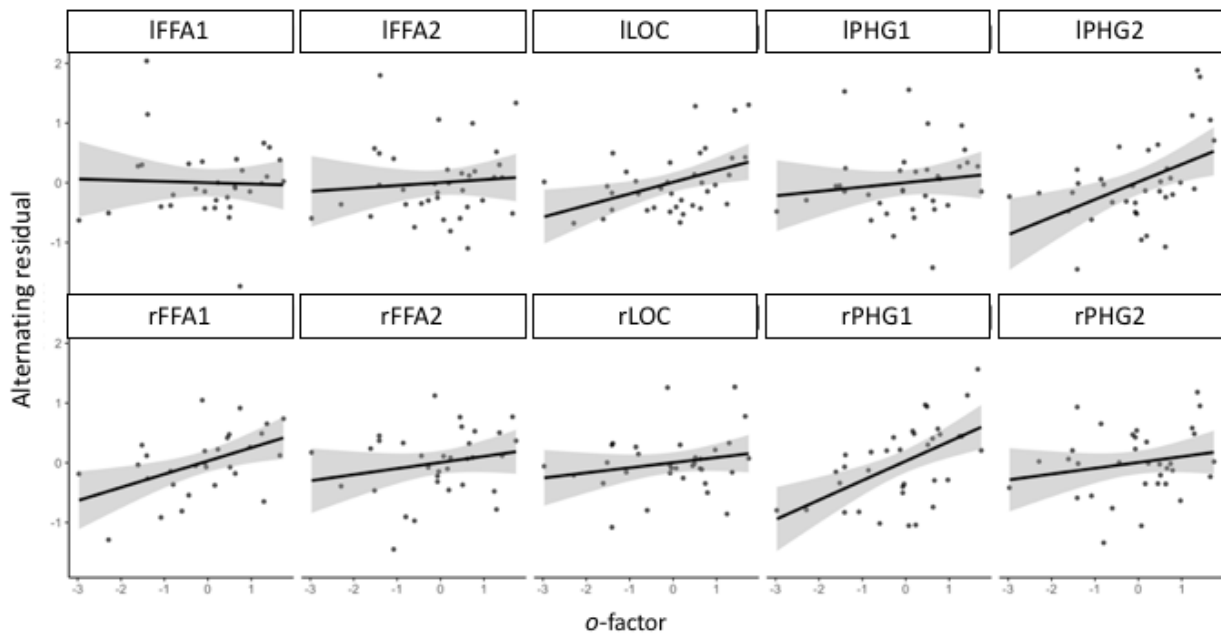

Figure 15. Scatterplots of *o*-factors versus alternating residuals for each ROI. Shaded regions represent 95% confidence intervals.

The ROIs that significantly correlated with *o*-factors also all significantly correlated with one another (rs = 0.34-0.51, Table 9), suggesting common variance between these ROIs. Indeed, if the common variance between these ROIs is removed by using a multiple regression to predict *o*-factors with rFFA1, lPHG2, rPHG1 and lLOC alternating residuals, none of the ROIs are significant predictors (*t*s = 0.99-1.38, *p*s = 0.18-0.33). This further suggests that the correlations between these ROIs and *o* is driven by variance shared across a network. Future work could use more complex statistical methods to further examine this shared variance.

Whole brain analysis

We conducted an exploratory search throughout the brain for correlates of *o*, first fitting a linear model to the four adaptation runs with a regressor for each condition (alternating, repeating and fixation), six movement parameters (x-translation, y-translation, z-translation, pitch, roll, yaw), and a regressor for each run. This model was convolved with the standard HRF function and filtered with a high-pass, 128-second temporal filter. To get one index of the signal for each condition, the beta-weights for each run were averaged together by condition for each subject voxelwise (using SPM's ImCalc function, e.g. beta-weights for the repeating condition for runs 1, 2, 3, and 4 were averaged per subject). Then a multiple regression was performed across subjects, using AFNI's 3dMVM function (Chen, Saad, Adleman, Leibenluft, & Cox, 2015). The model predicted average alternating beta-weights from *o*-factors and average repeating betas-weights entered as a voxelwise covariate. The resulting *t*-values for the *o*-factor regressor were used to find significant clusters. Ten clusters survived an

uncorrected threshold of $p < .001$ and cluster-size minimum of 3 voxels (Table 10, Figure 16,

made using SUMA software; Saad, Reynolds, Argall, Japee, & Cox, 2004).

Cluster	Num Voxels	Mean X	Mean Y	Mean Z	Alt λ2	Rep λ2	Residual reliability	r	Brain Region
1	21	-41.4	-75.6	0.60	0.84	0.65	0.59	0.59	Left Inferior Occipital Gyrus
2	7	-36.0	-66.6	-16.4	0.71	0.34	0.62	0.47	Left Fusiform Gyrus
3	7	-22.7	-79.9	30.7	0.80	0.67	0.27	0.62	Left Middle Occipital Gyrus
4	3	28.0	-66.0	-10.0	0.80	0.66	0.68	0.62	Right Fusiform Gyrus
5	3	-49.0	-63.0	-10.0	0.56	-0.50	0.43	0.24	Left Inferior Occipital Gyrus
6	3	18.0	-71.0	6.0	0.10	0.71	0.06	0.20	Right Lingual Gyrus
7	3	-2.0	-71.0	10.0	0.62	0.71	0.62	0.32	Left Lingual Gyrus
8	3	42.0	-75.0	11.0	0.59	0.26	0.43	0.60	Right Middle Occipital Gyrus
9	3	37.0	-45.0	48.0	0.83	0.49	0.83	0.49	Right Inferior Parietal Lobule
10	3	-34.0	-59.0	35.0	0.70	0.41	0.24	-0.20	Left Angular Gyrus

Table 10. Clusters from multiple regression analysis. Mean of MNI coordinates and number of voxels for each cluster are reported along with the approximate brain region of each cluster, Guttman's λ2 for alternating and repeating conditions, reliabilities of alternating residuals for each cluster, and correlation coefficient from PSC analysis.

Because the cluster analysis of the multiple regression was performed voxelwise at

thresholds not corrected for multiple comparisons (because no voxels survived this correction),

we analyzed the data from each cluster as a whole (averaged across voxels) to better

understand the correlations between o-factors and alternating residuals. Moreover, the

multiple regression was conducted with beta-weights because of software constraints, so to

provide a more direct comparison of these results with those from the ROI analysis, we

characterized the effects of each cluster using PSCs extracted from these regions. To this end,

data from these clusters were extracted and analyzed in the same way as in the ROI analysis

(extracting PSCs, regressing repeating PSC from alternating PSC, etc.). Notably, using either
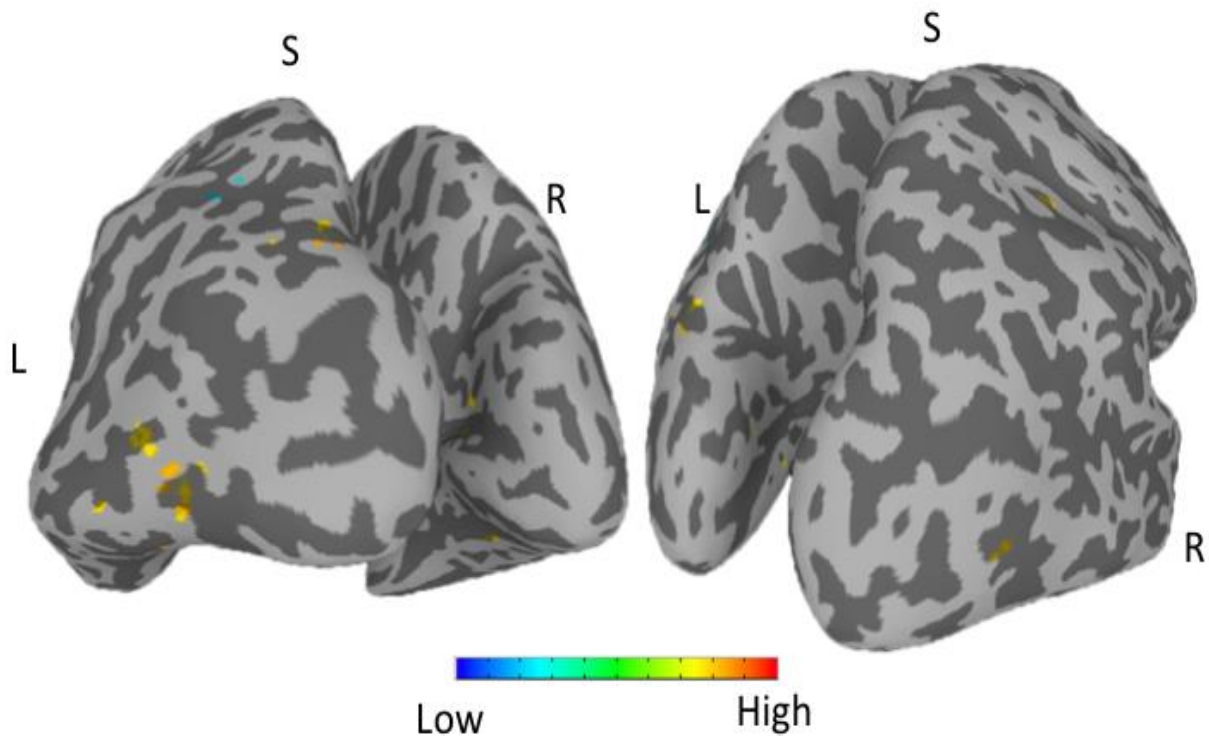
Figure 16. Map of clusters from whole brain analysis. T-statistics of each cluster overlaid onto an inflated cortex of the MNI N27 brain template for visualization purposes using SUMA. L=Left, R=right, S = superior.

averaged beta-weights or PSCs produced similar results (correlations between beta-weights and PSCs across subjects within clusters ranging from 0.47-0.87), and none of the results qualitatively differed when beta-weights were used rather than PSCs (i.e. the correlations between beta-weights with *o*-factors and PSCs with *o*-factors across clusters were very similar with r_8 = 0.93, *p* < .001). Thus, for consistency with the ROI analysis, we report the results using average PSCs extracted from each cluster. Reliabilities for each cluster are reported in Table 10. Alternating PSC residuals from all clusters correlated significantly with *o*-factors (Cluster 1: r_{34} = 0.59, 95% CI [.32, .77], r^2 = 0.35, *p* < .001, Cluster 2: r_{34} = 0.47, 95% CI [.16, .69], r^2 = 0.22 *p* =

.004, Cluster 3: $r_{34} = 0.62$, 95% CI [.36, .79], $r^2 = 0.38$, $p < .001$, Cluster 4: $r_{34} = 0.62$, 95% CI [.37,

.79], $r^2 = 0.38$, $p < .001$, Cluster 7: $r_{34} = 0.32$, 95% CI [-.01, .59], $r^2 = 0.10$, $p = .05$, Cluster 8: $r_{34} =$

0.60, 95% CI [.33, .77], $r^2 = 0.36$, $p < .001$, Cluster 9: $r_{34} = 0.49$, 95% CI [.19 .70], $r^2 = 0.24$, $p =$

.003; Figure 17), except clusters 5, 6, and 10 (which showed trending significance with ps of

0.17, 0.24 and 0.25 respectively, although they had correlations between their beta-weights

and o-factors below the p < .05 level). All significant correlations with o-factors were positive

except Cluster 10, which showed a negative, relatively weak correlation ($r_{34} = -0.20$, 95% CI [-.49
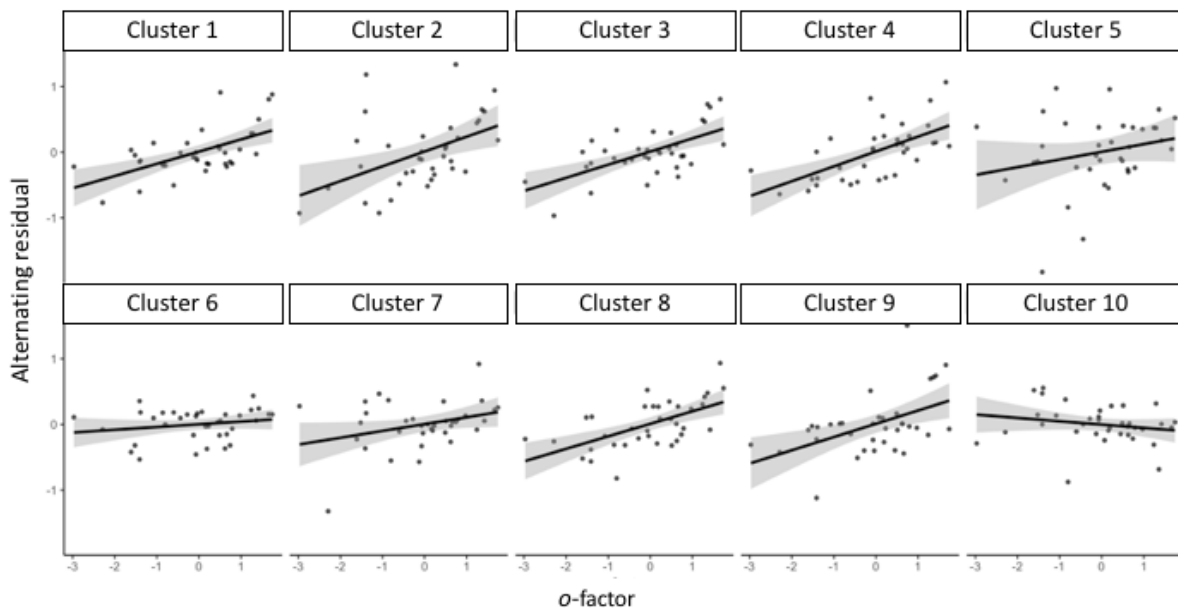
.14], $r^2 = 0.04$, $p = .25$).

Figure 17. Correlations between alternating residuals and o-factors in each cluster. Shaded regions represent 95% confidence intervals.

None of the clusters overlapped with any group-averaged ROIs that significantly

correlated with o (lLOC, lPHG2, rFFA1 and rPHG1). The smallest Euclidean distance between any

regions showing a relation with *o* (both ROIs and clusters) was between rPHG1 and Cluster 4 (distance ~ 2.0 mm), with group-averaged rPHG1 residing approximately 1.5 mm anterior to Cluster 4. Cluster 1 was also located relatively close to group-averaged lLOC (distance ~ 8.2 mm), with lLOC residing approximately 7 mm superior and 5 mm posterior to Cluster 1.

Discussion

This chapter presented exploratory findings about the neural correlates of domain-general object recognition ability, *o*. We found evidence for a positive relation between *o*-factors and neural sensitivity in regions throughout temporal and parietal lobes. In the ROI analysis, neural sensitivity in several functionally-defined, object-selective regions and one face-selective region correlated with *o*-factors. The whole brain analysis revealed other brain regions located primarily near the fusiform, lingual and occipital gyri where sensitivity in these regions correlated with *o*-factors. Together, these results indicated the first evidence that neural correlates of domain-general object recognition ability can be found in occipito-temporal regions where neural sensitivity to objects varies across subjects.

Because previous work found strong expertise effects in FFA2s (Golarai, Liberman, & Grill-Spector, 2017; McGugin et al., 2014, 2017; McGugin, Van Gulick, Tamber-Rosenau, et al., 2015), we could have found domain-general correlates within the same regions, to suggest that the neural correlates of experience-dependent and experience-independent object recognition performance overlap. Another possibility was that we would find effects in regions outside FFA2, either localized effects in a single region (for example, finding correlates of *o* only in FFA1) or distributed effects in several regions. Our results generally supported the latter possibility,

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that the neural correlates of o are distributed and do not overlap with the effects of expertise that are found in FFA2. Specifically, our ROI analysis revealed that neural sensitivity in object-selective right-parahippocampal, left-parahippocampal, left lateral occipital and face-selective right fusiform regions (rPHG1, lPHG2, lLOC and rFFA1) correlated with o-factors and the whole brain analysis implicated other regions, bilaterally, along the fusiform, occipital and lingual gyri. Generally, we found that repetition effects in small regions (27-567 mm^3 voxels) that have been associated with high-level visual-processing (e.g. Malach et al., 1995) throughout the temporal and parietal lobes correlated with o. This suggests the neural processing underlying experience-independent, domain-general object recognition is both distributed and bilateral. This finding may not be surprising given that other constructs like intelligence tend to show distributed correlates (Basten, Hilger, & Fiebach, 2015; Jung & Haier, 2007). Interestingly, neither FFA2s, which have shown relatively local correlations with experience-dependent measures in past research (Golarai et al., 2017; McGugin et al., 2014, 2017; McGugin, Van Gulick, Tamber-Rosenau, et al., 2015), correlated with o-factors in the present study. We speculate that novel object processing in novices recruits several distributed high-level visual regions. Then, as an individual gains domain-specific experience, more specialized processing of objects from a domain can occur (perhaps by honing in on domain-specific diagnostic features), and this processing recruits representations in the FFA2. An important aspect of this hypothesis is the type of domain-specific experience. Specifically, work has shown that subordinate-level training can produce focal effects in FFA regions whereas basic-level training produces more distributed effects in occipitotemporal regions (Wong, Palmeri, Rogers, Gore, & Gauthier, 2009). These focal effects in FFA2 are correlated with individual differences in holistic processing (Ross et al.,

2018), which also increases with subordinate-level experience (Chua & Gauthier, in press; Gauthier & Tarr, 2002; Gauthier, Williams, Tarr, & Tanaka, 1998; A. Wong, Palmeri, & Gauthier, 2009). Conversely, other types of experience, or even just simple exposure, may modify pre-existing representations that are distributed throughout high-level visual areas (Op de Beeck & Baker, 2010). Thus, in relation to the present findings, the hypothesized narrowing to FFA2 may only occur (or be more pronounced) with subordinate-level experience as compared with basic-level experience.

In addition to the location of neural correlates of *o*, the nature of these correlations is also informative. The correlations between *o* and neural sensitivity were consistently positive, meaning that increased neural sensitivity predicted increased domain-general object recognition ability. This indicates that individuals in the upper range of *o* are more sensitive to differences between objects, as reflected in the corresponding neural representations, giving rise to greater release from adaptation. Further studies replicating this work and extending it using neuroimaging methods capable of probing neural representations (like multi-voxel pattern analysis) could further investigate how the neural representations of objects relates to domain-general object recognition ability. Future studies could also investigate what differences between objects are driving this suppression, which could help inform what object features (e.g. shape or configuration) are most relevant to individual differences in *o*.

Along with the direction of observed correlations, the strengths of these correlations were also fairly consistent, ranging from 0.43 - 0.55 in the ROI analysis and 0.22 - 0.62 in the whole brain analysis. These moderate correlations suggest moderate effects of *o,* accounting for approximately one-fourth of the variance in neural sensitivity. Future work can explore how

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other constructs, either behavioral (e.g. fluid intelligence) or neural (e.g. structure or connectivity) may account for additional portions of this variance. It is also important to note that the reliabilities of each region found to correlate with o were not perfect (Tables 7 and 10, Guttman's $\lambda2$ ranging from 0.37 - 0.69 in the ROI analysis and 0.27 - 0.83 in the whole brain analysis), and thus could have attenuated the observed correlations (Nunnally, 1970). After correcting for attenuation due to measurement error, the range of correlations from the ROI analysis is 0.57-0.71 and 0.41-1.0 in the whole brain analysis, which represent upper limits for these correlations if both measures being correlated contained no measurement error.

In investigating the nature of the correlations between neural sensitivity and o, we also found that the shared variance indicated by these correlations tends to overlap within our ROI analysis, suggesting that the regions found to correlate with o do so through common variance between ROIs. We found evidence for this both in the fact that neural sensitivity in these regions correlate with one another (Table 9, minimum r = 0.34 (lPHG2 and lLOC), maximum r = 0.51 (lPHG2 and rPHG1)) and in our multiple regression model (in which none of the ROIs were significant predictors of o-factors, ts = 0.99-1.38, ps = 0.18-0.33). It is also interesting to note that neural sensitivity in rFFA1 significantly correlated with o-factors (r = 0.49) even though no significant difference between alternating and repeating conditions was observed on average for this region (Figure 14). This exemplifies the difference between group approaches concerned with average effects compared with individual differences approaches focused on variability.

Lastly, though our main focus in the present work was relating neural sensitivity to o, we also found that overall activity in lPHG2 and rPHG1 correlated with o-factors. This indicates that

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the general responsiveness of these regions to the presentation of objects can predict an individual's domain-general object recognition ability. Interestingly, these regions also show correlations between their neural sensitivity and o-factors, such that no region was found where overall activation in response to objects was related to o without further finding that this region responded specifically to changes in object identity. On the one hand, it is possible that increased sensitivity in parahippocampal areas results in increased activation (i.e. more energy is required to support this increased sensitivity) such that the correlation between o and general activation follows from the correlation between o and neural sensitivity. On the other hand, it is possible that, with regard to parahippocampal regions, domain-general object recognition performance is driven both by functions performed on the neural representations of object identity (reflected in neural sensitivity) and general increases in activity, such that the coupling of increased activation and increased sensitivity results in better performance, but each contribute separately. Though we cannot parse out these two possibilities in the present data, it is worth noting that neural sensitivity and general activation significantly correlated in all ROIs (rs = 0.42-0.95, ps ≤ .01). Follow-up work can further assess these relations using paradigms better optimized to measure both adaptation and overall activity, unlike the current paradigm (which was optimized only for adaptation).

The findings discussed here result from exploratory analyses and have several limitations. First, the clusters localized in the whole brain analysis were found using a threshold not corrected for multiple comparisons (because no clusters survived this correction) and should thus be interpreted cautiously. Second, though our sample size of thirty-six was larger than previous work looking at correlations with neural sensitivity (Epstein et al., 2005; Furl et

al., 2011; Natu et al., 2016) and was based on a power analysis, it was only a fraction of the 100

or even 250 subjects some have suggested is desirable for individual differences MRI work

(Dubois & Adolphs, 2016; Schönbrodt & Perugini, 2013). Because of this, we believe it will be

critical for confirmatory studies to not only attempt to replicate the correlations reported here

with larger sample sizes, but also to assess the predictive power of neural sensitivity to predict

o-factors in individuals outside the correlation sample (see Dubois & Adolphs, 2016). Lastly, our

current sample had a fairly restricted age range (range = 18-34), and so the results found here

may not generalize to older or younger samples. Age modulates face recognition ability

(Germine, Duchaine, & Nakayama, 2011), and studies have found evidence for age-related

differential item functioning (using Item Response Theory) in a test of car recognition ability but

not in a test of face recognition ability (Cho, Wilmer, Herzmann, McGugin, & Fiset, 2015; Lee,

Cho, McGugin, Van Gulick, & Gauthier, 2015), though some of this differential item functioning

may be due to format of these specific tests (Sunday, Lee, & Gauthier, 2018). The age range in

our sample reflected not only our choice to recruit subjects from the behavioral study in

Chapter II, which relied mostly on an undergraduate student research pool, but also safety

limitations imposed by the 7T scanner (i.e. younger subjects are less likely to have any medical

implants, surgeries, etc. that would exclude them from being scanned at the high field

strength). Future work could use samples with larger age ranges to determine not only how or

if *o* fluctuates with age, but also whether this impacts the neural correlates of *o*, as neural

representations and the sensitivity of BOLD responses have also been shown to fluctuate with

age (Goh, Suzuki, & Park, 2010; Liu et al., 2013).

In sum, the present study is the first attempt to localize cortical regions related to domain-general object recognition. We find several bilateral regions throughout the temporal and parietal lobes that positively correlate with o, suggesting distributed neural correlates. These neuroimaging results open the door for future studies aimed at replicating and further characterizing these correlates, and the neural mechanisms that support object recognition ability. Furthermore, analysis of the data collected but not reported in this study (structural, resting-state and diffusion data) will provide more insight into the structural and connectivity correlates of o.

Chapter IV

General Discussion

The work presented here serves to further characterize the recently-discovered domain-general object recognition construct *o* (Richler et al., 2019). Using a latent variable framework, the behavioral work presented in Chapter II furthers our understanding of how a domain-general novel object recognition construct relates to domain-general familiar object recognition. The results show that novel and familiar object factors relate quite strongly, which has important implications. Researchers wishing to measure familiar object recognition will need to consider that performance on a given measure will be influenced both by experience and domain-general ability. Moreover, the finding that familiar and novel domains recruit *o* to similar extents suggests that individuating objects from familiar domains, at least domains with basic-level familiarity (e.g. knowledge of what is a bird versus a plane), is similar to individuating objects from novel domains. This could mean that basic-level familiarity does not influence recognition performance and it is only once subordinate-level familiarity is reached that recognition performance begins to reflect both *o* and experience. Further work is needed to test this hypothesis with several familiar domains, especially with either sets of domains for which we would expect greater variability in subordinate-level familiarity or samples recruited specifically to vary in their subordinate-level familiarity with chosen domains.

The results additionally hint at the real-world relevance of *o*, which presents exciting new avenues for translational research. Applications of future research could be especially

useful in professions where recognition abilities are critical. For example, radiologists are faced with an enormous challenge of finding malignant abnormalities in radiological images and airport security agents must search for dangerous items quickly and efficiently as luggage is scanned. There is already some evidence that individual differences in medical detection may relate to novel object recognition ability (Sunday, Donnelly, et al., 2017, 2018; Trueblood et al., 2017) and that visual search consistency may relate to airport screening accuracy in security screening professionals (Biggs et al., 2013). These studies suggest possible starting points for investigations into the predictive validity of *o*. When investigating the role of *o* in professions like these, it will be critical to consider *o* in conjunction with constructs like experience and fluid intelligence, since for complex tasks like nodule detection there will likely be multiple sources of variance. For example, recent work in a sample of radiologists found that about fifty percent of variance on a measure of nodule detection ability could be accounted for by self-reported experience, but that an additional fifteen percent of the variance could be accounted for by fluid intelligence and novel object recognition ability (Sunday, Donnelly, et al., 2018). In addition, translational work should cautiously and conservatively draw inferences since confounds like self-selection and variability in medical training are difficult to control in correlational work. In high-stakes occupations like medical imaging and security, overstated conclusions can have unfortunate consequences (the least of which could be a loss of trust in the researchers). Nevertheless, empirically addressing the real-world value of *o* will undoubtedly further interest in the field and provide concrete examples of the field's relevance.

The neuroimaging work presented in Chapter III describes the first attempt to find neural correlates of a domain-general object recognition ability. Neural sensitivity in temporal

and parietal regions were found to positively correlate with *o*, suggesting that experience-independent neural correlates of object recognition reside in brain regions often implicated in general object processing. This result paves the way for more studies into the neural mechanisms underlying *o* by localizing regions that may causally relate to domain-general object recognition. For example, this work can inform future studies investigating questions like whether *o* can be manipulated through neuromodulators like transcranial direct current stimulation. Moreover, in perceptual expertise research, correlates to expertise levels are often distributed (Harel, Gilaie-Dotan, Malach, & Bentin, 2010; Martens et al., 2018; McGugin, Gauthier, et al., 2012; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006), but only some of these distributed regions still correlate with expertise levels when attentional demands are raised (McGugin, Van Gulick, Tamber-Rosenau, et al., 2015). Future work could explore whether a similar effect occurs with correlates to *o*, in which some of the distributed correlates found here would no longer correlate with *o* with increased attentional demands, leaving only the most robust correlates of *o*.

When considering the neuroimaging results in conjunction with neuroimaging perceptual expertise work, these results raise the intriguing possibility that experience-independent object recognition may be supported by distributed processing throughout the visual cortex, and with the acquisition of experience these correlates are replaced with local representations in regions implicated in many perceptual expertise studies (like the FFA2). If this were true, one might predict that individuals with higher levels of *o*, and therefore high levels of neural sensitivity in distributed occipito-temporal regions, would show selectivity for trained domains in FFA2 regions more quickly than individuals with lower levels of *o*, or reach greater levels of

selectivity. Before any training studies are done to empirically assess this prediction, the findings presented in Chapter II will have to be addressed. Specifically, since familiar and novel object recognition were found to correlate in the present study, it will be important to determine if there is a point at which enough experience is acquired for recognition in a given domain to diverge from o. In other words, is there something akin to a saturation level at which experience begins to account for a significant portion of variance in recognition, and if so, how much training is required to reach this level.

Overall, both the behavioral and neuroimaging work further the burgeoning line of research on individual differences in high-level vision and open the door for future work. For example, work investigating the heritability of a domain-general object recognition ability (similar to the work done in Shakeshaft & Plomin, 2015; Wilmer et al., 2010) or potential relations between this ability and brain chemistry will help to further characterize this ability. In addition, research into whether evidence can be found for the existence of o in other species could lead to animal models and elucidate the possible evolution of o (similar to Arden & Adams, 2016).

REFERENCES

Anastasi, J. S., & Rhodes, M. G. (2005). An own-age bias in face recognition for children and older adults. *Psychonomic Bulletin & Review*, *12*(6), 1043–1047.

Andrews, T. J., Baseler, H., Jenkins, R., Burton, A. M., & Young, A. W. (2016). Contributions of feature shapes and surface cues to the recognition and neural representation of facial identity. *Cortex*, *83*, 280–291. https://doi.org/10.1016/j.cortex.2016.08.008

Andrews, T. J., & Ewbank, M. P. (2004). Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *NeuroImage*, *23*(3), 905–913. https://doi.org/10.1016/j.neuroimage.2004.07.060

Apšvalka, D., Gadie, A., Clemence, M., & Mullins, P. G. (2015). Event-related dynamics of glutamate and BOLD effects measured using functional magnetic resonance spectroscopy (fMRS) at 3T in a repetition suppression paradigm. *NeuroImage*, *118*, 292–300. https://doi.org/10.1016/j.neuroimage.2015.06.015

Arden, R., & Adams, M. J. (2016). A general intelligence factor in dogs. *Intelligence*, *55*, 79–85. https://doi.org/10.1016/j.intell.2016.01.008

Balas, B., & Saville, A. (2015). Neuropsychologia N170 face specificity and face memory depend on hometown size. *Neuropsychologia*, *69*, 211–217. https://doi.org/10.1016/j.neuropsychologia.2015.02.005

Balas, B., & Saville, A. (2017). Hometown size affects the processing of naturalistic face variability. *Vision Research*. https://doi.org/10.1016/j.visres.2016.12.005

Barron, H. C., Garvert, M. M., & Behrens, T. E. J. (2016). Repetition suppression: A means to index neural representations using BOLD? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1705). https://doi.org/10.1098/rstb.2015.0355

Barton, J. J. S., Hanif, H., & Ashraf, S. (2009). Relating visual to verbal semantic knowledge: The evaluation of object recognition in prosopagnosia. *Brain*, *132*(12), 3456–3466. https://doi.org/10.1093/brain/awp252

Basten, U., Hilger, K., & Fiebach, C. J. (2015). Where smart brains are different: A quantitative meta-analysis of functional and structural brain imaging studies on intelligence. *Intelligence*, *51*, 10–27. https://doi.org/10.1016/j.intell.2015.04.009

Benton, A. L., Hamsher, K. D., Varney, N. R., & Spreen, O. (1983). *Contributions to Neuropsychological Assessment*.

Biederman, I., Margalit, E., Maarek, R. S., Meschke, E. X., Shilowich, B. E., Juarez, J. J., … Herald, S. B. (2014). What is the Nature of the Perceptual Deficit in Congenital Prosopagnosia ? In *Annual Meeting of the Vision Sciences Society*.

Biggs, A. T., Cain, M. S., Clark, K., Darling, E. F., & Mitroff, S. R. (2013). Assessing visual search performance differences between Transportation Security Administration Officers and nonprofessional visual searchers. *Visual Cognition*, *21*(3), 330–352. https://doi.org/10.1080/13506285.2013.790329

Bilalic, M., Grottenthaler, T., Nagele, T., & Lindig, T. (2016). The Faces in Radiological Images: Fusiform Face Area Supports Radiological Expertise. *Cerebral Cortex*, *26*(3), 1004–1014. https://doi.org/10.1093/cercor/bhu272

Bilalić, M., Langner, R., Ulrich, R., & Grodd, W. (2011). Many faces of expertise: Fusiform face area in chess experts and novices. *The Journal of Neuroscience*, *31*(28), 10206–10214. https://doi.org/10.1523/JNEUROSCI.5727-10.2011

Brainard, D. H. (1997). The Pyschophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Brett, M., Anton, J.-L., Valabregue, R., & Poline, J.-B. (2002). Region of interest analysis using an SPM toolbox. *NeuroImage*, *16*(2).

Brigham, J. C., & Malpass, R. S. (1985). The Role of Experience and Contact in the Recognition of Faces Of Own- and Other-Race Persons. *Journal of Social Issues*, *41*(3), 139–155. https://doi.org/10.1111/j.1540-4560.1985.tb01133.x

Busey, T. A., & Vanderkolk, J. R. (2005). Behavioral and electrophysiological evidence for configural processing in fingerprint experts. *Vision Research*, *45*(4), 431–448. https://doi.org/10.1016/j.visres.2004.08.021

Ćepulić, D. B., Wilhelm, O., Sommer, W., & Hildebrandt, A. (2018). All categories are equal, but some categories are more equal than others: The psychometric structure of object and face cognition. *Journal of Experimental Psychology: Learning Memory and Cognition*, *44*(8), 1254–1268. https://doi.org/10.1037/xlm0000511

Chen, G., Saad, Z. S., Adleman, N. E., Leibenluft, E., & Cox, R. W. (2015). Detecting the subtle shape differences in hemodynamic responses at the group level. *Frontiers in Neuroscience*, *9*, 1–18. https://doi.org/10.3389/fnins.2015.00375

Cho, S.-J., Wilmer, J. B., Herzmann, G., McGugin, R. W., & Fiset, D. (2015). Item Response Theory Analyses of the Cambridge Face Memory Test (CFMT). *Psychological Assessment*, *27*(2), 552–566.

Chua, K. W., Bub, D. N., Masson, M. E. J., & Gauthier, I. (2017). Grasp Representations Depend on Knowledge and Attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, (June).

Chua, K. W., & Gauthier, I. (2019). Domain-Specific Experience Determines Individual Differences in Holistic Processing. *Journal of Experimental Psychology: General*.

Collins, J. A., & Curby, K. M. (2013). Conceptual knowledge attenuates viewpoint dependency in visual object recognition. *Visual Cognition*, *21*(8), 945–960. https://doi.org/10.1080/13506285.2013.836138

CreaceedSPRL. (2008). MorphAge.

Curby, K., Hayward, W. G., & Gauthier, I. (2004). Laterality effects in the recognition of depth-rotated novel objects. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(1), 100–111.

Davies-Thompson, J., Newling, K., & Andrews, T. J. (2013). Image-invariant responses in face-selective regions do not explain the perceptual advantage for familiar face recognition. *Cerebral Cortex*, *23*(2), 370–377. https://doi.org/10.1093/cercor/bhs024

Davis, J. P., Lander, K., Evans, R., & Jansari, A. (2016). Investigating Predictors of Superior Face Recognition Ability in Police Super- recognisers. *Applied Cognitive Psychology*, *30*, 827–840. https://doi.org/10.1002/acp.3260

De Baene, W., & Vogels, R. (2010). Effects of adaptation on the stimulus selectivity of macaque inferior temporal spiking activity and local field potentials. *Cerebral Cortex*, *20*(9), 2145–2165. https://doi.org/10.1093/cercor/bhp277

De Heering, A., De Liedekerke, C., Deboni, M., & Rossion, B. (2010). The role of experience during childhood in shaping the other-race effect. *Developmental Science*, *13*(1), 181–187.

https://doi.org/10.1111/j.1467-7687.2009.00876.x

Deary, I. J., Penke, L., & Johnson, W. (2010). The neuroscience of human intelligence differences. *Nature Reviews Neuroscience*, *11*(3), 201–211. https://doi.org/10.1038/nrn2793

DeGutis, J., Wilmer, J. B., Mercado, R. J., & Cohan, S. (2013). Using regression to measure holistic face processing reveals a strong link with face recognition ability. *Cognition*, *126*(1), 87–100. https://doi.org/10.1016/j.cognition.2012.09.004

Dennett, H. W., McKone, E., Tavashmi, R., Hall, A., Pidcock, M., Edwards, M., & Duchaine, B. (2012). The Cambridge Car Memory Test: a task matched in format to the Cambridge Face Memory Test, with norms, reliability, sex differences, dissociations from face memory, and expertise effects. *Behavior Research Methods*, *44*(2), 587–605. https://doi.org/10.3758/s13428-011-0160-2

Denys, K., Vanduffel, W., Fize, D., Nelissen, K., Peuskens, H., Van Essen, D., & Orban, G. A. (2004). The Processing of Visual Shape in the Cerebral Cortex of Human and Nonhuman Primates: A Functional Magnetic Resonance Imaging Study. *Journal of Neuroscience*, *24*(10), 2551–2565. https://doi.org/10.1523/jneurosci.3569-03.2004

Dubois, J., & Adolphs, R. (2016). Building a Science of Individual Differences from fMRI. *Trends in Cognitive Sciences*, *20*(6), 425–443.

Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia*, *44*(4), 576–585. https://doi.org/10.1016/j.neuropsychologia.2005.07.001

Echavarria, C., Nasr, S., & Tootell, R. (2016). Smooth versus Textured Surfaces: Feature-Based Category Selectivity in Human Visual Cortex. *Eneuro*, *3*(5). https://doi.org/10.1523/ENEURO.0051-16.2016

Epstein, R. A., Higgins, J. S., & Thompson-Schill, S. L. (2005). Learning Places from Views: Variation in Scene Processing as a Function of Experience and Navigational Ability. *Journal of Cognitive Neuroscience*, *17*(1), 73–83. https://doi.org/10.1162/0898929052879987

Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Furl, N., Garrido, L., Dolan, R. J., Driver, J., & Duchaine, B. (2011). Fusiform Gyrus Face Selectivity Relates to Individual Differences in Facial Recognition Ability. *Journal of Cognitive Neuroscience*, *23*(7), 1723–1740. https://doi.org/10.1162/jocn.2010.21545

Gauthier, I. (2018). Domain-Specific and Domain-General Individual Differences in Visual Object Recognition. *Current Directions in Psychological Science*, *27*(2), 97–102. https://doi.org/10.1177/0963721417737151

Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience*, *11*(4), 349–370. https://doi.org/10.1162/089892999563472

Gauthier, I., Curran, T., Curby, K. M., & Collins, D. (2003). Perceptual interference supports a non-modular account of face processing, *6*(4). https://doi.org/10.1038/nn1029

Gauthier, I., McGugin, R. W., Richler, J. J., Herzmann, G., Speegle, M., & Van Gulick, A. E. (2014). Experience moderates overlap between object and face recognition, suggesting a common

ability. *Journal of Vision*, *14*(8), 7–7. https://doi.org/10.1167/14.8.7

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*(2), 191–197. https://doi.org/10.1038/72140

Gauthier, I., & Tarr, M. J. (1997). Becoming a "Greeble" expert: Exploring mechanisms for face recognition. *Vision Research*, *37*(12), 1673–1682. https://doi.org/10.1016/S0042-6989(96)00286-6

Gauthier, I., & Tarr, M. J. (2002). Unraveling Mechanisms for Expert Object Recognition : Bridging Brain Activity and Behavior, *28*(2), 431–446. https://doi.org/10.1037//0096-1523.28.2.431

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects. *Nature Neuroscience*, *2*(6), 568–73. https://doi.org/10.1038/9224

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, a W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, *12*(3), 495–504. https://doi.org/10.1162/089892900562165

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

Germine, L. T., Duchaine, B., & Nakayama, K. (2011). Where cognitive development and aging meet: Face learning ability peaks after age 30. *Cognition*, *118*(2), 201–210. https://doi.org/10.1016/j.cognition.2010.11.002

Gilbert, A. L., Regier, T., Kay, P., & Ivry, R. B. (2006). Whorf hypothesis is supported in the right visual field but not the left. *Proceedings of the National Academy of Sciences*, *103*(2), 489–494.

Goh, J. O., Suzuki, A., & Park, D. C. (2010). Reduced neural selectivity increases fMRI adaptation with age during face discrimination. *NeuroImage*, *51*(1), 336–344. https://doi.org/10.1016/j.neuroimage.2010.01.107

Golarai, G., Liberman, A., & Grill-Spector, K. (2017). Experience Shapes the Development of Neural Substrates of Face Processing in Human Ventral Temporal Cortex. *Cerebral Cortex*, *27*(2), 1229–1244. https://doi.org/10.1093/cercor/bhv314

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*(1), 14–23. https://doi.org/10.1016/j.tics.2005.11.006

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, *24*(1), 187–203. https://doi.org/10.1016/S0896-6273(00)80832-6

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*(1), 293–321. https://doi.org/10.1016/S0001-6918(01)00019-1

Haberman, J., Brady, T. F., & Alvarez, G. A. (2015). Individual differences in ensemble perception reveal multiple, independent levels of ensemble representation. *Journal of Experimental*

Psychology: General, *144*(2), 432–446. https://doi.org/10.1037/xge0000053

Halpern, S. D., Andrews, T. J., & Purves, D. (1999). Interindividual variation in human visual performance. *Journal of Cognitive Neuroscience*, *11*(5), 521–534.

Harel, A., Gilaie-Dotan, S., Malach, R., & Bentin, S. (2010). Top-Down engagement modulates the neural expressions of visual expertise. *Cerebral Cortex*, *20*(10), 2304–2318. https://doi.org/10.1093/cercor/bhp316

Harris, R. J., Young, A. W., & Andrews, T. J. (2012). Morphing between expressions dissociates continuousfrom categorical representations of facial expressionin the human brain. *Proceedings of the National Academy of Sciences*, *109*(51), 21164–21169. https://doi.org/10.1073/pnas.1212207110/-/DCSupplemental/pnas.201212207SI.pdf

Hendel, R. K., Starrfelt, R., & Gerlach, C. (2019). The good, the bad, and the average: Characterizing the relationship between face and object processing across the face recognition spectrum. *Neuropsychologia*, *124*(June 2018), 274–284. https://doi.org/10.1016/j.neuropsychologia.2018.11.016

Herbort, O., & Butz, M. V. (2011). Habitual and goal-directed factors in (everyday) object handling. *Experimental Brain Research*, *213*(4), 371–382. https://doi.org/10.1007/s00221-011-2787-8

Horst, J. S., & Hout, M. C. (2016). The Novel Object and Unusual Name (NOUN) Database: A collection of novel images for use in experimental research. *Behavior Research Methods*, *48*(4), 1393–1409. https://doi.org/10.3758/s13428-015-0647-3

Hsiao, J. H., & Cottrell, G. W. (2009). Not All Visual Expertise Is Holistic, but It May Be Leftist. *Psychological Science*, *20*(4), 455–463. https://doi.org/10.1111/j.1467-9280.2009.02315.x

Huang, L., Song, Y., Li, J., Zhen, Z., Yang, Z., & Liu, J. (2014). Individual differences in cortical face selectivity predict behavioral performance in face recognition. *Frontiers in Human Neuroscience*, *8*(July), 1–10. https://doi.org/10.3389/fnhum.2014.00483

Jax, S., & Buxbaum, L. (2010). Response interference between functional and structural actions linked to the same familiar object. *Cognition*, *115*(2), 350–355. https://doi.org/10.1016/j.cognition.2010.01.004.Response

Jung, R. E., & Haier, R. J. (2007). The Parieto-Frontal Integration Theory (P-FIT) of intelligence: converging neuroimaging evidence. *Behavioral and Brain Sciences*, *30*(2), 135–54. https://doi.org/10.1017/S0140525X07001185

Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, *3*(8), 759–763. https://doi.org/10.1038/77664

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*(11), 4302–11. https://doi.org/10.1098/Rstb.2006.1934

Konar, Y., Bennett, P. J., & Sekuler, A. B. (2010). Holistic processing is not correlated with face identification accuracy. *Psychological Science*, *21*(1), 38–43. https://doi.org/10.1177/0956797609356508

Kourtzi, Z., Erb, M., Grodd, W., & Bülthoff, H. H. (2003). Representation of the perceived 3-D object shape in the human lateral occipital complex. *Cerebral Cortex*, *13*(9), 911–920. https://doi.org/10.1126/science.1061133

Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *The Journal of Neuroscience*, *20*(9), 3310–8.

Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., & Logothetis, N. K. (2003). Integration of local features into global shapes: Monkey and human fMRI studies. *Neuron*, *37*(2), 333–346. https://doi.org/10.1016/S0896-6273(02)01174-1

Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S., & Baker, C. I. (2009). Circular analysis in systems neuroscience: the dangers of double dipping. *Nature Neuroscience*, *12*(5), 535.

Kunda, M., Mcgreggor, K., & Goel, A. (2011). Two visual strategies for solving the Raven's Progressive Matrices intelligence test. *Proceedings of the 25th AAAI Conference*, 1555–1558.

Larsson, J., Solomon, S. G., & Kohn, A. (2016). fMRI adaptation revisited. *Cortex*, *80*, 154–160. https://doi.org/10.1016/j.cortex.2015.10.026

Lee, W.-Y., Cho, S.-J., McGugin, R. W., Van Gulick, A. E., & Gauthier, I. (2015). Differential item functioning analysis of the Vanderbilt Expertise Test for cars. *Journal of Vision*, *15*(13), 23. https://doi.org/10.1167/15.13.23

Leek, E. C., Cristino, F., Conlan, L. I., Patterson, C., Rodriguez, E., & Johnston, S. J. (2012). Eye movement patterns during the recognition of three-dimensional objects: Preferential fixation of concave surface curvature minima. *Journal of Vision*, *12*(1), 7–7. https://doi.org/10.1167/12.1.7

Li, L., Miller, E. K., & Desimone, R. (1993). The representation of stimulus familiarity in anterior inferior temporal cortex. *Journal of Neurophysiology*, *69*(6), 1918–1929.

Liu, P., Hebrank, A. C., Rodrigue, K. M., Kennedy, K. M., Section, J., Park, D. C., & Lu, H. (2013). Age-related differences in memory-encoding fMRI responses after accounting for decline in vascular reactivity. *NeuroImage*, *78*, 415–425. https://doi.org/10.1016/j.neuroimage.2013.04.053

Lupyan, G. (2008). From Chair to " Chair ": A Representational Shift Account of Object Labeling Effects on Memory. *Journal of Experimental Psychology: General*, *137*(2), 348–369. https://doi.org/10.1037/0096-3445.137.2.348

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

Martens, F., Bulthé, J., van Vliet, C., & Op de Beeck, H. P. (2018). Domain-general and domain-specific neural changes underlying visual expertise. *NeuroImage*, *169*(July 2017), 80–93. https://doi.org/10.1016/j.neuroimage.2017.12.013

Matlab. (2016). Natick, Massachusetts: MathWorks.

McGugin, R. W., & Gauthier, I. (2016). The reliability of individual differences in face-selective responses in the fusiform gyrus and their relation to face recognition ability. *Brain Imaging and Behavior*, *10*(3), 707–718. https://doi.org/10.1007/s11682-015-9467-4

McGugin, R. W., Gauthier, I., Gatenby, C., & Gore, J. C. (2012). High-resolution imaging of expertise reveals reliable object selectivity in the FFA related to perceptual performance. *Proceedings of the National Academy of Sciences*, *109*(42), 17063–17068. https://doi.org/10.1167/12.9.1281

McGugin, R. W., Newton, A. T., Gore, J. C., & Gauthier, I. (2014). Robust expertise effects in right FFA. *Neuropsychologia*, *63*, 135–144. https://doi.org/10.1016/j.neuropsychologia.2014.08.029

McGugin, R. W., Richler, J. J., Herzmann, G., Speegle, M., & Gauthier, I. (2012). The Vanderbilt Expertise Test reveals domain-general and domain-specific sex effects in object recognition. *Vision Research*, *69*, 10–22. https://doi.org/10.1016/j.visres.2012.07.014

McGugin, R. W., Ryan, K. F., Tamber-Rosenau, B. J., & Gauthier, I. (2017). The Role of Experience in the Face-Selective Response in Right FFA. *Cerebral Cortex*, 1–14. https://doi.org/10.1093/cercor/bhx113

McGugin, R. W., Van Gulick, A. E., & Gauthier, I. (2015). Cortical Thickness in Fusiform Face Area Predicts Face and Object Recognition Performance. *Journal of Cognitive Neuroscience*, 282–294. https://doi.org/10.1162/jocn

McGugin, R. W., Van Gulick, A. E., Tamber-Rosenau, B. J., Ross, D. A., & Gauthier, I. (2015). Expertise effects in face-selective areas are robust to clutter and diverted attention, but not to competition. *Cerebral Cortex*, *25*(9), 2610–2622. https://doi.org/10.1093/cercor/bhu060

McMahon, D. B. T., & Olson, C. R. (2007). Repetition Suppression in Monkey Inferotemporal Cortex: Relation to Behavioral Priming. *Journal of Neurophysiology*, *97*(5), 3532–3543. https://doi.org/10.1152/jn.01042.2006

Mollon, J. D., Bosten, J. M., Peterzell, D. H., & Webster, M. A. (2017). Individual differences in visual science: What can be learned and what is good experimental practice? *Vision Research*, *141*(November), 4–15. https://doi.org/10.1016/j.visres.2017.11.001

Muthén, L. K., & Muthén, B. O. (1998). Mplus User's Guide. Eigth Edition. Los Angeles, CA.

Nasr, S., Echavarria, C. E., & Tootell, R. B. H. (2014). Thinking Outside the Box: Rectilinear Shapes Selectively Activate Scene-Selective Cortex. *Journal of Neuroscience*, *34*(20), 6721–6735. https://doi.org/10.1523/JNEUROSCI.4802-13.2014

Natu, V. S., Barnett, M. A., Hartley, J., Gomez, J., Stigliani, A., & Grill-Spector, K. (2016). Development of Neural Sensitivity to Face Identity Correlates with Perceptual Discriminability. *The Journal of Neuroscience*, *36*(42), 10893–10907. https://doi.org/10.1523/JNEUROSCI.1886-16.2016

Noppeney, U., Price, C. J., Penny, W. D., & Friston, K. J. (2006). Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex*, *16*(3), 437–445. https://doi.org/10.1093/cercor/bhi123

Norman, J. F., Phillips, F., Cheeseman, J. R., Thomason, K. E., Ronning, C., Behari, K., … Lamirande, D. (2016). Perceiving object shape from specular highlight deformation, boundary contour deformation, and active haptic manipulation. *PLoS ONE*, *11*(2), 1–15. https://doi.org/10.1371/journal.pone.0149058

Nunnally, J. C. (1970). *Introduction to psychological measurement.*

Op de Beeck, H. P., & Baker, C. I. (2010). The neural basis of visual object learning. *Trends in Cognitive Sciences*, *14*(1), 22–30. https://doi.org/10.1016/j.tics.2009.11.002

Op de Beeck, H. P., Baker, C. I., DiCarlo, J. J., & Kanwisher, N. G. (2006). Discrimination Training Alters Object Representations in Human Extrastriate Cortex. *Journal of Neuroscience*, *26*(50), 13025–13036. https://doi.org/10.1523/jneurosci.2481-06.2006

Op de Beeck, H. P., Torfs, K., & Wagemans, J. (2008). Perceived Shape Similarity among Unfamiliar Objects and the Organization of the Human Object Vision Pathway. *Journal of Neuroscience*, *28*(40), 10111–10123. https://doi.org/10.1523/JNEUROSCI.2511-08.2008

Palermo, R., Rossion, B., Rhodes, G., Laguesse, R., Tez, T., Hall, B., … McKone, E. (2017). Do

People Have Insight into their Face Recognition Abilities? *Quarterly Journal of Experimental Psychology*, *70*(2), 218–233. https://doi.org/10.1080/17470218.2016.1161058

Picci, G., & Scherf, K. S. (2016). From Caregivers to Peers: Puberty Shapes Human Face Perception. *Psychological Science*, *27*(11), 1461–1473. https://doi.org/10.1177/0956797616663142

Pinsk, M. A., Arcaro, M., Weiner, K. S., Kalkus, J. F., Inati, S. J., Gross, C. G., & Kastner, S. (2008). Neural Representations of Faces and Body Parts in Macaque and Human Cortex: A Comparative fMRI Study. *Journal of Neurophysiology*, *101*(5), 2581–2600. https://doi.org/10.1152/jn.91198.2008

Raven, J. (2000). The Raven's Progressive Matrices: Change and Stability over Culture and Time. *Cognitive Psychology*, *41*, 1–48. https://doi.org/10.1006/cogp.1999.0735

Raykov, T., Goldammer, P., Marcoulides, G. A., Li, T., & Menold, N. (2018). Reliability of Scales With Second-Order Structure: Evaluation of Coefficient Alpha's Population Slippage Using Latent Variable Modeling. *Educational and Psychological Measurement*, *78*(6), 1123–1135.

Reavis, E. A., Lee, J., Wynn, J. K., Engel, S. A., Jimenez, A. M., & Green, M. F. (2017). Cortical Thickness of Functionally Defined Visual Areas in Schizophrenia and Bipolar Disorder. *Cerebral Cortex*, *27*(5), 2984–2993. https://doi.org/10.1093/cercor/bhw151

Richler, J. J., Cheung, O. S., & Gauthier, I. (2011). Holistic Processing Predicts Face Recognition. *Psychological Science*, *22*(4), 464–471. https://doi.org/10.1177/0956797611401753

Richler, J. J., Floyd, R. J., & Gauthier, I. (2015). About-face on face recognition ability and holistic processing. *Journal of Vision*, *15*(9), 15. https://doi.org/10.1167/15.9.15

Richler, J. J., Gauthier, I., & Palmeri, T. J. (2011). Automaticity of Basic-Level Categorization Accounts for Labeling Effects in Visual Recognition Memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *37*(6), 1579–1587. https://doi.org/10.1037/a0024347

Richler, J. J., Tomarken, A., Sunday, M. A., Vickery, T. J., Ryan, K. F., Floyd, R. J., … Gauthier, I. (2019). Individual Differences in Object Recognition. *Psychological Review*, *126*(2), 226–251.

Richler, J. J., Wilmer, J. B., & Gauthier, I. (2017). General object recognition is specific: Evidence from novel and familiar objects. *Cognition*, *166*, 42–55. https://doi.org/10.1016/j.cognition.2017.05.019

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

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

Roberson, D. E. B., & Davidoff, J. (2000). The categorical perception of colors and facial expressions: The effect of verbal interference. *Memory & Cognition*, *28*(6), 977–986.

Rogosa, D. R., Brandt, D., & Zimowski, M. (1982). Quantitative methods in psychology: A growth curve approach to the measurement of change. *Psychological Bulletin*, *92*(3), 726–748.

Ross, D. A., Tamber-Rosenau, B. J., Palmeri, T., Zhang, J., Xu, Y., & Gauthier, I. (2018). High-resolution functional magnetic resonance imaging reveals configural processing of cars in right anterior fusiform face area of car experts. *Journal of Cognitive Neuroscience*, *30*(7),

973–984.

Rotshtein, P., Henson, R. N. A., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience*, *8*(1), 107–113. https://doi.org/10.1038/nn1370

Ryan, K. F., & Gauthier, I. (2016). Gender differences in recognition of toy faces suggest a contribution of experience. *Vision Research*, *129*, 69–76. https://doi.org/10.1016/j.visres.2016.10.003

Saad, Z. S., Reynolds, R. C., Argall, B., Japee, S., & Cox, R. W. (2004). SUMA: An interface for surface-based intra- and inter-subject analysis with AFNI. *2004 2nd IEEE International Symposium on Biomedical Imaging: Macro to Nano (IEEE Cat No. 04EX821)*, 1510–1513. https://doi.org/10.1109/ISBI.2004.1398837

Sangrigoli, S., Pallier, C., Argenti, A. M., Ventureyra, V. A. G., & De Schonen, S. (2005). Reversibility of the Other-Race Effect in Face Recognition During Childhood. *Psychological Science*, *16*(6), 440–444. https://doi.org/10.1111/j.0956-7976.2005.01554.x

Sawamura, H., Georgieva, S., Vogels, R., Vanduffel, W., & Orban, G. A. (2005). Using Functional Magnetic Resonance Imaging to Assess Adaptation and Size Invariance of Shape Processing by Humans and Monkeys. *Journal of Neuroscience*, *25*(17), 4294–4306. https://doi.org/10.1523/jneurosci.0377-05.2005

Schönbrodt, F. D., & Perugini, M. (2013). At what sample size do correlations stabilize ? *Journal of Research in Personality*, *47*, 609–612. https://doi.org/10.1016/j.jrp.2013.05.009

Scott, L. S., Tanaka, J. W., Sheinberg, D. L., & Curran, T. (2006). A reevaluation of the electrophysiological correlates of expert object processing. *Journal of Cognitive Neuroscience*, *18*(9), 1453–1465. https://doi.org/10.1162/jocn.2006.18.9.1453

Shakeshaft, N. G., & Plomin, R. (2015). Genetic specificity of face recognition. *Proceedings of the National Academy of Sciences*, *112*(41), 201421881. https://doi.org/10.1073/pnas.1421881112

Short, L. A., Balas, B., & Wilson, C. (2017). The effect of educational environment on identity recognition and perceptions of within-person variability. *Visual Cognition*, *25*(9–10), 940–948. https://doi.org/10.1080/13506285.2017.1360974

Spearman, C. (1904). General Intelligence: Objectively Determined and Measured. *The American Journal of Psychology*, *15*(2), 322–326.

Sunday, M. A., Dodd, M. D., Tomarken, A. J., & Gauthier, I. (2018). How faces (and cars) may become special. *Vision Research*.

Sunday, M. A., Donnelly, E., & Gauthier, I. (2017). Individual differences in perceptual abilities in medical imaging: the Vanderbilt Chest Radiograph Test. *Cognitive Research: Principles and Implications*, *2*(1), 36. https://doi.org/10.1186/s41235-017-0073-4

Sunday, M. A., Donnelly, E., & Gauthier, I. (2018). Both fluid intelligence and visual object recognition ability relate to nodule detection in chest radiographs. *Applied Cognitive Psychology*, *32*(6), 755–762. https://doi.org/10.1002/acp.3460

Sunday, M. A., Lee, W., & Gauthier, I. (2018). Age-related differential item functioning in tests of face and car recognition ability. *Journal of Vision*, *18*(1), 2–2.

Sunday, M. A., McGugin, R. W., & Gauthier, I. (2017). Domain-specific reports of visual imagery vividness are not related to perceptual expertise. *Behavior Research Methods*, *49*(2), 733–738. https://doi.org/10.3758/s13428-016-0730-4

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

Tanaka, J. W., Kiefer, M., & Bukach, C. M. (2004). A holistic account of the own-race effect in face recognition: Evidence from a cross-cultural study. *Cognition*, *93*(1), 1–9. https://doi.org/10.1016/j.cognition.2003.09.011

Tanaka, J. W., & Pierce, L. J. (2009). The neural plasticity of other-race face recognition. *Cognitive, Affective and Behavioral Neuroscience*, *9*(1), 122–131. https://doi.org/10.3758/CABN.9.1.122

Trueblood, J. S., Holmes, W. R., Seegmiller, A. C., Douds, J., Compton, M., Woodruff, M., … Eichbaum, Q. (2017). Investigating the Cognitive Processes Involved in Cancer Cell Image Identification. *ArXiv, arXiv:1709*.

Van Gulick, A. E., McGugin, R. W., & Gauthier, I. (2016). Measuring nonvisual knowledge about object categories: The Semantic Vanderbilt Expertise Test. *Behavior Research Methods*, *48*(3), 1178–1196. https://doi.org/10.3758/s13428-015-0637-5

Verhoef, B.-E., Kayaert, G., Franko, E., Vangeneugden, J., & Vogels, R. (2008). Stimulus Similarity-Contingent Neural Adaptation Can Be Time and Cortical Area Dependent. *Journal of Neuroscience*, *28*(42), 10631–10640. https://doi.org/10.1523/jneurosci.3333-08.2008

Vuilleumier, P., Henson, R. N., Driver, J., & Dolan, R. J. (2002). Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nature Neuroscience*, *5*(5), 491–499. https://doi.org/10.1038/nn839

Ward, J., Rothen, N., Chang, A., & Kanai, R. (2016). The structure of inter-individual differences in visual ability: Evidence from the general population and synaesthesia. *Vision Research*. https://doi.org/10.1016/j.visres.2016.06.009

Warrington, E. (1984). Recognition Memory Test: Rmt. (Words). Test Booklet 1.

Watson, M., Voloh, B., Naghizadeh, M., & Womelsdorf, T. (2017). Quaddles : A multidimensional 3D object set with parametrically-controlled and customizable features. *Bioarxiv*.

Wechsler, D. (1955). *Manual for the Wechsler adult intelligence scale.*

Weiner, K. S., Sayres, R., Vinberg, J., & Grill-Spector, K. (2010). fMRI-Adaptation and Category Selectivity in Human Ventral Temporal Cortex: Regional Differences Across Time Scales. *Journal of Neurophysiology*, *103*(6), 3349–3365. https://doi.org/10.1152/jn.01108.2009

Wiggett, A. J., Pritchard, I. C., & Downing, P. E. (2009). Animate and inanimate objects in human visual cortex: Evidence for task-independent category effects. *Neuropsychologia*, *47*(14), 3111–3117. https://doi.org/10.1016/j.neuropsychologia.2009.07.008

Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: The SHINE toolbox. *Behavior Research Methods*, *42*(3), 671–684. https://doi.org/10.3758/BRM.42.3.671

Wilmer, J. B. (2008). How to use individual differences to isolate functional organization, biology, and utility of visual functions; with illustrative proposals for stereopsis. *Spatial Vision*, *21*(6), 561–579. https://doi.org/10.1163/156856808786451408.How

Wilmer, J. B., Germine, L., Chabris, C. F., Chatterjee, G., Williams, M., Loken, E., … Duchaine, B. (2010). Human face recognition ability is specific and highly heritable. *Proceedings of the National Academy of Sciences*, *107*(11), 5238–5241.

https://doi.org/10.1073/pnas.0913053107

Winston, J. S. (2004). fMRI-Adaptation Reveals Dissociable Neural Representations of Identity and Expression in Face Perception. *Journal of Neurophysiology*, *92*(3), 1830–1839. https://doi.org/10.1152/jn.00155.2004

Wong, A., & Hayward, W. G. (2005). Constraints on view combination: effects of self-occlusion and differences among familiar and novel views. *Journal of Experimental Psychology. Human Perception and Performance*, *31*(1), 110–121. https://doi.org/10.1037/0096-1523.31.1.110

Wong, A., Palmeri, T. J., & Gauthier, I. (2009). Conditions for facelike expertise with objects: Becoming a ziggerin expert - but which type? *Psychological Science*, *20*(9), 1108–1117. https://doi.org/10.1111/j.1467-9280.2009.02430.x

Wong, A., Palmeri, T. J., Rogers, B. P., Gore, J. C., & Gauthier, I. (2009). Beyond shape: How you learn about objects affects how they are represented in visual cortex. *PLoS ONE*, *4*(12), 1–7. https://doi.org/10.1371/journal.pone.0008405

Wong, Y., & Gauthier, I. (2010). Holistic processing of musical notation : Dissociating failures of selective attention in experts and novices. *Cognitive, Affective, & Behavioral Neuroscience*, *10*(4), 541–551. https://doi.org/10.3758/CABN.10.4.541

Xu, B., Rourke, L., Robinson, J. K., & Tanaka, J. W. (2016). Training Melanoma Detection in Photographs Using the Perceptual Expertise Training Approach. *Applied Cognitive Psychology*, *30*(5), 750–756. https://doi.org/10.1002/acp.3250

Xu, Y. (2005). Revisiting the role of the fusiform face area in visual expertise. *Cerebral Cortex*, *15*(8), 1234–1242. https://doi.org/10.1093/cercor/bhi006

Yoon, E. Y., Heinke, D., & Humphreys, G. W. (2002). Modelling direct perceptual constraints on action selection: The Naming and Action Model (NAM). *Visual Cognition*, *9*(4–5), 615–661. https://doi.org/10.1080/13506280143000601

Yue, X., Pourladian, I. S., Tootell, R. B. H., & Ungerleider, L. G. (2014). Curvature-processing network in macaque visual cortex. *Proceedings of the National Academy of Sciences*, *111*(33), E3467–E3475. https://doi.org/10.1073/pnas.1412616111