

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/261878792>

Expertise and Object Recognition

Chapter · February 2015

DOI: 10.1016/B978-0-12-397025-1.00038-5

CITATION

1

READS

233

2 authors:



Heida Maria Sigurdardottir

University of Iceland

13 PUBLICATIONS 69 CITATIONS

[SEE PROFILE](#)



Isabel Gauthier

Vanderbilt University

245 PUBLICATIONS 13,414 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Visual factors in dyslexia [View project](#)



Visual expertise [View project](#)

Expertise and object recognition

Heida Maria Sigurdardottir¹ and Isabel Gauthier²

¹Department of Neuroscience, Brown University, Providence, RI, USA

²Department of Psychology, Vanderbilt University, Nashville, TN, USA

Full contact information for each author:

Heida Maria Sigurdardottir

Phone: 401 863 6876

Fax: 401 863 1074

Email: heidamaria@gmail.com

Department of Neuroscience
Brown University
Box G-LN
Providence, RI 02912

Isabel Gauthier

Phone: 615 322 1778

Fax: 615 322 4706

Email: isabel.gauthier@vanderbilt.edu

REGULAR MAIL (via U.S. Postal Service)
Vanderbilt University
PMB 407817
2301 Vanderbilt Place

Nashville, TN 37240-7817
COURIER MAIL (via Fed Exp, UPS)
Vanderbilt University
Department of Psychology
111 21st Avenue South
301 Wilson Hall
Nashville, TN 37240

To appear in: A. W. Toga, M. M. Mesulam & S. Kastner (Eds.), *Brain Mapping: An Encyclopedic Reference*. Oxford, UK: Elsevier.

Keywords: Domain specificity, expertise, faces, FFA, learning, objects, plasticity, training, visual perception, visual representations.

50-100 word synopsis of the article, which will be used to summarize the work online: This chapter examines how extensive experience in a specific domain leads to perceptual expertise in visual object recognition. The visual system appears to optimize the processing of objects for the tasks that were carried out on them in the past. The study of perceptual expertise illustrates how long-term experience with associating specific task demands with an object category can shape the visual system.

Suggestions for cross-references to other articles within the work: High Field Acquisition, Limits of spatial resolution, temporal resolution, and interpretability in fMRI, fMRI at high field - spatial resolution limits and applications, Large-Scale Organization, Motor learning, Shape perception, Visual object recognition, Face processing, Category-Specificity in object recognition, Visual perceptual learning, Modulating cortical systems to stimulate plasticity, Functional studies, Face Perception, Sex differences, Higher visual cortex, Semantic processing, Naming, Category learning, Statistical learning

Biographies and photos of each author, to be included with the article when published online:

Heida Maria Sigurdardottir



Heida Maria Sigurdardottir is a Research Associate in the Department of Neuroscience at Brown University, and a Postdoctoral Fellow at the Department of Psychology at the University of Iceland. She works on the visual system with a focus on object perception, visual attention, plasticity and learning. She is the receiver of the 2007 International Fulbright Science and Technology Award.

Isabel Gauthier



Isabel Gauthier is a cognitive neuroscientist currently holding the position of David K. Wilson Professor of Psychology. She heads the Object Perception Lab at Vanderbilt University. She has received the Young Investigator Award from the Cognitive Neuroscience Society in 2002, the APA Distinguished Scientific Award for Early Career Contribution to Psychology in the area of Behavioral/Cognitive Neuroscience in 2003 and the Troland research award from the National Academy of Sciences in 2008. She has researched many topics involved in perception, with a focus on the role of perceptual expertise in category-specific effects in domains such as faces, letters or musical notation.

Nature vs. Nurture

The *C. elegans* roundworm has exactly 302 neurons, and the wiring of each one of these neurons is the same in every individual of the species (White, Southgate, Thomson, & Brenner, 1986; WormAtlas, 2002-2013). Arguably, this is as hardwired as a nervous system can get. Yet, even these simple organisms have the ability to *learn*, to change the workings of their nervous system through experience (Rankin, Beck, & Chiba, 1990). It should therefore come as no surprise that the human nervous system, with its estimated 11.5 billion cortical neurons (Haug, 1987; Roth & Dicke, 2005), goes through adaptive changes through a person's entire lifespan. It is easy to see that human behavior — the output of the nervous system — needs to be flexible to deal with ever-changing circumstances. It is less obvious why perception — on the input side of the human nervous system — could and should extensively change through experience. After all, our world works more or less in the same way as it ever did. Light shines from above and not below, things fall down and not up, people have faces with two eyes, a nose, and a mouth, and so on. It might make sense to hardwire this kind of information into the human perceptual system. But a completely hardwired system is still an immutable one, and an immutable system by definition cannot adapt to changes in the structure of the environment. In this chapter, we will talk about how experience shapes perceptual representations, in particular how extensive experience in a specific domain leads to perceptual expertise in visual object recognition.

Domain Specificity vs. Generality

The perceptual expertise literature was initially largely driven by questions concerning the domain-specificity versus domain-generality of the visual system. In its essence, domain-

specificity within the visual system indicates that a brain region is specialized for the perception of particular stimuli, such as manipulable objects, body parts, or faces. Domain-general accounts instead emphasize that the organization of cortical space is determined by function, and that similar computations can be made on several different inputs (Gauthier, 2000).

The debate about the domain-specificity of face processing has been particularly lively. Recognizing people by their faces is obviously incredibly important for human social behavior. It is therefore somewhat reasonable to assume that a part of visual cortex could be devoted to the detection and subsequent recognition of these complex visual objects. Indeed, work on brain damaged patients (Bentin, Deouell, & Soroker, 1999; Farah, Levinson, & Klein, 1995; McNeil & Warrington, 1993; Moscovitch, Winocur, & Behrmann, 1997) and functional neuroimaging studies (Haxby et al., 1994; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Sergent, Ohta, & MacDonald, 1992; Tsao, Freiwald, Tootell, & Livingstone, 2006) both pointed to the possibility that one or more relatively circumscribed cortical regions could be selectively responsive to faces, and that damage to these areas could impair face recognition while sparing the ability to recognize other types of objects.

One of these regions, the fusiform face area (FFA), reliably responds more to faces when contrasted with a set of objects from several other categories (see figure 1), and has been proposed to be a module specialized for the perception of faces (Kanwisher et al., 1997). Face recognition, however, might impose particular computational needs that do not apply to our most of our interactions with objects. For example, while it might in many cases suffice to classify objects into general categories such as cat, dog, tree etc., our goal typically is not to just detect faces but to individuate them. Because one's eyes, nose and mouth are very similar to many others' face parts, we apparently solve the problem of individuating faces by also using subtle

differences in the configuration or relations between different visual features (Farah, Wilson, Drain, & Tanaka, 1998; Sergent, 1988; Tanaka & Farah, 1993; Tanaka & Sengco, 1997), such as the distance between the eyes relative to the overall size of the face. A region such as the FFA could hypothetically be specialized for such within-category recognition, which has been proposed to depend on configural and holistic processing. Configural processing is broadly defined as using the spatial relations between parts, while holistic processing has been used in the same manner (Rossion, 2013), but in research on expertise, the most useful meaning of holistic processing has been to describe an inability to ignore parts of an object even when under instructions to do so (but see Richler, Palmeri, & Gauthier, 2012, p. for the many definitions of holistic processing). The FFA might be recruited for objects other than faces if previous task requirements made such computations particularly beneficial and experience allowed for these strategies. People's expertise with classifying faces might have led to the specific routing to this cortical region whenever faces are seen.

Expertise Effects in the FFA

Studies have now shown that the fusiform gyrus is recruited for visual objects of expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Tarr & Gauthier, 2000; A. C.-N. Wong, Palmeri, Rogers, Gore, & Gauthier, 2009; but see Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006). For example, when people are trained for thousands of trials to tell apart visually similar nonsense objects ("Greebles"), they will not only become better at this task, but their performance will start to show signs of increased holistic and configural processing, even for new objects in the category for which they have become visual experts (Gauthier, Williams, Tarr, & Tanaka, 1998). Objects from a category

of expertise will also start to evoke greater activity in the FFA (Gauthier et al., 1999; see figure 1).

Real-world experts also recruit the FFA for the objects of their expertise. As an example, James and James (2012) studied children with an intense interest in Pokémon trading cards at an age where face expertise has not reached its peak. These children show a greater BOLD activation in the FFA for Pokémon characters than age-matched controls, but not for Digimon characters found on other types of trading cards. Of course, Pokémon characters have faces, begging the question that FFA is only important for the visual processing of objects of expertise if those objects have faces or face-like qualities. This, however, does not appear to be a necessity. Compared to other children, the experts also show greater FFA activation for so-called Pokémon objects which do not have faces (in the FFA defined individually, see James & James, 2012, supplementary material). It therefore seems like expertise with a stimulus, and not just its visual appearance, is an important factor.

This is bolstered by further evidence. For instance, when compared to novices, chess experts show greater FFA BOLD activity for full-board chess positions (Bilalić, Langner, Ulrich, & Grodd, 2011). Chess boards are complex objects with multiple parts in meaningful spatial relations, yet they look quite distinct from faces. FFA activity in chess experts alone was also sensitive to the disruption of relational information in the chess boards, such as when the boards were turned upside-down or the position of the chess pieces was randomized, consistent with the hypothesis that the FFA is important for configural processing of visual objects. As people become greater experts with chess, they will also show increased holistic processing of chess boards (Boggan, Bartlett, & Krawczyk, 2012). Curiously, this increase goes hand in hand with decreased holistic processing for faces (Boggan et al., 2012). This trade-off indicates that face

and chess recognition share a common process in people who presumably are experts in both domains (see also McGugin, McKeeff, Tong, & Gauthier, 2011; McKeeff, McGugin, Tong, & Gauthier, 2010).

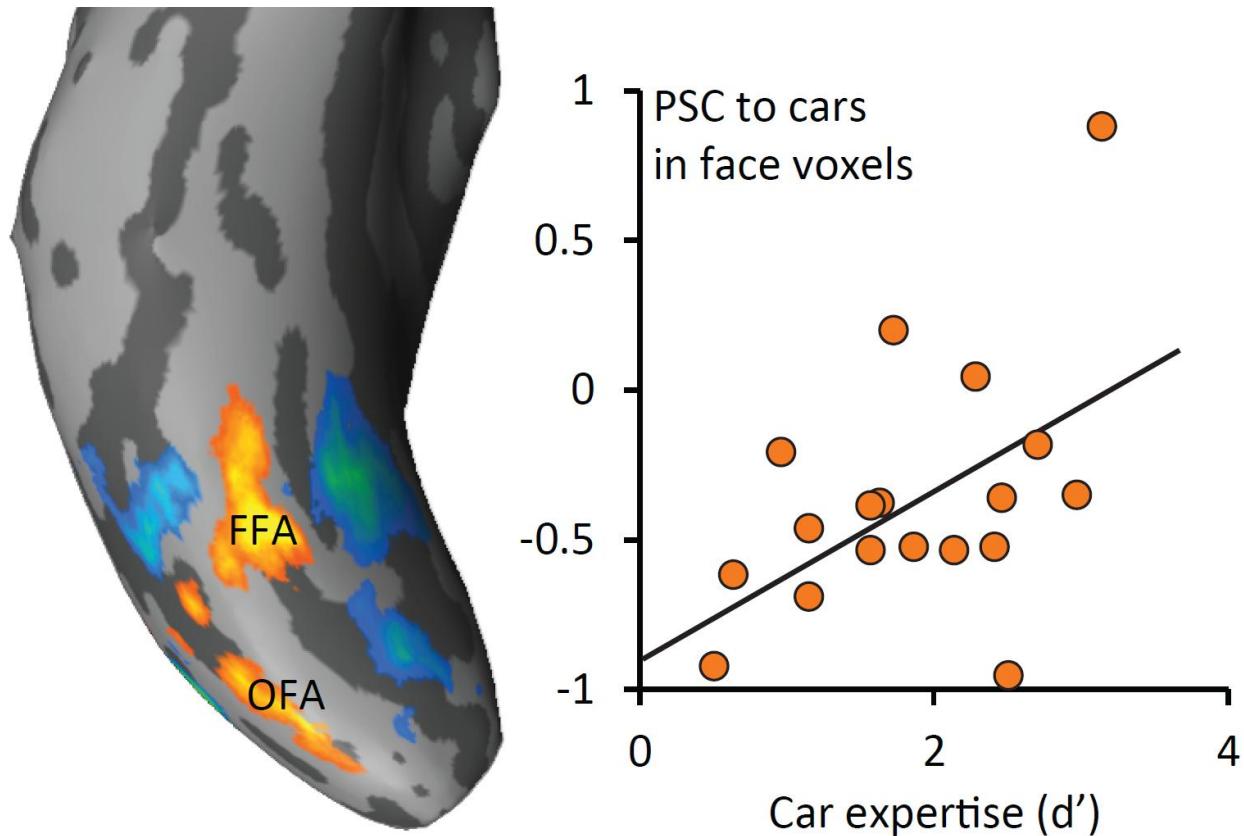


Figure 1. Left: An example subject's right fusiform face area (FFA) and right occipital face area (OFA) are shown on an inflated cortical surface. Regions marked in yellow/red respond to a greater extend to faces when contrasted with a variety of other visually presented objects. Regions in green/blue respond less to faces than to other visually presented objects. Standard resolution voxels were used (12 mm^3). **Right:** Percent signal change (PSC) to cars (relative to the neural response for animals) in face-selective high resolution voxels (2 mm^3) within the functionally defined right FFA (surface area: 100 mm^2). Activation for visually presented cars increases with greater perceptual expertise for cars. Adapted from McGugin, Gatenby, Gore, & Gauthier (2012).

Functional neuroimaging might be considered a rather crude method for studying neural specificity; in a typical fMRI experiment, BOLD signal within a single voxel is caused by the summed activity of millions of individual neurons. A truly face-specific region in the fusiform cortex might therefore be spatially distinct from a region utilized for objects of expertise, but signals from neurons in these two brain areas could become intermingled in a standard-sized voxel. McGugin, Gatenby, Gore, and Gauthier (2012) sought to explore this possibility by utilizing the greater signal-to-noise ratio of an ultra-high field strength magnet (7 Tesla) to image activity within and around the FFA at a finer spatial resolution. They scanned people with varying degrees of car expertise, measured as the degree to which they could judge whether images (shown outside the scanner) depicted cars from the same make and model.

Consistent with other studies (Gauthier et al., 2000), McGugin, Gatenby, et al. (2012) found that when people viewed cars, the FFA was recruited to an increasing degree with greater levels of car expertise. This is also compatible with the finding that cars are processed holistically by experts (Bukach, Phillips, & Gauthier, 2010) and that holistic processing relies on the FFA. Crucially, this expertise effect was found even in the most face selective voxels within the FFA (see figure 1). Expertise effects are found in a highly face-selective patch of cortex, a little over a cubic millimeter in volume, where according to neurophysiology in the monkey brain (Tsao et al., 2006) 97% of the neurons are face-selective. If the single cell recording results generalize to the human brain, this suggests that face-selective neurons also respond to a great degree to other objects of expertise that, like faces, tend to be processed in a holistic manner.

How to Measure Expertise?

The FFA is functionally defined as a contiguous cortical region that responds more to faces than to other objects. This reveals that faces activate a particular region of cortex more than some kind of average object, but such an average of apples and oranges might not be particularly meaningful and can mask any differences between non-face objects. Objects of expertise are also often compared only to faces and perhaps to a single non-expertise category, such as when perceptual performance for cars is compared to that for birds (Gauthier, Curran, Curby, & Collins, 2003; Gauthier et al., 2000; Harel, Gilai-Dotan, Malach, & Bentin, 2010; McGugin & Gauthier, 2010; Xu, 2005). Here, too, only a fractured picture emerges. Very little is revealed about the similarities and differences in recognition abilities for separate object categories. If you are much better at recognizing cars than you are for birds, you could be exceptionally good with cars and average for birds, average for cars and terrible with birds, good with man-made objects and bad with living objects, and a number of other possibilities. If you perform particularly well with both cars and birds, you might be an expert in both domains, or you could simply have excellent domain-general capability for recognizing objects.

To measure expertise in object recognition, it is therefore crucial to compare perceptual skills for many different categories of visual objects. The Vanderbilt Expertise Test (VET, McGugin, Richler, Herzmann, Speegle, & Gauthier, 2012) was developed for precisely this purpose, where people's perceptual capabilities are measured and contrasted for several visually homogeneous categories. McGugin, Richler, et al. (2012) found that people who are good at recognizing objects belonging to one category in general are to some extent also good at recognizing objects within other categories, indicating a common underlying factor relevant for

domain-general object recognition. But performance on the VET also revealed domain-specificity that suggests that experience may be important.

For instance, sex differences were found (McGugin, Richler, et al., 2012) where women were better than men at recognizing natural objects, while men on average outperformed women when recognizing man-made objects. These differences can possibly be explained through gender-dependent visual experience. In current western cultures, men on average show more interest in and have more experience with things such as cars and motorcycles, while the same might be true for women and natural categories such as birds and butterflies. Men and women might therefore be likely to develop perceptual expertise for different kinds of visual objects.

The dependence or independence of facial recognition and the recognition of non-face objects was again moderated by sex (McGugin, Richler, et al., 2012); women's performance when recognizing faces was only predicted based on their performance with other natural categories and appeared to be unrelated to their performance with man-made objects; the opposite was true for men, whose facial recognition was only predicted by taking into account their recognition of man-made objects. These results illustrate how performance with a single object category cannot adequately capture one's ability to recognize "objects". And it may not be valid to claim that face perception is or is not qualitatively different from that of other objects unless other factors that can influence experience are taken into account.

Experience Influences Representations

So far we have talked about visual expertise as an experience-dependent change where perceptual processing of objects increasingly resembles that of faces by relying on holistic and

relational information. As it turns out, however, not all visual experience with objects leads to such a change; merely seeing lots of cars does not necessarily make you a car expert in the aforementioned sense. Visual expertise instead seems driven by the kind of experience that one has.

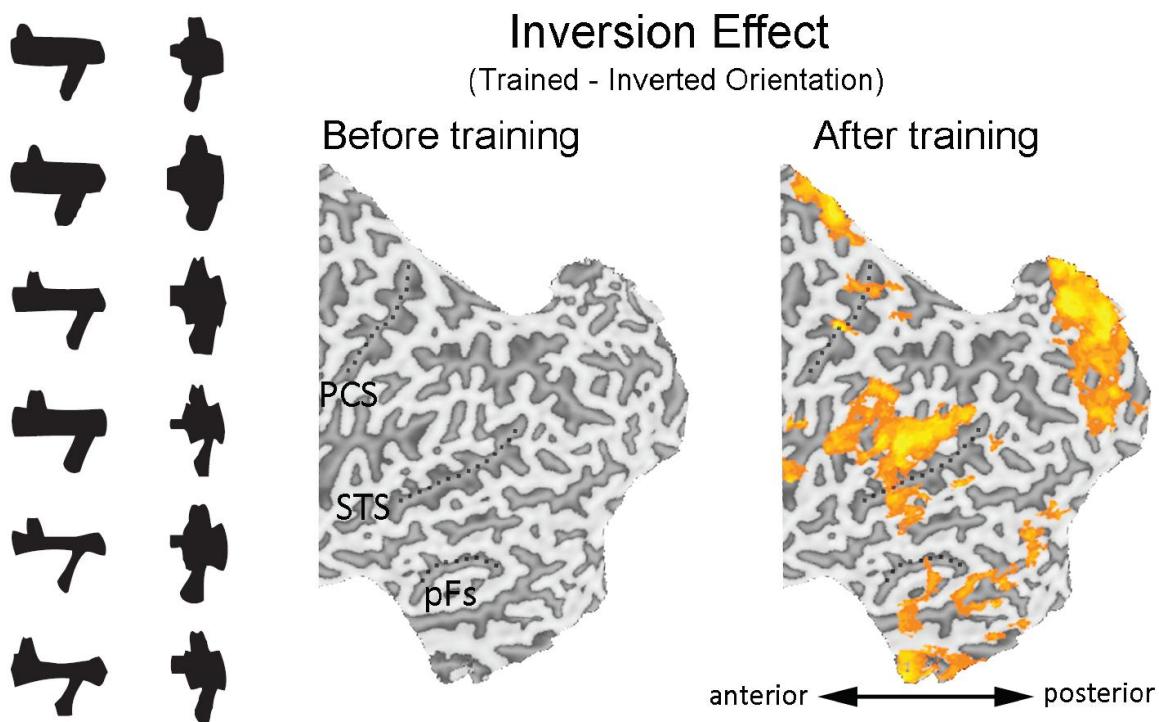


Figure 2. Left: Example silhouettes of unfamiliar "Ziggerin" objects. **Right:** People underwent fMRI brain scanning while performing a visual search task where they searched for a Ziggerin object of a particular orientation. Outside the scanner, they were then trained to search for Ziggerins from one particular category in a specific orientation (perceptual learning). After this training, they were scanned again while performing the same visual search task as before. Training induced extensive changes throughout visual cortex, where searching for new exemplars of Ziggerins in the trained orientation now evoked greater activity than when searching for Ziggerins presented in a different orientation. Another type of perceptual expertise training with the same kinds of novel objects evokes different cortical plasticity in visual regions (not shown). PCS – post-central sulcus; STS – superior temporal sulcus; pFg – posterior fusiform gyrus. Adapted from Y. K. Wong, Folstein, & Gauthier (2012).

For example, A. C.-N. Wong, Palmeri, and Gauthier (2009) trained people on different tasks with the same set of unfamiliar objects ("Ziggerins", see figure 2). Ziggerin objects within a particular category or class had the same parts and general structure, but there were subtle differences (e.g. part aspect ratio) between individual Ziggerins of the same class. One group of participants was trained to categorize or classify the Ziggerins, while the other learned to individuate them. Categorization training sped up categorization of new exemplars of the learned classes, while individuation mainly increased the speed of individuating the new Ziggerins, and only the latter group showed an increase in holistic processing for Ziggerins. Both tasks were challenging, and both groups clearly benefited from their training and could therefore be said to have increased visual expertise for Ziggerins. However, different task demands clearly lead to qualitatively different types of visual expertise.

Accordingly, different experience with the same stimuli can differentially drive plasticity in the visual system. For instance, only participants who had learned to individuate Ziggerins showed increased activity for these objects in the right fusiform (A. C.-N. Wong, Palmeri, Rogers, et al., 2009) In a different study using silhouettes of Ziggerins, always shown in the peripheral visual field (Y. K. Wong, Folstein, & Gauthier, 2011, 2012), one group learned to visually search for Ziggerin objects of a particular orientation (perceptual learning). Performance for this group specifically improved for the trained orientation as in prior perceptual learning studies with simpler objects (Sigman et al., 2005) even for new examples of Ziggerins, but did not generalize to Ziggerins of other orientations or classes. Another group learned to individuate Ziggerins by associating each individual object with a unique name. This kind of perceptual expertise training increased people's sensitivity for fine shape discriminations for Ziggerins within the trained class. These training paradigms led to qualitatively different changes within

the visual system. The former mainly induced changes in early visual regions. The latter led to changes in higher level visual regions (such as the fusiform gyrus) and included both face- and object-selective cortical areas. Experience clearly influences visual object representations throughout cortex (see figure 2), well outside the FFA, and the precise nature of that experience dictates where and almost surely how the workings of neurons are modified by learning.

Summary

Our brains are constantly being modified by new experience. The visual system appears to optimize the processing of objects for the tasks that were carried out on them in the past. While some of the most influential theories of object recognition focus almost entirely on a bottom-up process based on visual attributes of objects (Biederman, 1987; Jiang et al., 2006; Perrett & Oram, 1993; Riesenhuber & Poggio, 1999), there has been an increasing interest in top-down influences in vision (e.g. Gilbert & Li, 2013). The study of perceptual expertise illustrates how long-term experience associating specific task demands with an object category can shape the visual system.

This chapter was supported by the International Fulbright Science and Technology Award to H. M. S., and the National Science Foundation (Grant SBE-0542013), the Vanderbilt Vision Research Center (Grant P30-EY008126) and the National Eye Institute (Grant R01 EY013441-06A2) to I. G.

References

- Bentin, S., Deouell, L. Y., & Soroker, N. (1999). Selective visual streaming in face recognition: Evidence from developmental prosopagnosia. *NeuroReport*, 10(4), 823-827.
- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, 94(2), 115-147.
- 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.
- Boggan, A. L., Bartlett, J. C., & Krawczyk, D. C. (2012). Chess masters show a hallmark of face processing with chess. *Journal of Experimental Psychology: General*, 141(1), 37-42.
- Bukach, C. M., Phillips, W. S., & Gauthier, I. (2010). Limits of generalization between categories and implications for theories of category specificity. *Attention, Perception, & Psychophysics*, 72(7), 1865-1874.
- Farah, M. J., Levinson, K. L., & Klein, K. L. (1995). Face perception and within-category discrimination in prosopagnosia. *Neuropsychologia*, 33(6), 661-674.
- Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is "special" about face perception? *Psychological Review*, 105, 482-498.
- Gauthier, I. (2000). What constrains the organization of the ventral temporal cortex? *Trends in Cognitive Sciences*, 4(1), 1-2.
- Gauthier, I., Curran, T., Curby, K. M., & Collins, D. (2003). Perceptual interference supports a non-modular account of face processing. *Nature Neuroscience*, 6(4), 428-432.
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, 3(2), 191-197.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nature Neuroscience*, 2(6), 568-573.

Gauthier, I., Williams, P., Tarr, M. J., & Tanaka, J. (1998). Training 'greeble' experts: A framework for studying expert object recognition processes. *Vision Research*, 38(15), 2401-2428.

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, 14(5), 350-363.

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.

Haug, H. (1987). Brain sizes, surfaces, and neuronal sizes of the cortex cerebri: A stereological investigation of man and his variability and a comparison with some mammals (primates, whales, marsupials, insectivores, and one elephant). *American Journal of Anatomy*, 180(2), 126-142.

Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *Journal of Neuroscience*, 14(11), 6336-6353.

James, T. W., & James, K. H. (2012). Expert individuation of objects increases activation in the fusiform face area of children. *NeuroImage*.

Jiang, X., Rosen, E., Zeffiro, T., VanMeter, J., Blanz, V., & Riesenhuber, M. (2006). Evaluation of a shape-based model of human face discrimination using fMRI and behavioral techniques. *Neuron*, 50(1), 159-172.

- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17(11), 4302-4311.
- McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, 9(5), 605-610.
- McGugin, R. W., Gatenby, J. C., Gore, J. C., & Gauthier, I. (2012). High-resolution imaging of expertise reveals reliable object selectivity in the fusiform face area related to perceptual performance. *Proceedings of the National Academy of Sciences*, 109(42), 17063-17068.
- McGugin, R. W., & Gauthier, I. (2010). Perceptual expertise with objects predicts another hallmark of face perception. *Journal of Vision*, 10(4), 1-12.
- McGugin, R. W., McKeeff, T. J., Tong, F., & Gauthier, I. (2011). Irrelevant objects of expertise compete with faces during visual search. *Attention, Perception, & Psychophysics*, 73(2), 309-317.
- 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.
- McKeeff, T. J., McGugin, R. W., Tong, F., & Gauthier, I. (2010). Expertise increases the functional overlap between face and object perception. *Cognition*, 117(3), 355.
- McNeil, J. E., & Warrington, E. K. (1993). Prosopagnosia: A face-specific disorder. *The Quarterly Journal of Experimental Psychology*, 46(1), 1-10.
- Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, 9(5), 555-604.

- Op de Beeck, H. P., Baker, C. I., DiCarlo, J. J., & Kanwisher, N. G. (2006). Discrimination training alters object representations in human extrastriate cortex. *The Journal of Neuroscience*, 26(50), 13025-13036.
- Perrett, D., & Oram, M. (1993). Neurophysiology of shape processing. *Image and Vision Computing*, 11(6), 317-333.
- Rankin, C. H., Beck, C., & Chiba, C. M. (1990). *Caenorhabditis elegans*: A new model system for the study of learning and memory. *Behavioural brain research*, 37(1), 89-92.
- Richler, J. J., Palmeri, T. J., & Gauthier, I. (2012). Meanings, mechanisms, and measures of holistic processing. *Frontiers in Psychology*, 3:553. doi: 10.3389/fpsyg.2012.00553
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, 2(11), 1019-1025.
- Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, 9(5), 250-257.
- Sergent, J. (1988). Face perception and the right hemisphere. In L. Weiskrantz (Ed.), *Thought without language. A Fyssen Foundation symposium* (pp. 108-131). New York, NY, US: Clarendon Press/Oxford University Press.
- Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing: A positron emission tomography study. *Brain*, 115(1), 15-36.
- Sigman, M., Pan, H., Yang, Y., Stern, E., Silbersweig, D., & Gilbert, C. D. (2005). Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron*, 46(5), 823-835.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology*, 46(2), 225-245.

- Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory & Cognition*, 25(5), 583-592.
- Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience*, 3, 764-770.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, 311(5761), 670-674.
- White, J. G., Southgate, E., Thomson, J. N., & Brenner, S. (1986). The structure of the nervous system of the nematode *Caenorhabditis elegans*. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 314(1165), 1-340. doi: 10.1098/rstb.1986.0056
- Wong, A. C.-N., Palmeri, T. J., & Gauthier, I. (2009). Conditions for facelike expertise with objects becoming a Zigerin expert—but which type? *Psychological Science*, 20(9), 1108-1117.
- Wong, A. C.-N., Palmeri, T. J., Rogers, B. P., Gore, J. C., & Gauthier, I. (2009). Beyond shape: How you learn about objects affects how they are represented in visual cortex. *PLOS ONE*, 4(12), e8405.
- Wong, Y. K., Folstein, J. R., & Gauthier, I. (2011). Task-irrelevant perceptual expertise. *Journal of Vision*, 11(14), 1-15.
- Wong, Y. K., Folstein, J. R., & Gauthier, I. (2012). The nature of experience determines object representations in the visual system. *Journal of Experimental Psychology: General*, 141(4), 682-698.
- WormAtlas. (2002-2013). WormAtlas Z. F. Altun & D. H. Hall (Eds.), Retrieved from <http://www.wormatlas.org>

Xu, Y. (2005). Revisiting the role of the fusiform face area in visual expertise. *Cerebral Cortex*, 15(8), 1234-1242.