

## Categorization

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The survival of most organisms demands that they discriminate predator from prey, edible from inedible, or family from foe. Organisms have to be able to recognize things as *kinds of things*, not as isolated instances, because what is learned about one thing should generalize to other things of the same kind. We call these kinds of things *categories*. Recognizing something in the world as a kind of thing is *categorization*. Organisms may also *identify* unique objects as individuals, but arguably this *identification* can be considered a fine-grained form of categorization because matching different views of the same object, or even the same object changing over time, requires labeling different experiences as belonging to the same category.

Once a thing is categorized or identified, all of the knowledge we might have about that category can be brought to bear. What's the most appropriate course of action? Flee? Eat it? Pick up and dial?

Humans take categorization to dizzying degrees. First there is the mundane. We easily categorize chairs from tables, trees from shrubs, and birds from dogs. And there is the remarkable. Experts from various domains may easily discriminate subspecies of particular kinds of plants or animals, judge cancerous from noncancerous growths, or distinguish Porsche models just by the shape of the headlight. While this may seem impressive, remember that many everyday categorizations prove remarkable when you consider the processing demands involved. We easily identify the people we know at a glance. Yet structurally, people may be as similar to one another as different chimpanzees. For most people, all chimpanzees look the same but people look much more different. Right now you are engaging in another everyday categorization: With remarkable speed and ease, the letters and words in this sentence are categorized

as just the first step of comprehending (at least we hope) our written language. Face and letter perception are examples of domains in which most people have gained considerable expertise and are very important domains of study.

This chapter mainly addresses how people categorize visual objects. People can also categorize things based on their sound, touch, taste, or smell. But outside of speech perception, the majority of categorization research has focused on the visual modality. More complex visual events can also be categorized, such as “a nod” or “a touchdown” or “an armstand back double somersault tuck,” but this has been for the most part studied separately from object categorization (e.g., Zacks, Speer, Swallow, Braver, & Reynolds, 2007). In keeping with the aims of this *Handbook*, in each section of this chapter we lay out a variety of fundamental behavioral manifestations of object categorization and review some of the key findings from neurophysiology, electrophysiology, neuropsychology, and functional brain imaging that have deepened our understanding of object categorization. We also look to computational cognitive neuroscience models grounded in neuroanatomy and neurophysiology.

We begin our discussion with the issue of abstraction. By its very nature, categorization is abstraction. We live in a world of particular experiences. Yet recognizing an object as not simply an isolated perceptual experience but also as an instance of a kind of thing that has been experienced before—as a member of a category—is to abstract from the particular to the general. Does this ability to abstract from particular experience mean that what we know about an object category is itself an abstraction? At first blush, it may seem like the answer is obviously yes. How could we categorize objects abstractly if our knowledge about categories was not itself abstract? But as we will see, decades of behavioral research wrestled with this basic issue and recent neuroscientific evidence has shed important light on this question.

We then turn to two parallel issues that have dominated much of the recent research on object categories: (a) The

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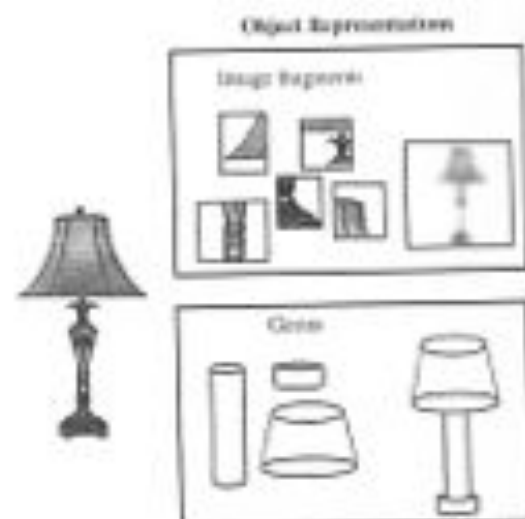
study of when different kinds of knowledge representations, abstract or not, come into play, and whether the variety of categorization behaviors we can observe is best explained by different learning and memory systems in the brain; and (b) whether objects from different domains may be categorized in different ways and by different brain systems. For instance, there may be specialized systems in the brain to process objects from especially important categories such as letters and faces. Whether and how we acquire such specialization through learning, or whether we have evolved systems for some special categories, has been a topic of debate.

### ROLE OF ABSTRACTION IN CATEGORIZATION

Categorization is abstraction. To begin with, we never see the same object twice, even if it is the very same physical object. When an object is viewed from a different position or under different lighting, the projection of that object onto our retina will vary, often quite dramatically. What is remarkable is that, despite the visual signal being very different, we perceive the same object (Palmer & Gauthier, 2004; Palmer & Tarr, 2008). Moreover, physically different objects can be perceived as very different, yet even very young children know that they are the same thing—not the same object, but the same kind of thing (Quinn, 1999). Humans have developed complex systems that permit objects to be categorized at multiple levels of abstraction, from specific (e.g., “Gladys” or “American White Pelican”), to basic level categories (e.g., “chair” or “bird”), to extremely abstract superordinate categories (e.g., “living thing”; Rosch, Mervis, Gray, Johnson, & Boyes-Braun, 1976).

Categorization is a form of abstraction, but does this necessarily imply that the mental representations and processes involved are inherently abstract? Early theories of object categorization took it as nearly an axiom that the goal of visual cognition was to create an abstract representation of the viewing world.

Early structural description theories of object recognition assumed that the goal of vision was to mentally reconstruct the abstract three-dimensional structure of objects (Marr & Nishihara, 1978). Recognition-by-components (Biederman, 1987) assumes that objects are mentally represented in terms of a small set of qualitative three-dimensional primitives known as *geons* (Figure 20.1). Geons are uniquely recovered by attending to various configurations of view-invariant properties in the two-dimensional retinal image. Objects are represented in terms of their geon components and their relative spatial



**Figure 20.1** Illustration of object representations in image-based versus structural description models.

**Note:** (Top) Image-based models. The object (lamp) is represented in terms of image-based fragments of intermediate complexity. (Bottom) Structural description models. The object (lamp) is represented in terms of geometric primitives (*geons*) and the spatial relations between them.

configuration. As a consequence of this reconstruction into a geon-defined structure, many sources of variability are eliminated entirely from a mental representation of an object. Different views of the same object and different exemplars within a category such as dog or lamp map onto the same object representation.

Early concept models also assumed that our knowledge about object categories is abstract. Semantic network models (e.g., Collins & Quillian, 1969) conceptually organized one kind of thing with another kind of thing through propositional structures. Knowledge is stored efficiently, so that object properties that are *new* of a superordinate category are only stored at the most general level and only properties unique to subordinate categories or specific individuals are stored at lower levels of the conceptual hierarchy (E. Smith, Shoben, & Rips, 1974). According to this view, what we know about particular object categories is also abstracted away from our experience with objects. By such abstractionist views, categorization of an object requires applying logical rules to object properties (e.g., Bruner, Goodnow, & Austin, 1956; Johnson & Palser, 2002) or comparing an object to an abstract category prototype or schema (e.g., Lakoff, 1987). Category abstraction is achieved because our knowledge about categories is abstract.

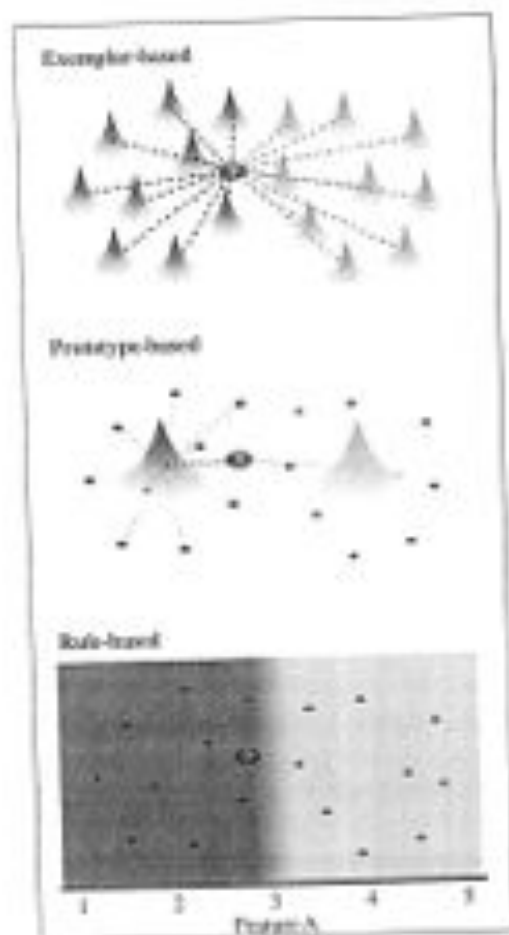
However, later work showed that we do not need viewpoint-invariant and instance-invariant representations in order to achieve categorization that appears invariant across viewing conditions and invariant across instances of a category. Careful experimentation revealed that object categorization can be systematically affected by the particular

viewpoints and category instances that have been experienced (see Palmeri & Gauthier, 2004; Palmeri & Tarr, 2008).

While there are conditions under which humans readily recognize and categorize objects irrespective of viewpoint (Biederman & Gerhardstein, 1993; Tarr & Bulthoff, 1998), numerous studies have found that if observers learn to recognize novel objects from specific viewpoints, they are both faster and more accurate at recognizing these same objects from familiar viewpoints relative to unfamiliar viewpoints (Bulthoff & Edelman, 1992; Tarr & Bulthoff, 1995; Tarr & Pinker, 1989). Even the recognition of single geometrical objects, originally proposed to support view-invariant performance with more complex objects, is sensitive to changes in viewpoint (Tarr, Williams, Hayward, & Gauthier, 1998). Instead, human object recognition was proposed to rely on multiple views, where each view encodes the appearance of an object under specific viewing conditions, including viewpoint, pose, configuration, and lighting (Tarr, 1995; Tarr, Kemon, & Bulthoff, 1998) and a collection of such views constitutes the enduring visual representation of a given object.

These ideas are instantiated in image-based models of object recognition (e.g., Edelman, 1997, 1999; Poggio & Edelman, 1990). Rather than assume that the goal of vision is to reconstruct the three-dimensional world, image-based models stress the importance of generalizing from past experiences to the present experience (Shepard, 1987, 1994). This is done by remembering past views of objects and generalizing based on similarity to those stored views. Such models account well for patterns of interpolation and extrapolation to new views. Furthermore, since physically similar objects in the world viewed under similar conditions will be similar to the same set of stored views, generalization to new objects can occur without any explicit representation of three-dimensional shape. For purposes of object recognition and categorization, representation of three-dimensional shape may not be necessary. Instead, such information may be stored in parts of the brain involved in acting on objects (Goodale & Milner, 1992).

Similar computational principles are also at work in exemplar-based models of object categorization. The core principle of these models is that object categories are mentally represented in terms of the specific category exemplars that have been previously experienced (Kruschke, 1992; Medin & Schaffer, 1978; Nosofsky, 1986). Categorization is based on the relative similarity of an object to these stored exemplars. In that sense, you judge that a certain object is a cell phone because of its similarity to many other cell phones in memory. While no abstraction occurs, exemplar models can readily account for a range of prototypicality effects that might at first blush appear to demonstrate abstract prototype representations for categories (Basson, Dewey, & Madsen, 1984; Hutzman, 1986;

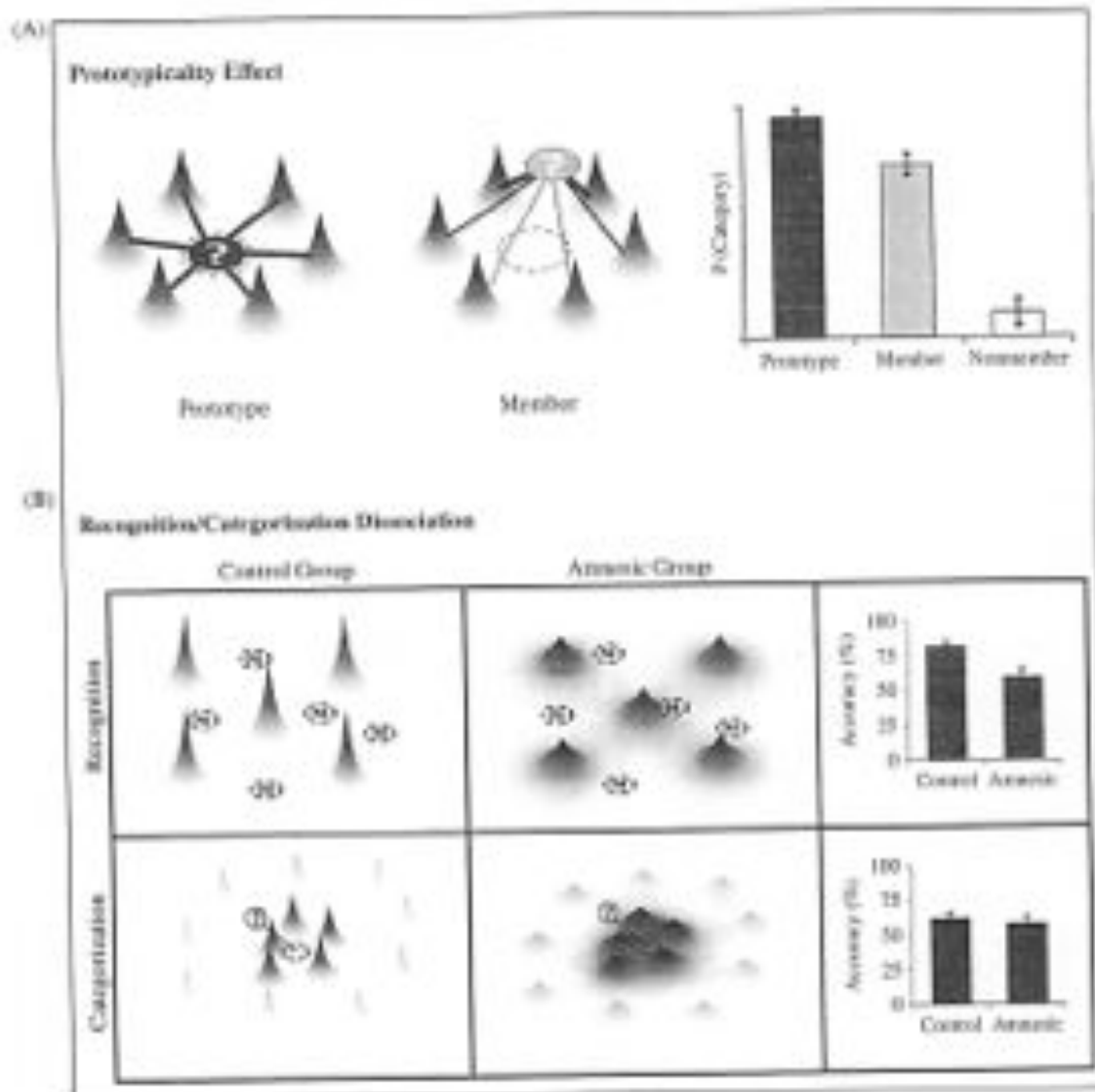


**Figure 20.3** Top: Exemplar-based models of categorization assume that object categories are represented by storing category exemplars that were previously experienced. Middle: Prototype models assume category knowledge is based on a stored prototype abstracted from the experienced category examples. Bottom: Rule-based models represent category knowledge with logical rules along individual features.

Note: (Top) Exemplars are represented as points in multidimensional psychological space, with similarity a function of distance in that space, and the generalization gradient around an object indicated by the graded shading around each exemplar. The exemplars on the left (darker circles) represent one category and the exemplars on the right (lighter circles) represent a different category. A probed object (question mark) is categorized based on the relative similarity to stored exemplars in each category. (Middle) A probed object (question mark) is categorized based on the relative similarity to the different category prototypes. (Bottom) These rules partition psychological space into different regions. A probed object (question mark) is categorized according to what region it lies within relative to the category rule.

Nosofsky, 1988; Shin & Nosofsky, 1992; see Figures 20.2 and 20.3). These models also account for a range of category exemplar effects (Nosofsky, Kruschke, & McKinley, 1992) and the time course of categorization (Lamberts, 2000; Nosofsky & Palmeri, 1997; Palmeri, 1997).

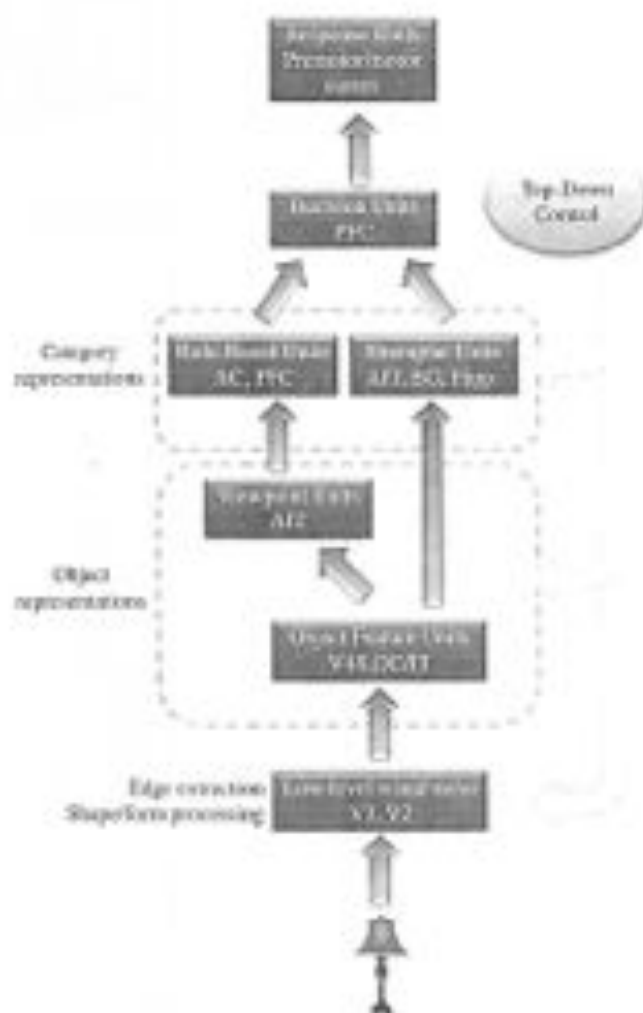
Neurophysiological evidence supports many important assumptions underlying a host of image-based and exemplar-based models of object categorization (refer to Figure 20.4



**Figure 20.3** Exemplar-based models can account for two important phenomena that on the surface seem to challenge exemplar-based models.

**Note:** At the top panel illustrates prototypicality effects. Category prototypes are readily categorized as well as and sometimes better than category exemplars, even if the category prototypes have never been seen before (far right graph). This result is typically viewed as strong evidence for prototype abstraction. How else could an object that's never been seen before be classified as well as objects that have been trained on, unless that unseen prototype is in fact abstracted during learning and stored just like an experienced exemplar? But assuming that categorization is based on similarity to stored exemplars only, this prototypicality effect falls out quite naturally. The left and middle figures illustrate how category exemplars and the category prototype might be represented in a psychological space, with the prototype in the middle, the exemplars around the prototype, and distance between objects related to their psychological similarity; the cloud around each point represents the generalization gradient around each stored exemplar. As shown in the left figure, the prototype to be classified (indicated by T) is similar to many exemplars, yielding a lot of evidence in favor of category membership. By contrast, as shown in the middle figure, an individual category exemplar to be classified (indicated by T) may only be similar to a subset of exemplars, yielding weaker

category evidence compared to that for an unseen prototype. **B:** The bottom panel illustrates dissociations between categorization and recognition memory. As discussed in the text, whereas amnesic individuals and controls show similar performance on categorization, amnesic individuals are significantly impaired at recognition memory (far right graph). This behavior dissociation suggests a functional dissociation between categorization and recognition. As in the top panel, individual exemplars are represented as points in a psychological space with the clearly stored exemplars representing the generalization gradients. Following Neofsky and Zohary (1995) we assume here that amnesic individuals have far poorer exemplar recollection than controls, as indicated by the far more diffuse generalization gradients because of impaired memory for amnesic individuals. For categorization, all of the category exemplars are stored together in the same general region of psychological space. Having fairly good or diffuse exemplar memories has little impact on categorization because all of the category members are in the same part of the psychological space. However, having fairly good or diffuse exemplar memories does have significant impact on recognition because the space of old and new patterns is distributed uniformly throughout psychological space; having more diffuse recollection makes it far more difficult to discriminate between old objects that have been seen and stored, about points, from new objects.



**Figure 28.4** Stages of processing in object recognition and categorization according to a range of models.

*Note:* Low-level features such as edges are processed in early visual areas. Object representations are created by processing object features with in the V4, lateral occipital cortex (LOCC), and/or inferotemporal cortex (IT) and by processing viewpoint in anterior intraparietal cortex (AIT). Category representations arise from rule-based units in the anterior cingulate (AC) and prefrontal cortex (PFC), or from exemplar units in the anterior inferotemporal cortex (AIT), the basal ganglia (BG), and the hippocampus (Hipp). Information from the category representation is passed to decision units in PFC, which determines category membership and initiates the selection of the appropriate category response in the premotor cortex for execution by the motor cortex. Low-level processing, object representations, and category representations can all be modulated by factors such as attention and various task demands via top-down control.

for brain areas discussed in this section). The responses of inferotemporal (IT) neurons to objects depends on stimulus size and viewpoint (Perrett, Oram, & Ashbridge, 1998; K. Tanaka, 1996). Even accepted notions of retinal position invariance in IT (Tovee, Rolls, & Azzopardi, 1996) have been challenged (DiCarlo & Maunsell, 2003; Op de Beeck & Vogels, 2000). Surprisingly few neural responses in IT are invariant to position, size, or viewpoint (DiCarlo & Maunsell,

2003; Logothetis & Sheinberg, 1996; but also see Booth & Rolls, 1998). When trained on particular object views, monkeys recognize novel object views according to their similarity to experienced views, and neurons respond in a similarly graded fashion to particular trained views (Logothetis & Pauls, 1995; Logothetis, Pauls, Bülthoff, & Poggio, 1994; Logothetis, Pauls, & Poggio, 1995). Perrett et al. (1998) provided one suggestion for how object recognition could take the form of an accumulation of evidence across all neurons selective for aspects of a given object. By assuming a neural variant of stochastic accumulation of evidence models (Nowofsky & Palmeri, 1997; P. Smith & Ratcliff, 2004) and by assuming that the rate of accumulation depends on the similarity between visible features in the presented viewpoint and those to which individual neurons are tuned, systematic effects of object recognition time and accuracy with changes in viewpoint can be well accounted for.

When monkeys are trained to categorize objects, their behavior is consistent with exemplar generalization and not with the abstraction of a prototype (Sigala, Gabbiani, & Logothetis, 2002). IT neurons will respond selectively to specific exemplars that have been studied, not to an average category prototype that was never studied (Freedman, Riesenhuber, Poggio, & Miller, 2003; Op de Beeck, Wagemans, & Vogels, 2001, 2008; Vogels, Biederman, Bar, & Loricz, 2001). Furthermore, many exemplar models of object categorization assume that similarity between objects is heavily influenced by matches or mismatches along dimensions that are diagnostic of category membership (Gauthier & Palmeri, 2002; Kruschke, 1992; Lambert, 2000; Nowofsky, 1984, 1986), and neural responses are modulated by dimensional diagnosticity in a similar manner (Sigala & Logothetis, 2002).

While responses of IT neurons can be specific to particular exemplars that have been experienced, IT neurons do not seem to respond in a category-specific manner. Instead, category-specific, but not exemplar-specific, neural responses are observed in the prefrontal cortex (Freedman et al., 2003; Long et al., 2007; Rotshtein, Henson, Treves, Driver, & Dolan, 2005). These neurophysiological results may seem at odds with the apparent category specificity observed using functional magnetic resonance imaging (fMRI) and in the patterns of deficits in category-specific agnosia due to focal brain injury, which we discuss later in this chapter. One way to reconcile these results is to first consider the vast differences in spatial resolution between single-unit recordings and fMRI or brain lesions. Although individual neurons may respond in a way that highlights exemplar-specific (not category-specific) information, neighboring regions of the cortex may respond to similar objects or objects that are processed in a similar fashion. So objects in the same category may recruit the same area

of the cortex as measured by fMRI or may be impaired in a category-specific fashion by brain injury, yet the underlying neural activity may respect exemplar-specific and view-specific coding, not category-specific coding per se.

Some recent neurally plausible computational models have instantiated this division of labor between learned object representations in IT and learned category representations elsewhere in the brain. For example, the theoretical work of Riesenhuber and Poggio (2000) represents a recent instantiation of a tradition of image-based models of object recognition (Edelman, 1997; Poggio & Edelman, 1990). This model builds on classical models where complex cells are built from simple cells in early visual areas, extending this hierarchy of processing throughout the higher-level visual cortex to view-tuned and exemplar-tuned units. At each level of the hierarchy, these units have Gaussian-shaped receptive fields (radial-basis functions) that respond preferentially to a particular stimulus property, whether that be edges or junctions at the lowest level, or views or exemplars at the highest level. Category-specific units that can represent knowledge of the basic-level category of an object or the subordinate-level identity of an object are thought to reside in the prefrontal cortex. Other computational models have proposed a similar division of labor between exemplar-like object representations in IT and category representations elsewhere, implicating brain structures such as the basal ganglia as well as the prefrontal cortex in mapping object-specific representations to category-specific representations (Ashby, Essiis, & Spiering, 2007; but see Lewis & Gureckin, 2007).

The hierarchical object representations instantiated in such models make us reflect on one key difference between classic structural description and image-based theories: Under the cartoon view of the world, structural descriptions represent objects in terms of viewpoint-independent three-dimensional parts and their spatial relations (Biederman, 1987), and views represent objects in terms of holistic images of the entire object (Edelman, 1997). However, intuition and empirical evidence (e.g., Garner, 1974; Sankiewicz, 2002; Tversky, 1977) suggest that we often represent complex objects in a compositional manner—objects are decomposable into parts. In addition, most exemplar-based and related models of object categorization assume that objects have parts, features, or dimensions that can be selectively attended according to how diagnostic they are for categorization decisions. Is there a way to marry the best qualities of image-based theories with the compositional representations seen in structural-description theories?

Some studies attempt to uncover image features that are most informative for classification, based on the mutual information (or mutual dependence) of features and specified categories (Scleris & Rodin, 1997; Ullman, Vidal-Naquet,

& Sali, 2002). Some of this work has found that features of “intermediate complexity” are best for basic-level classification (see Figure 20.1). For faces, what features emerge from this analysis are those we would generally call the “parts of a face” such as the eyes or the nose, even though the features are not selected a priori to correspond to meaningful parts per se; and for cars, parts such as the wheels or the driver’s side window emerge. In this context, we mean “emerge” in the sense that these features are uncovered by a computational analysis of hundreds of images as they relate to categories of objects without any kind of intervention from a human teacher. It is tempting to speculate about the relationship between such “ad hoc” image-based features to the observed feature selectivity of neurons in IT (K. Tanaka, 1996, 2003). The best responses for individual IT neurons are elicited by somewhat odd patterns that do not correspond to what we might typically think of as distinct object parts. These appear to be ad hoc. And they appear to be of intermediate complexity. So representations of object parts, as well as objects themselves, seem to be tuned by specific experience with objects in the world; object parts are not general-purpose parts such as those instantiated in models like recognition-by-components.

#### MEMORY AND LEARNING SYSTEMS THAT SUPPORT CATEGORIZATION

The role of abstraction in categorization defined much of the early research and debates about categorization (Murphy, 2002). Initial accounts assumed that categories are represented by abstracting logical rules (Figure 20.2) that define the necessary and sufficient conditions for category membership (Bourne, 1970; Bruner et al., 1956; Levine, 1975; Trabasso & Bower, 1968). While rule-based accounts described well how people learned categories defined by explicit rules, natural categories were found to have a graded structure that suggested instead notions like “family resemblance” and “similarity” as core constructs (Barsalou, 1985; Rosch, 1973; Wittgenstein, 1953). It is easier to categorize a robin as a bird than a penguin as a bird, the argument goes, because a robin is more similar to the prototypical bird (Rosch & Mervis, 1975). Such results suggested that prototypes (Figure 20.2), not rules, define natural categories and that prototypes are learned by abstracting core properties of the category from experience with category members (Horn, Cross, Cornell, Goldman, & Schwartz, 1973; Posner & Keele, 1968; J. D. Smith & Minda, 1998). But as discussed earlier, later work showed that models assuming specific exemplar representations (Figure 20.2), instead of abstract prototype representations, can account well for prototype effects.

a whole host of other behavioral effects, and are consistent with a significant amount of the neurophysiological data (Figure 20.3). Arguably, most successful models of categorization have an exemplar model as a critical component (Erickson & Kroschke, 1998; Palmeri, 1997) or fall on a continuum between prototype abstraction models and pure exemplar models (Ashby & Waldron, 1999; Love, Medin, & Oroscois, 2004; Rosseel, 2002). Much of this early work was grounded in an assumption—a perfectly reasonable parsimonious assumption—that all kinds of categories are represented the same way at all stages of learning. Categories are represented by rules or prototypes or exemplars. More recent work has instead asked whether different kinds of category representations are used for learning different kinds of categories, under different kinds of conditions, and at different stages of learning. Some kinds of categories can be learned using rules, but others cannot. Perhaps people try to use rules when they first learn a category, but make use of other less explicit kinds of category knowledge with experience. The burgeoning interest in cognitive neuroscience over the past decade has led researchers quite naturally to ask how categories are represented in the brain. If categories can be represented in different ways at different points in learning under different conditions, it is likely that there are multiple memory and learning systems in the brain that support categorization. We should note that in this context we use the term *system* in the broadest possible sense: A system could reflect functionally independent kinds of representations and processes, or interacting systems, or different critical subcomponents of a single processing architecture (e.g., Palmeri & Flanery, 2002; Roediger, Beckner, & McDermott, 1999).

### Categorization and Rules

Despite the success of exemplar models of categorization, there have always been some lingering concerns about the processing and storage requirements that come with theories that demand individual memory traces of each and every experience with an object (e.g., Logan, 1988). One response to this criticism has been to view pure exemplar models as a sort of theoretical ideal point, whereas in reality categories may be represented by a subset of the space of experienced exemplars that produces a sufficient level of performance (e.g., Ashby & Waldron, 1999; Kroschke, 1992; Rosseel, 2002). But an alternative response has been to reconsider whether people might use simple rules to categorize objects.

What possessed researchers to reconsider an idea that was largely abandoned decades earlier? To begin with, many subjects asked to learn novel categories will say they are forming rules, even if the rules they verbalize

do not account all that well for their own categorization behavior. In addition, it is clear that novices are often taught categories using rules. For example, field guides for identifying birds, butterflies, or mushrooms certainly include many pictures but they also include lists of critical features for distinguishing different species. In the case of mushrooms, these explicit rules can be particularly important because edible and poisonous mushrooms often look quite similar. One important factor driving this theoretical shift was the finding that when subjects were told to use a particular categorization rule, exemplar-based models could not account for the observed categorization behavior (e.g., Nosofsky, Clark, & Shiu, 1989). The RULEX model (Nosofsky, Palmeri, & McKahey, 1994) posits that even when people are not given a rule or are not told to create a rule they form simple rules anyway when learning a category. What distinguishes RULEX from earlier rule-based models is that it is a rule-plus-exception model, hence the name RULEX: People form simple rules that may work pretty well and then store in memory any exceptions to those rules (see also Nosofsky & Palmeri, 1998; Palmeri & Nosofsky, 1995; Sakamoto & Love, 2004). RULEX accounts extremely well for a wide array of phenomena that are also consistent with prototype and exemplar models; and under some conditions individual subject behavior is more consistent with RULEX than exemplar or prototype models (Johansen & Palmeri, 2002; Nosofsky et al., 1994). RULEX was perhaps the first of a class of hybrid categorization models combining rules with other nonanalytic forms of category representations (Ashby, Alfonso-Reese, Turkes, & Waldron, 1998; Erickson & Kroschke, 1998; Goodman, Tenenbaum, Feldman, & Griffiths, 2008; Nosofsky & Palmeri, 1998; Palmeri, 1997). The success of a model like RULEX provides just one illustration of how difficult it can be to distinguish abstract rule-based from exemplar-based (or more generally similarity-based) models of categorization (see also Johansen & Palmeri, 2002; Nosofsky & Johansen, 2000). What are arguably polar extremes of the representational continuum can produce remarkably similar behavioral predictions.

Researchers have more recently looked to cognitive neuroscience data for evidence for a rule-based mode of categorization. Motivated by hypotheses about the underlying neural systems supporting different kinds of categorization, Ashby, Maddox, and colleagues have conducted a series of behavioral experiments that attempt to selectively influence rule-based versus similarity-based categorization. For example, introducing certain kinds of secondary distractor tasks during category learning can selectively interfere with rule-based but not similarity-based categorization (Waldron & Ashby, 2001, but see Nosofsky & Kroschke, 2001), whereas delaying corrective feedback

can selectively interfere with similarity-based but not rule-based categorization (Maddox, Ashby, & Bohil, 2003). Neuropsychological evidence also suggests a role for rule-based categorization and provides clues as to the specific brain structures involved. For example, patients with prefrontal cortex lesions are impaired at the Wisconsin Card Sorting Test (WCST), a task that requires sorting cards according to logically defined rules (Milner, 1963; Robinson, Heaton, Lehan, & Stilson, 1980). Parkinson's disease patients also seem to show selective impairment in rule-based but not similarity-based categorization (Ashby, Noble, Filoteo, Waldron, & Ell, 2003; Brown & Stubbs, 1988; Cools, van den Bercken, van Spaendonck, & Berger, 1984; Downes et al., 1989). Parkinson's disease has been linked to basal ganglia damage, specifically in the head of the caudate nucleus, which has reciprocal connections to the prefrontal cortex. Additional evidence for a rule-based system comes from neuroimaging data in healthy adults. One early study contrasted similarity-based versus rule-based categorization strategies (Allen & Brooks, 1991) that seemed to recruit different networks of brain areas as revealed by PET (E. E. Smith, Patalano, & Jonides, 1998). fMRI during rule-based categorization reveals activation in the right dorsal-lateral prefrontal cortex (Konishi et al., 1998; Seger & Cincotta, 2005) and the head of the right caudate nucleus (Konishi et al., 1998; see also Lombardi et al., 1999; Monchi, Petrides, Petre, Worsley, & Dagher, 2001; Seger & Cincotta, 2005). A variety of computational cognitive neuroscience models have implicated an interactive role for the prefrontal cortex and the basal ganglia (specifically the caudate nucleus of the striatum) in important aspects of various cognitive tasks (Ashby et al., 1998; Frank & Claus, 2006; Houk & Wise, 1995), but these models differ in important details regarding whether the basal ganglia is the core locus of learning or plays a more modulatory role. Overall, the converging results from behavioral, neuropsychological, neuroimaging, and computational studies suggest the existence of a network of brain areas, including the prefrontal cortex and the caudate, that are critically involved in rule-based categorization (Ashby & O'Brien, 2005).

### Categorization as a Skill

While some categorizations require explicit rules—and sometimes complex rules at that—other categorizations are made quickly and effortlessly, and perhaps without conscious intention. Such categorization has a qualitatively different flavor from rule use and can be considered something more like a habit or a skill that can be executed automatically. Palmeri (1997) explored how categorizations as skills can become automatized through an elaboration of Logan's

(1988) instance theory of automaticity. Instance theory is a general theory of automaticity of cognitive skills that posits a shift from more algorithmic or rule-based processing early in learning to memory retrieval of specific experienced instances later in learning (for some fMRI evidence consistent with instance theory, see Dobbins, Schnyer, Verfaellie, & Schacter, 2004; see also Logan, 1990, 2002; Palmeri, Wong, & Gauthier, 2004). Palmeri (1997) conceptualized the development of automaticity as a race between a rule-based categorization process and an exemplar-based categorization process (Nosofsky & Palmeri, 1997). Early in learning, rules are executed faster than category exemplars can be retrieved. But as more and more exemplars are experienced and are stored as part of the category representation, the exemplar-based categorization process eventually wins the race. Categorization is automatic when it's based on exemplar retrieval instead of rule use.

Ashby et al. (2007) proposed a computational cognitive neuroscience model called Subcortical Pathways Enable Expertise Development (SPEED) that shares some important computational principles with instance theory and exemplar-based models of categorization (Nosofsky & Palmeri, 1997; Palmeri, 1997). Like exemplar models, SPEED is a member of a family of computational theories called "nonparametric classifiers" (Ashby & Alfonso-Reese, 1995). These models are nonparametric in the sense of a contrast with so-called "parametric classifiers" like prototype theories that assume a specific (often normal) distribution of category members (Ashby, 1992). But SPEED specifically assumes a shift from category representations mediated by cortico-striatal loops to category representations mediated by direct cortico-cortico connections. Cortico-striatal loops appear to play an important role in category learning (Ashby et al., 1998), even if more permanent long-term category knowledge may ultimately rely on direct cortical representations.

Significant evidence suggests an important role for the basal ganglia, specifically the striatum, in categorization—at least for certain kinds of categorization and at certain points in learning (Shohamy, Myers, Kalanithi, & Gluck, 2008). Huntington's disease (HD) and Parkinson's disease (PD) are characterized by damage to the basal ganglia (for HD there is direct damage to the striatum whereas for PD there is damage to the substantia nigra that interacts critically with the striatum). HD and PD are classically characterized by their severe motor impairments, but it has long been known that these diseases also more generally impair motor skill learning and other procedural learning tasks (e.g., Mishkin, Malamut, & Bachevalier, 1984; Saint-Cyr, Taylor, & Lang, 1988). HD and PD also impair certain kinds of category learning as well, such as those involving a probabilistic association of cues to categories



(e.g., Knowlton, Mangels, & Squire, 1996; Knowlton, Squire, et al., 1996) and those involving an integration of information across multiple stimulus dimensions (e.g., Ashby et al., 2003; Filoteo, Maddox, & Davis, 2001; Maddox, Aparicio, Marchant, & Ery, 2005; Maddox & Filoteo, 2001). These patterns of deficits in HD and PD implicate an important role of the striatum in novel category learning (Ashby & O'Brien, 2005). In addition to such neuropsychological studies, a body of fMRI data also implicates the basal ganglia, specifically the striatum, in these kinds of novel category learning tasks (Poldrack et al., 2001; Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; Poldrack & Rodriguez, 2004; Seger & Cincotta, 2005).

### Categorization and Episodic Memory

Having an episodic memory allows us to recognize when we have seen particular objects in particular situations. For example, in order to recognize that you have previously seen a yawning orange cat sitting on a green bench in a grassy park, you must be able to access a coherent memory trace that includes all of the characteristics of this scene. The relationship, both computational and neuroanatomical, between the memories used to support explicit recognition of objects and the representations used to support object categorization has been vigorously debated. On the one hand, exemplar-based models propose that the same exemplar memories used to support categorization are used to support explicit recognition as well (e.g., Nosofsky, 1991, 1992). On the other hand, some have argued that while exemplar memories may be used to support some relatively ad hoc categories (Ashby & O'Brien, 2005), they play little or no role in most kinds of categorization (e.g., Ashby et al., 2007). The primary source of evidence against any close relationship between episodic memory and categorization and their underlying neural underpinnings comes from studies testing individuals with anterograde amnesia, a condition characterized by profound explicit memory deficits caused by damage to the hippocampus and neighboring medial temporal brain areas.

Specifically, Knowlton and Squire (1993; Squire & Knowlton, 1995; see also Reed, Squire, Palano, E. T. Smith, & Jondes, 1999) observed a behavioral dissociation between recognition and categorization, whereby individuals with anterograde amnesia who are significantly impaired at explicit recognition memory perform normally at categorization. According to Knowlton and Squire, this behavioral dissociation between categorization and recognition provided a direct falsification of exemplar-based models. But dissociations, and even double dissociations, are only weak evidence in favor of modular theories (Platt, 1995; Shallice, 1988). A direct instantiation of an exemplar

model, whereby simulated individuals with amnesia have significantly degraded exemplar memories compared to simulated controls, predicts the very dissociation Knowlton and Squire claimed as a falsification of exemplar models (Nosofsky & Zaki, 1998; Palmeri & Flanery, 2002). Other research supporting a functional dissociation between categorization and recognition (Filoteo et al., 2001; Reed et al., 1999; J. D. Smith & Minda, 2001) suffers from a variety of theoretical, statistical, and methodological problems (Kinder & Shanks, 2001; Palmeri & Flanery, 1999, 2002; Zaki, 2005; Zaki & Nosofsky, 2001, 2004). Moreover, there is research showing that individuals with explicit memory deficits show impairments in categorization as well (Graham et al., 2006; Hopkins, Myers, Shohamy, Grossman, & Gluck, 2004; Zaki, Nosofsky, Ramerail, & Urviztagi, 2003; see also Meiser, Myers, Shohamy, Hopkins, & Gluck, 2006).

The most widely studied cases of anterograde amnesia are caused by damage to the hippocampus and associated medial temporal lobe (MTL) structures (e.g., Squire, 2004). So debates about the relationship between categorization and episodic memory engender debates about the role of the hippocampus in categorization. According to some multiple memory systems theories, explicit episodic memory is supported by the hippocampus whereas categorization involves implicit procedural memory that is supported by the basal ganglia and cortex (Squire & Zola, 1996). Some computational cognitive neuroscience models eschew entirely any role for the hippocampus in categorization (e.g., Ashby et al., 1998, 2007; Ashby & O'Brien, 2005) or do not discuss whether the hippocampus has any role (e.g., Rieserhuber & Poggio, 1999, 2002).

But evidence is building for a role of the hippocampus in categorization. As discussed previously, hippocampal damage in individuals with anterograde amnesia does lead to significant categorization deficits. These results mirror other neuropsychological findings that suggest the hippocampus is involved in purportedly implicit forms of memory (e.g., Chan & Phelps, 1999). In addition, functional brain imaging provides evidence that the hippocampus is recruited during categorization. Reber, Gielman, Parrish, and Mesulam (2003) found greater MTL activation when healthy adults learned categories intentionally compared to when they learn them implicitly. Poldrack et al. (1999, 2001; see also Fenske, Knowlton, & Poldrack, 2006; Seger & Cincotta, 2005) observed a trade-off between hippocampal and basal ganglia activation during novel category learning, suggesting an interaction in the computations performed by these two important neural systems (Poldrack & Rodriguez, 2004). The recruitment of the hippocampus appears to be more pronounced early in learning novel categories. One hypothesis is that the MTL helps set up the representations

of novel stimuli that are then used by other brain areas (such as the basal ganglia or prefrontal cortex) to assign those stimuli to categories. This role as a novel representational engine has been proposed in computational models (e.g., Gluck & Myers, 1993; Meeter, Myers, & Gluck, 2005). Specifically, SUSTAIN (Supervised and Unsupervised STRatified Adaptive Incremental Network; Love et al., 2004) is a cognitive model of categorization that shares properties with various exemplar, prototype, and rule-based models, and has accounted for an array of fundamental categorization phenomena. More recently, the computational mechanisms within SUSTAIN have been grounded in a network of brain areas, with the hippocampus playing a critical role in encoding novel stimuli that cannot be accommodated by the current category representations (Love & Gureckis, 2007). Instead of linking specific brain areas with particular kinds of cognitive tasks, whether episodic memory or categorization or priming, it seems more fruitful to consider the computations performed by those brain areas in the service of complex tasks (Palmeri & Flanery, 2002; Turke-Browne, Yi, & Chun, 2006).

### CATEGORY-SPECIFIC SYSTEMS FOR CATEGORIZATION

Some arguments for multiple systems for categorization are based on structural aspects of the categories to be learned (e.g., whether they permit single rules or not), aspects of the task (e.g., the timing and quality of feedback), and the amount of learning. In the following section, we introduce work from a different tradition that studies the organization of the neural substrates responsible for the perception of different object categories in the brain. In this work, claims of multiple categorization systems have also been made. Specifically, that some categories are special in that they engage specialized brain areas. Specialized systems dedicated to perception of specialized categories have been claimed for faces (Kanwisher, McDermott, & Chun, 1996, 1997), places (Epstein, Harris, Stanley, & Kanwisher, 1999), body parts (Downing, Jiang, Shuman, Kanwisher, 2001), words (Cohen et al., 2000; Nobre, Allison, & McCarthy, 1994), letterstrings (Polk et al., 2002), and even single letters (K.H. James, James, Jobard, Wong, & Gauthier, 2005). We provide an overview of the evidence that has led researchers to postulate category-specific perceptual systems and then discuss some alternative interpretations of these results. To the extent that categorization studies are performed with visual stimuli such as faces (e.g., Goldstone & Styvers, 2001) or novel items that may be animal-like (Allen & Brooks, 1991; Reed et al., 1999) or not (Knowlton & Squire, 1993; Posner & Keele, 1968),

understanding the systems involved in their perception may be crucial. We often use face processing as the main example domain in what follows because it has been studied the most extensively.

Studies of patients with brain damage resulting in deficits in the visual recognition of objects suggest that the visual system, at least on a fairly coarse scale, may be organized around categories. While most cases of brain damage to the visual cortex result in deficits with virtually any category tested, in relatively rare cases, category-specific deficits are observed. These patients have difficulty identifying visually presented objects from certain categories, despite good basic visual skills. For example, when shown a picture of a banana, a patient may be unable to say "banana" or retrieve semantic information about bananas, but they may be able to describe its shape and identify that the object is yellow. Category-specific agnosias have been found for biological objects (e.g., Hillis & Caramazza, 1991; McCarthy & Warrington, 1988; Warrington & Shallice, 1984) artifacts (e.g., Hillis & Caramazza, 1991; Warrington & McCarthy, 1983, 1987), faces (e.g., Farah, 1996; Farah, Levinson, & Klein, 1995; Henke, Schweinberger, Grigo, Klos, & Sommer, 1998), and words (e.g., Warrington & Shallice, 1980). One patient presented with deficits in recognizing any object or word, except for extremely well-preserved face recognition skills (Moscovitch, Winocur, & Behrmann, 1997). At the other end of the spatial scale, neurophysiology in the monkey reveals selectivity of single cells for particular objects, such as faces, in several regions of the temporal lobe (e.g., Baylis & Rolls, 1987; Desimone, Albright, Gross, & Bruce, 1984; Gross, Bender, & Rocha-Miranda, 1969) and elsewhere in the brain such as the amygdala (e.g., Rolls, 1992) and the frontal cortex (e.g., Wilson, Scalaidhe, & Goldman-Rakic, 1993) although the cells selective for any category are only a fraction, typically about 20%, of the population of neurons recorded from. Recent work, however, suggests that when using single cell recording within the face-selective patches localized with fMRI in the monkey brain, virtually all neurons are selective for faces (Tsao, Freiwald, Tootell, & Livingstone, 2006). Thus, neuropsychology and neurophysiology together suggest category-selective responses that are distributed over the ventral cortex, with at least some categories showing a high degree of spatial clustering.

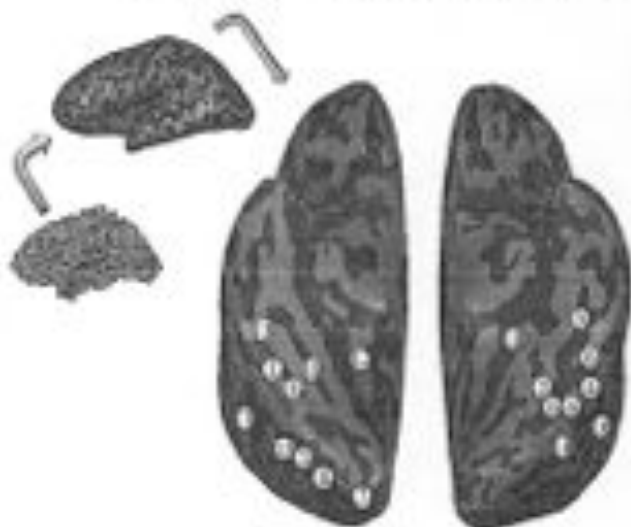
Much of our knowledge about the organization of the visual recognition system in the human brain comes from much less invasive work using brain imaging in normal subjects. For instance, scalp recordings reveal face-selective (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 2000) and letter-selective (e.g., Wong, Gauthier, Woroch, DeBuse, & Curran, 2005) potentials that peak about 170 ms after the presentation of the image.

But the evidence that has perhaps received the most attention comes from studies using fMRI, a technique with better spatial resolution than event-related potentials (ERP), and which reveals brain regions selectively engaged by faces (Gauthier, Tarr, Maylan, Anderson, & Gore, 2000; fusiform gyri, lateral occipital gyri, superior temporal sulcus; e.g., Kanwisher et al., 1997; Puce, Allison, Bertin, Gore, & McCarthy, 1998; see also Sergent, Ohta, MacDonald, & Zuck, 1994), animals (lateral fusiform, e.g., Chao, Haxby, & Martin, 1999; Martin, Wiggs, Ungerleider, & Haxby, 1996), tools (left premotor area, medial fusiform gyrus; e.g., Chao et al., 1999; Martin et al., 1996), words, letter strings, and single letters (left fusiform, left occipito-temporal junction, e.g., Cohen et al., 2000; Flowers et al., 2004; K. H. James et al., 2005; Polk et al., 2002; Puce, Allison, Asgari, Gore, & McCarthy, 1996). Categories that are even more rarely selectively impaired in brain damage also reveal similar specialization. For instance, a "place area" was discovered in the parahippocampal gyrus that responds strongly to scenes, buildings, and other spatial landmarks (Agnaire, Zarahn, & D'Esposito, 1998; Epstein et al., 1999; Epstein & Kanwisher, 1998). Regions of the lateral occipito-temporal cortex (Downing et al., 2001) and fusiform gyrus (Poeles, Wiggan, & Dowling, 2006) were found to selectively respond to body parts and areas of the superior temporal sulcus respond selectively to biological motion (Grossman & Blake, 2002). The typical locus for some of these areas is shown in Figure 20.5.

There are several possible explanations for the apparent category specialization in the brain. One option is to take the compartmentalization observed in fMRI maps at face value and conclude that there may be separate modules responsible for processing different object categories. In this context, modularity does not simply refer to an anatomically distinct neural area, but instead invokes a Fodorian (Fodor, 1983) sense of modules as specialized, encapsulated mental subsystems that handle specific information—they are domain-specific entities that function independently of one another and of background beliefs of the subject. Modular claims are found throughout psychology and cognitive neuroscience and it is rare that they do not lead to heated debates. We briefly summarize some of the evidence that has led researchers to question the idea that category specialization in the ventral visual system represents modular organization.

### Modular Accounts

Modular accounts of category specialization often suggest that evolutionary pressures caused the creation of specific modules for processing categories that are relevant to survival, like animals, plants, and conspecifics, more quickly



**Figure 20.5** Typical location of some category-selective peak activations shown on a ventral view of brain.

*Note:* An individual brain was segmented and then inflated so as to make the sulci (dark grey) as well as the gyri (light grey) visible. 1 = Right fusiform face area (Gauthier, Skudlarski, et al., 2000); 2 = Left fusiform face area (Gauthier, Skudlarski, et al., 2000); 3 = Right occipital face area (Gauthier, Skudlarski, et al., 2000); 4 = Visual word form area (K. H. James et al., 2005); 5 = Single letters (K. H. James et al., 2005); 6 = Letter strings (K. H. James et al., 2005); 7, 8, and 9 = Animals (Chao et al., 1999); 10 = Tools (Chao et al., 1999); 11 = Left parahippocampal place area (Epstein et al., 1999); 12 = Right parahippocampal area (Epstein et al., 1999); 13 = Fusiform body area (Poeles et al., 2006); 14 = Left extrastriate body area (Poeles et al., 2006); 15 = Right extrastriate body area (Poeles et al., 2006); 16 = Left biological motion area (Grossman & Blake, 2002); 17 = Right biological motion area (Grossman & Blake, 2002).

(Caramazza & Shelton, 1998): Is that animal a potential predator, a potential food source, or a potential mate? Is this plant poisonous, edible, or medicinal? Similarly, if you are walking alone at night, recognizing the face of the person coming toward you as either a friend or an enemy is a decision you would want to make rapidly and accurately. A specialized processing module for important categories of objects would confer survival advantage. It is clear, however, that for some domains of apparent modularity, such as reading, it begs reason to suggest that such specialization would be innate. Therefore, modules, if they exist, can be either innate or learned.

Generally, modular accounts do not predict that there is a module in the brain for every object category we interact with. Instead, a few categories are thought to have a special status either because of evolutionary pressures or experience. For instance, there is a double dissociation between living and nonliving things, with some patients showing an impairment for living but not nonliving things (e.g., Farah, McMullen, & Meyer, 1991; Hillis & Caramazza, 1991; McCarthy & Warrington, 1988; Sheridan & Humphreys,

1993) and other patients show the opposite deficit (e.g., Hillis & Caramazza, 1991; Sacchi & Humphreys, 1992; Warrington & McCarthy, 1983, 1987). However, the cases of deficits recognizing living things far outnumber the reported cases of deficits recognizing nonliving things. This suggests that it is the processing of living things that is specialized, or at least more localized (Caramazza & Shelton, 1998).

A similar double dissociation has been observed with faces and objects, where patients with either acquired or congenital deficits with a condition known as prosopagnosia are impaired at recognizing faces, although recognition of other objects is relatively unimpaired (e.g., Duchaine, 2000; Farah, 1996; Farah et al., 1995). In very rare cases, when object recognition is impaired, face recognition can be spared (Moscovitch et al., 1997; Rumiati & Humphreys, 1997). Though rare, the existence of patients who show a selective impairment in a domain that is more frequently preserved is crucial to the modularity argument: Their existence refutes the idea that one domain (e.g., face perception) may simply be more difficult than another domain (e.g., object perception).

### Distributed Representations

Modular explanations of the mind and the brain capture the imagination and capture the attention of the press. The apparent discovery of brain modules responsible for recognizing body parts (Downing et al., 2001), intelligence (Duncan et al., 2000), and moral reasoning (Greene, Sommerville, Nyström, Dwyer, & Cohen, 2001) are covered by the press in much the same way as the discovery of a new dinosaur skeleton, a new planet, or a new bird species. Yet, neuropsychologists have long recognized significant challenges for inferring modularity from patterns of behavioral deficits caused by brain damage: Deficits result from large lesions that vary considerably between patients and the behavioral dissociations are rarely all that "clean." For example, in the case of the living/nonliving dissociation, the majority of patients possess deficits that cross the living/nonliving boundaries (Buckch, Bah, Masson, & Lindsay, 2004; Warrington & McCarthy, 1987; Warrington & Shallice, 1984). Similarly, prosopagnosic patients, whether acquired by brain damage or through congenital defect, often present with problems in air-free perception (Behrmann, Avidan, Marota, & Kimchi, 2005; Gauthier, Behrmann, & Tarr, 1999). A common interpretation of this pattern of results is that the lesions in most patients extend beyond the boundaries of a single module (e.g., Farah, 1990). And even if this is correct, it is clear that dissociations may be caused by a different modular organization from what might be apparent at first blush. For example, the living/nonliving dissociation

may actually represent modular organization along visual features versus functional features (Farah & McClelland, 1991; Warrington & Shallice, 1984). But another interpretation of double dissociations based on rare patients is that these rare patients are simply outliers who are not representative of the underlying population of brain structures. Unfortunately, brain insults happen on a daily basis. Yet, category-specific deficits occur in just a tiny fraction of cases. Simulated brain damage in neural networks that have no modular organization whatsoever can yield a small number of cases that appear to suggest modularity (Plaut, 1995). If modules exist, then we should expect double dissociations. But double dissociations are not sufficient to prove the existence of modules (Shallice, 1988). This makes it necessary to use converging evidence from many techniques to help interpret patterns of deficits.

Category representations can be fairly distributed and overlapping in the brain yet brain damage can produce, in some rare cases, quite selective deficits that suggest modularity. There is now considerable evidence that the representations of different categories are distributed and overlapping. In a classic study, Haxby et al. (2001) found that objects from different categories elicit replicable (and partly overlapping) patterns of activation across the entire ventral temporal cortex, rather than selective activation in a localized region. Subjects in the scanner were shown images of objects from various categories such as faces, houses, bottles, cats, and shoes. The pattern of activity for these categories over thousands of voxels was found to replicate between two halves of the data set, demonstrating how one could decode what a subject is seeing from the brain activity alone. This demonstration led many scientists to consider the importance of more distributed patterns of cortical activity. Some of the most exciting methods for analyzing fMRI data were inspired by that work (Kamitani & Tong, 2005; Norman, Polyn, Detre, & Haxby, 2006). Nonetheless, other researchers still emphasize the significance of the maximal response elicited in a specific brain area rather than the distributed pattern (Op de Beeck, 2008; Spiridon & Kanwisher, 2002). While the finding of distributed and partly overlapping maps for different categories is generally accepted, what remains vigorously debated is whether all categories are represented in this manner or if some special categories, such as faces, are much more localized (Hasson & Halchenko, 2008; Spiridon & Kanwisher, 2002).

That category representations are distributed within the visual system may seem even less surprising when considering evidence that categories are in fact distributed over the whole brain. For instance, according to Barsalou's (1999) perceptual symbol systems theory (Barsalou, 2008; Martin, 2007), concepts are represented in the collection

of modal systems for perception and action, rather than amodal symbols. Concepts, even abstract concepts, are thought to recruit a distributed representation across the brain because information from different sensory modalities is stored in modality-specific systems. When participants engage in a verbal conceptual task with words from different categories (e.g., animals and tools), the resulting activation is highly similar to the patterns evoked by the presence of physical objects from different categories (Chao et al., 1999). Modality-specific information associated with a concept appears to be automatically engaged, regardless of the task.

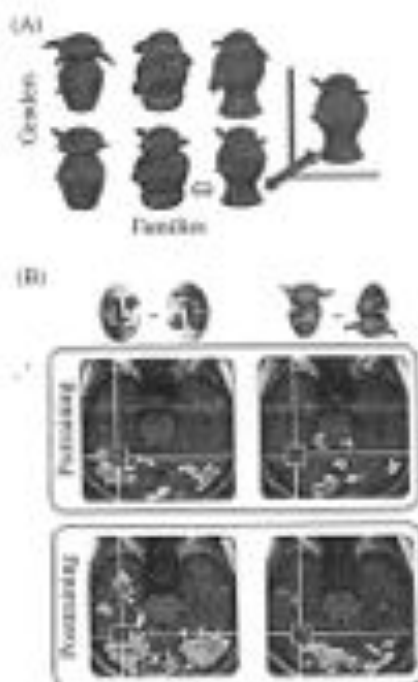
Such findings are relevant to the interpretation of studies where objects from different categories are contrasted. Not only do objects from the same category look alike, but they are likely associated with similar semantic knowledge. These associations influence the pattern of brain activity observed in response to the presentation of the object. This was demonstrated in a study where arbitrary semantic information was associated with novel objects through a short training task, and where these features appeared to be engaged automatically upon object perception (T. W. James & Gauthier, 2003). Outside of the scanner, objects were first associated with verbal labels describing auditory features (e.g., “whistles,” “hisses”) or motion features (e.g., “hops,” “crawls”). Later in the scanner, subjects performed visual matching judgments on pairs of objects. Strikingly, modality-specific cortices (the auditory cortex and an area that responds to biological motion) were engaged automatically based on prior associations that were completely irrelevant to the visual matching task. If these effects can emerge after a short training procedure, there could be a challenge in interpreting patterns of selectivity to visually presented familiar objects that subjects have acquired a lifetime of associations. Cats and faces and bottles have different shapes and they are also associated with different semantic information, making it difficult to know whether the distributed object maps in the visual system are maps of shape per se or maps of other dimensions (Op de Beeck, 2008).

### Experience and Expertise

Another alternative to a modular account for how different categories are represented in the brain is that the observed cortical representation of categories represents the interaction between processing biases in the cortex and the varied task demands associated with the objects. One specific account, the process map hypothesis (Gauthier, 2000), argues that category-selectivity reflects the automatization of strategies that are learned during experience with a category. Automatic strategies associated with category membership could produce patterns of category-selectivity

in the brain even if there were no maps of object shape or of object categories. This could happen if the ventral temporal cortex shows organization that reflects intersecting gradients in processing. For example, a gradient of eccentricity exists over the topographic extent of the visual cortex in the temporal lobe, and a continuum from local parts to holistic representations has been proposed (Hasson, Levy, Behrmann, Hendler, & Malach, 2001; Lerner, Hendler, Ben-Bashat, Harel, & Malach, 2001). Whatever the nature of the underlying dimensions relevant to processing (and they are largely unknown), the general idea is that any point in such a map would be unique and best suited to learn a specific visual categorization task. For instance, faces have to be identified at the subordinate level, and for that purpose, metric relations between parts (also called configural information) appear to be particularly useful (Tanaka & Sengco, 1997; Young, Hellawell, & Hay, 1987). Training at the subordinate level encourages participants to use a more “holistic” strategy (Diamond & Carey, 1986), in which participants find it more difficult to ignore task-irrelevant parts of the object (Young et al., 1987). The process-map hypothesis suggests that faces come to engage the fusiform face area (FFA) because it is best suited for holistic processing, the default mode of processing for faces, and predicts that other objects recognized using the same strategy, regardless of their shape, should also engage the same area.

This prediction was first tested in a perceptual expertise training study with a set of artificial stimuli called “Greebles.” Greebles were designed to replicate some critical aspect of faces, such as the fact that they share a small number of parts in a common configuration (Figure 20.6). The training was modeled after the constraints of face recognition and other types of real-world expertise. That is, subjects learned to categorize Greebles in families and to name individual Greebles and to discriminate them from other visually similar Greebles, as we do every day with faces. Training continued until subjects were as quick to categorize Greebles at the individual level as they were at categorizing them at a more abstract “family” level. Fast individuation is a hallmark of expertise in real-world domains (e.g., Tanaka & Taylor, 1991). Behavioral studies of Greeble training showed that these objects were processed more like faces following training. In particular, Greeble experts processed Greebles more holistically, finding it difficult to selectively attend to part of these objects (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). A comparison of brain activity before and after Greeble training revealed an increase of activity for upright Greebles in face-selective areas in the occipital lobe (what is now called occipital face area or OFA), the mid-fusiform face area (FFA; Figure 20.6) and a face-selective region of the anterior



**Figure 20.6** (Figure C.28 in color section) **A:** Examples of the Greble objects used in the Gauthier and Tarr (1997), Gauthier et al. (1998), Gauthier and Tarr (2002), and Gauthier, Behrmann, et al. (1999) expertise studies. **B:** Average fMRI results before and after Greble expertise training.

**Note:** (A) Greble objects share a general configuration of parts, and their set is organized hierarchically with two genders (defined by all parts pointing up versus down) and several families (differed by body shape). Training required subjects to learn to discriminate Grebles of the same gender and family (red arrow) as far as they could discriminate two objects from different families (yellow arrow). (B) The highlighted region is centered on the FFA. Red and yellow areas responded more to upright than upside-down stimuli, while blue to purple areas responded more to upside-down images. Upright faces elicit more activity in this area than upside-down faces. However, the same effect is only observed for Grebles after expertise training with upright Grebles. From Gauthier, Tarr, Anderson, Skuffarski, & Gore (1998). Adapted with permission.

temporal lobe (Gauthier, Tarr, Moylan, Anderson, & Gore, 2000). Later work showed that behavioral increases in configural processing were correlated with changes of activity in the FFA across subjects (Gauthier & Tarr, 2002). The Greble work suggests that changes in the way that a category is processed with the acquisition of perceptual expertise are critical in recruiting specific areas of the ventral temporal cortex for its processing.

The recruitment of the FFA in expert perception has been confirmed in studies of real-world expertise with cars or birds, where the degree of FFA activity in response to images of cars, for example, shows a very strong correlation with a behavioral measure of expertise over several independent experiments (Gauthier, Skuffarski, Gore, & Anderson, 2000; Gauthier, Curby, Skuffarski, & Epstein,

2005; Xu, 2005). As might be predicted based on such results, individuals with Autism, who show abnormalities in face processing that can be apparent early in development (e.g., Klin & Jones, 2008), show reduced selectivity in faces in the fusiform gyrus (e.g., Hahl et al., 2003; Pierce, Müller, Ambrose, Allen, & Courchesne, 2001; Schultz et al., 2000). Consistent with the idea that this hypoactivity is due to a lack of expertise, a boy with Autism who acquired perceptual expertise with Digimon cartoon characters showed specialization for Digimon but not faces in the fusiform gyrus (Grelotti et al., 2005). Finally, consistent with an expertise account of face-selective effects, the N170 face-selective ERP component is larger in amplitude for various nonface homogeneous objects in expert observers (Busey & Vanderkolk, 2005; Gauthier, Curran, Carby, & Collins, 2005; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; J. W. Tanaka & Curran, 2001).

However, extensive practice with a category does not always recruit face-selective areas. A handful of fMRI training studies with object categories have been conducted and have led to inconsistent results in terms of the specific regions engaged. With close examination of the particulars of these studies, this inconsistency may not be surprising given that the studies varied greatly on several dimensions, including object geometry, amount of training, and the specific training task practiced by subjects (Jiang et al., 2007; Moore, Cohen, & Ramgoban, 2006; Op de Beeck, Baker, DeCarlo, & Kanwisher, 2006; Xue & Poldrack, 2007; Yee, Tjan, & Biederman, 2006). Despite these differences, one region, the lateral occipital complex, is a more consistent locus of change across studies, suggesting that it may be more sensitive to exposure to a category than to the specific constraints of the training. Human ERPs and recordings in monkeys reveal that responses to objects can change in the ventral occipital cortex due to mere exposure (Prinzig, Singer, Kawasaki, & Sheinberg, 2007; Scott, Tanaka, Sheinberg, & Curran, 2006). In contrast, the FFA may be more important when experts process objects holistically, a strategy that was only assessed directly in the Greble training study. The adoption of a holistic strategy by subjects was suggested in one study (Moore et al., 2006) where training led to an inversion effect (inversion disrupts holistic processing with faces; Tanaka & Sengco, 1997; Young et al., 1987) and in that study, a small training effect was obtained in the FFA. Clearly, there are domains of expertise with visual categories, such as print, that do not rely on configural perception and lead to specialization outside of the face-selective system (McCardell, Cohen, & Dehaene, 2000). Thus, exposure with objects may be enough to produce some changes in the visual system (Freedman, Riesenhuber, Poggio, &

Miller, 2006) but there may also be a record of the manner in which experience with a category is acquired, in terms of the perceptual strategy and neural substrates that come to be automatically engaged by category members.

Our ability to interpret patterns of differences across training studies is seriously limited by the fact that fMRI training studies almost never compare two types of trainings with the same object category. Wong (2007) trained two groups of subjects with the same set of objects. One group learned to individuate objects as in Greeble training, while the other group was given equal exposure to objects but learned to classify them rapidly at the basic level. Only the individuation group demonstrated a switch to configural processing and an increase of activity near the FFA, with the behavioral and neural changes correlated across subjects. In contrast, rapid basic-level processing led to changes in more lateral areas of the occipito-temporal cortex, near the standard visual word form area. This work is unique in contrasting different types of experiences for the same category, as the majority of fMRI studies contrast different object categories, leading to effects that can be interpreted as indicating that the pattern of selectivity in ventral temporal cortex codes for variations in the shape of objects. Although there is no question that objects with similar shapes tend to recruit similar neural substrates in the same subject, which part of the neural network is recruited for objects with a given geometry in a given individual may be to some extent determined by experience processing objects from that category.

Computational modeling supports the claim that the FFA is a subordinate-level, fine-grained visual discrimination area, whose main feature is performing transformations that magnify differences between highly similar visual items (Joyce & Cottrell, 2004). Tong, Joyce, and Cottrell (2007) first trained neural networks to discriminate several basic-level categories (e.g., cups, Grebbles, and cans). “Expert” networks were additionally trained to discriminate items within one of these categories at the subordinate level. In the second phase, the learned weights from the first phase of training were saved, and both the basic-level and expert-level networks were trained on new subordinate-level discriminations. Results showed that although in the first phase basic-level discriminations were learned more quickly than subordinate-level discriminations, once the “expert” network was trained, learning new subordinate-level discriminations occurred more rapidly for the expert network than the basic-level network. This suggests that a neural network trained to perform subordinate-level discriminations on one class of objects shows an advantage in learning a new class at the subordinate level—because of extensive early experience with faces,

the FFA becomes a skilled subordinate-level classifier for faces that is later recruited by other domains of visual expertise.

So far we have only considered the case of expertise for objects in homogeneous categories such as faces, cars, and birds, where the goal is rapid individuation. Recent work has also explored expertise for letters and words. In contrast to faces, birds, and cars, which are typically individuated at the subordinate level by experts, for letters the goal of experts is basic-level categorization (an A is an A regardless of changes in font or style; Wong & Gauthier, *in press*). However, to facilitate reading, one wants to rapidly perceive a sequence of items to make a word. This is made easier by regularity in font style—it is easier to READ THIS than it is to rEaD tHiS (Sanocki, 1987, 1988). Furthermore, this effect is not limited to Roman characters: Chinese readers are faster to serially scan a matrix of Chinese characters for targets when the characters are all in the same font, whereas subjects who do not read Chinese do not show this sensitivity to style (Gauthier, Wong, Hayward, & Cheung, 2006). Such sensitivity to font is one example of a perceptual strategy that is more useful for letter perception than for the processing of most other categories.

Neurally, several brain regions have been implicated in letter and word expertise: The visual word form area (VWFA; Cohen et al., 2000) responds more to words and pseudowords than nonpronounceable consonant strings. Surprisingly, this area does not show visual selectivity for letters or letter strings, for instance it is equally recruited by strings of Chinese characters in non-Chinese readers (K. H. James et al., 2005). In contrast, visual selectivity for letter strings and single letters is obtained in other parts of the left fusiform gyrus (Flowers et al., 2004; K. H. James et al., 2005; Polk et al., 2002). These findings are not restricted to one particular character set because Chinese-character and Roman-character selective areas overlapped in Chinese-English bilinguals (Baker et al., 2007; Wong, Jobard, James, James, & Gauthier, *submitted*). The N170 ERP potential is also obtained for words or letter strings (Bentin, Deouell, & Soroker, 1999) and for letters or other characters of expertise (Wong et al., 2005). Because of its selectivity for two very different types of expertise, the N170 may be a general marker of expert processes that can be localized in different brain areas. Scott et al. (2006) compared different trainings with bird categories revealing that both basic- and subordinate-level training enhanced the early N170 component, but only subordinate-level training amplified a later N250 component. Further comparisons of trainings in both ERP and fMRI could lead to a better understanding of the dynamics of perceptual expertise.

### High-Resolution Imaging and Competition Studies

In recent years, two different lines of research offer new data for interpreting category selectivity in the FFA. The first uses high-resolution imaging in an attempt to separate patterns of responses to faces and objects, while the second attempts to measure neural (and behavioral) competition that could result from functional overlap.

Standard fMRI has a resolution around 3 mm<sup>3</sup>. At that resolution, each voxel (3D pixel) in the FFA yields a maximal response to faces and a nonzero response to nonface objects. Recent work using higher resolution imaging looked "inside the voxel" to reveal the functional organization of the FFA at a finer spatial scale (1-mm<sup>3</sup>; Grill-Spector, Sayres, & Ress, 2006); this represents a 27-fold increase in resolution. The results revealed that all voxels were maximally selective to faces, but highly face-selective voxels are intermingled with voxels that also showed comparable responses for at least some nonface category, such as animals or cars. The reproducibility of face-selectivity at a finer scale in the FFA is consistent with single-cell recordings in macaque monkeys, within face-selective regions identified by fMRI where 97% of cells are found to be face-selective (Tsao et al., 2006). Analyses in a prior expertise study with car and bird experts had revealed that the single most face-selective FFA voxel at standard resolution showed a clear expertise effect (Gauthier, Skudlarski, et al., 2000), which suggests that expert object responses in the FFA would overlap with face-selectivity at high-resolution, and perhaps even at the single-cell level.

If a considerable number of neurons in the fusiform gyrus are selective for both faces and objects of expertise, interference between these two domains may be expected in some situations. There could also be interference between face and object perception even if there were no shared neurons, as long as the two populations were strongly interconnected. In other words, instead of focusing on spatial overlap, one can address functional overlap: Is face perception functionally independent from the perception of nonface objects, especially for cases of expertise where a face-like configural strategy is recruited? In one study (Gauthier et al., 2003), subjects with a range of car expertise saw a sequence of faces alternating with cars. Each car or face was made out of two parts (top and bottom) and subjects selectively attended to the bottom of these images and made 1-back judgments for both categories; in this way, the degree of holistic processing could be measured for both categories. In this dual task situation, car experts processed cars more holistically than car novices and processed faces *less* holistically in the context of cars: Simultaneous processing of faces and cars by car experts

appears to create a competition for common resources. This behavioral interference was correlated with the magnitude of the N170 face-selective ERP potential (see also Rossion, Kung, & Tarr, 2004; Rossion, Collins, Goffaux, & Curran, 2007). In more recent work, competition between car and face perception was also obtained in tasks where the cars were completely task-irrelevant (McKeeff, Tong, & Gauthier, 2007; Williams, 2007). Competition between face perception and objects of expertise suggests one or more functional bottlenecks in the brain for configural processing, and because the FFA responds to both faces and objects of expertise, it is tempting to assume that the FFA is one such bottleneck. This is difficult to verify with fMRI at standard resolution because the response to cars and faces cannot be separated, but this could be addressed in future work using high-resolution imaging.

### SUMMARY

Understanding how objects are categorized is a complex challenge that requires bridging the study of visual perception and visual cognition and cannot be studied without also considering how objects are perceived, identified, and remembered (Palmeri & Tarr, 2008). To date, different aspects of this problem, such as the format of visual object representations and the principles that govern decisions about the categories to which these objects belong, have been explored in separate fields. But more than once, such as on the issue of abstraction or modularity, these independent lines of research have faced similar debates or reached similar conclusions (Palmeri & Gauthier, 2004). The advent of cognitive neuroscience, which provides evidence and constraints from techniques as diverse as psychophysics, brain imaging, neuropsychology, and neurophysiology, may help blur old boundaries between approaches to produce more complete models of object categorization.

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