Functional specificity in the human brain: A window into the functional architecture of the mind

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Is the human mind/brain composed of a set of highly specialized components, each carrying out a specific aspect of human cognition, or is it more of a general-purpose device, in which each component participates in a wide variety of cognitive processes? For nearly two centuries, proponents of specialized organs or modules of the mind and brain—from the phrenologists to Broca to Chomsky and Fodor—have jousted with the proponents of distributed cognitive and neural processing—from Flourens to Lashley to McClelland and Rumelhart. I argue here that research using functional MRI is beginning to answer this long-standing question with new clarity and precision by indicating that at least a few specific aspects of cognition are implemented in brain regions that are highly specialized for that process alone. Cortical regions have been identified that are specialized not only for basic sensory and motor processes but also for the high-level perceptual analysis of faces, places, bodies, visually presented words, and even for the very abstract cognitive function of thinking about another person's thoughts. I further consider the as-yet unanswered questions of how much of the mind and brain are made up of these functionally specialized components and how they arise developmentally.

brain imaging | modularity | functional MRI | fusiform face area

Understanding the nature of the human mind is arguably the greatest intellectual quest of all time. It is also one of the most challenging, requiring the combined insights not only of psychologists, computer scientists, and neuroscientists but of thinkers in nearly every intellectual pursuit, from biology and mathematics to art and anthropology. Here, I discuss one currently fruitful component of this grand enterprise: the effort to infer the architecture of the human mind from the functional organization of the human brain.

The idea that the human mind/brain is made up of highly specialized components began with the Viennese physician Franz Joseph Gall (1758–1828). Gall proposed that the brain is the seat of the mind, that the mind is composed of distinct mental faculties, and that each mental faculty resides in a specific brain organ. A heated debate on localization of function in the brain raged over the next century (*SI Text*), with many of the major figures in the history of neuroscience weighing in (Broca, Brodmann, and Ferrier in favor, and Flourens, Golgi, and Lashley opposed). By the early 20th century, a consensus emerged that at least basic sensory and motor functions reside in specialized brain regions.

The debate did not end there, however. Today, a century later, two questions are still fiercely contested. First, how functionally specialized are regions of the brain? The concept of functional specialization is not all or none but a matter of degree; a cortical region might be only slightly more engaged in one mental function than another, or it might be exclusively engaged in a single mental function. Many neuroscientists today challenge the strong (exclusive) version of functional specialization. As one visual neuroscientist put it, "each extrastriate visual area, rather than performing a unique, one-function analysis, is engaged, as are most neurons in the visual system, in many different tasks" (1).

The second ongoing controversy concerns the question of whether only basic sensory and motor functions are carried out in functionally specialized regions, or whether the same might be true even for higher-level cognitive functions. Although one might think that Broca settled this matter with his demonstration that the left frontal lobe is specialized for aspects of language, the current status of this debate is far from clear. Indeed, a recent authoritative review of the brain-imaging literature on language concludes that "areas of the brain that have been associated with language processing appear to be recruited across other cognitive domains" (2). The case of language is not unique. Indeed, a backlash against strong functional specialization seems to be in vogue. A recent neuroimaging textbook argues that "unlike the phrenologists, who believed that very complex traits were associated with discrete brain regions, modern researchers recognize that . . . a single brain region may participate in more than one function" (3).

In this review, I address these ongoing controversies about the degree and nature of functional specialization in the human brain, arguing that recent neuroimaging studies have demonstrated that at least a few brain regions are remarkably specialized for single high-level cognitive functions. To make my case, I first describe three candidates for such functionally specific brain regions identified in my lab. I then consider how much of the brain is made up functionally specialized regions: are they found only for high-level perceptual functions or also for components of abstract thought? I then ask how these regions arise developmentally; that is, what are the exact roles of genes and experience in the development of these regions? In *SI Text*, I address a key challenge to the specificity of the fusiform face area (FFA) and parahippocampal place area (PPA), and I consider the computational advantages that may be afforded by specialized regions in the first place. I conclude by speculating that the cognitive functions implemented in specialized brain regions are strong candidates for fundamental components of the human mind.

Neuroimaging Evidence for Functional Specialization in the Ventral Visual Pathway

Ever since Broca, neurologists and cognitive neuroscientists have investigated cognitive impairments in people with focal brain lesions, providing extensive evidence for localization of at least some functions in the human brain. The study of neurological disorders is one of the few methods that allows powerful inferences about not just the engagement but also the necessity of a given brain region for a specific cognitive function in humans. However, even if a particular functionally specific region exists, a lesion is unlikely to affect all and only that region, so clean functional dissociations in the patient literature are rare. Brain imaging [and functional MRI (fMRI) in particular] thus provides

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a powerful complement to lesion studies, allowing neural activity in the normal human brain to be monitored safely and noninvasively at resolutions approaching the millimeter range. The principle underlying fMRI is that blood flow increases locally in active regions of the brain. Although the precise neural events that fMRI reflects are a matter of ongoing research, the general validity of the method as an indicator of neural activity is clear from studies replicating, with fMRI, the properties of visual cortex previously established by the gold-standard method of single-neuron recording in monkeys. Thousands of papers have used fMRI to ask about the relative contributions of different regions in the human brain to a wide variety of cognitive functions. My lab has focused especially on the question of whether any of these brain regions are specifically engaged in a single high-level cognitive function.

Supporting the idea that some brain regions are indeed engaged in specific mental functions, we have identified a number of cortical regions (Fig. 1) that respond selectively to single categories of visually presented objects: most notably, the FFA, which responds selectively to faces (4, 5), the PPA, which responds selectively to places (6), and the extrastriate body area (EBA), which responds selectively to bodies and body parts (7).

These three brain regions are not the only ones that have been argued to conduct specific perceptual functions (8). Probably the strongest other case is visual area MT/V5, shown much earlier with neurophysiological methods to play a key causal role in the perception of visual motion in monkeys (9–11), and later, identified in humans with brain imaging (12, 13). However, even this classic example of functional specificity does not process visual-motion information exclusively; this area also contains information about stereo depth (14). Another strong case of functional specificity for a simple visual dimension is color (15), for which recent evidence from both fMRI and single-unit recording indicates the existence of multiple millimeter-sized color-selective "globs" in posterior inferotemporal cortex in macaques (16, 17). Other brain regions have been reported to be selectively engaged in processing information about biological motion (18), visually guided reaching (19), and grasping (20). For most cases in the neuroimaging literature, however, the main claim is one of regional specificity (i.e., that the implicated function activates this region more than other brain regions) rather than of functional specificity (i.e., that the implicated region is more engaged for this function than other functions). In contrast, this article focuses primarily on the question of functional specificity, because this is the question that is critical for understanding the architecture of the human mind (Fig. 1).

The evidence we and others have collected on the FFA, PPA, and EBA provides unusually strong support for functional specificity of these regions for three reasons. First, each of these regions has been found consistently in dozens of studies across many labs; although their theoretical significance can be debated, their existence cannot. Indeed, these regions are found, in more or less the same place, in virtually every neurologically intact subject; they are part of the basic functional architecture of the human brain. Second, the category selectivity by which each region is defined is not merely statistically significant, but also large in effect size: Each of these regions responds about twice as strongly to stimuli from its preferred category as to any nonpreferred stimuli.* Although effect size is generally ignored in the brain imaging literature, it should not be, as it determines the strength of the inference you can draw: If you know how to double the response of a region, you generally have a better handle on its function than if you merely know how to change its response by a small amount. Third, the fact that these regions can be found easily in any normal subject makes possible a "region of interest" (ROI) research strategy whereby the region is first functionally identified in each subject individually in a short "localizer" scan, and then the response of that region is measured in any number of new conditions that test specific hypotheses about its exact function. It is precisely the fact that the responses of the FFA, PPA, and EBA have been quantified in each of now dozens of different stimulus and task manipulations that enables us to say with confidence that each of these regions is primarily, if not exclusively, engaged in processing its preferred stimulus class (faces, places, and bodies, respectively). Taken together, these three regions constitute some of the strongest evidence that at least some cortical regions are selectively engaged in processing specific classes of stimuli. Next I summarize the evidence for the specificity of each of these regions for a particular class of stimuli.

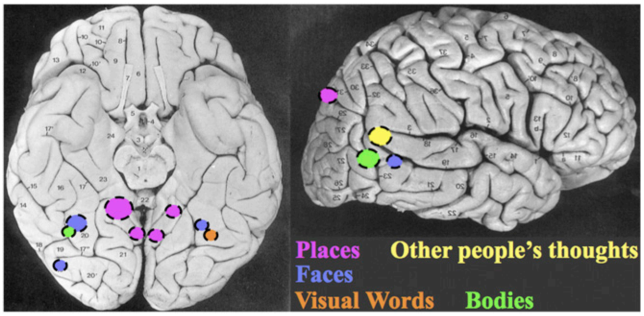

Fig. 1. This schematic diagram indicates the approximate size and location of regions in the human brain that are engaged specifically during perception of faces (blue), places (pink), bodies (green), and visually presented words (orange), as well as a region that is selectively engaged when thinking about another person's thoughts (yellow). Each of these regions can be found in a short functional scan in essentially all normal subjects.

FFA. The FFA is the region found in the midfusiform gyrus (on the bottom surface of the cerebral cortex just above the cerebellum) that responds significantly more strongly when subjects view faces than when they view objects (4, 5, 23). This region responds similarly to a wide variety of different kinds of face images (24), including photos of familiar and unfamiliar faces, schematic faces, cartoon faces, and cat faces as well as faces presented in different sizes, locations, and viewpoints (25, 26). Crucially, when relatively high-resolution imaging methods are used (including individual–subject analyses without spatial smoothing), no nonface object has been reported to produce more than one-half the response found for faces in this region. Further, the evidence (27, 28) allows us to reject alternative hypotheses proposed earlier that the FFA is not specifically responsive to faces but rather is more generally engaged in fine-grained discrimination of exemplars of any category or of any category for which the subject has gained substantial expertise. Importantly, the magnitude of the FFA response is correlated trial by trial with success both in detection of the presence of faces and in identification of individual faces (29, 30). Thus, as discussed further in *SI Text*, the FFA seems to play a central role in the perception of faces but to play little if any role in the perception of nonface objects. This hypothesis is consistent with evidence that (*i*) face-selective responses have been observed in approximately this location in subdural electrode recordings from the brains of subjects undergoing presurgical mapping for epilepsy treatment (31–33) and (*ii*) lesions in approximately this location can produce selective deficits in face perception (34).

Answering the question of what exactly the FFA does with faces has been more difficult. Current evidence indicates, however, that it is sensitive to multiple aspects of face stimuli including face parts

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*fMRI response magnitudes are typically measured as percent signal increases compared with a low baseline condition (e.g., fixating on a cross), so a 2-fold response difference might correspond to a 2% signal increase from fixation versus a 1% signal increases from fixation. Crucially, the magnitude of selectivity must be evaluated using data independent of that used to identify the region (21, 22). Selectivity is underestimated when low-resolution methods are used (e.g., when voxels are large or when spatial smoothing or group analyses are used).

(eyes, noses, and mouths), the T-shaped configuration of those features, and external features of faces like hair (35) and that representations extracted in the FFA show some invariance across changes in stimulus position and less invariance across changes in viewpoint (25), mirroring comparable behavioral results. The FFA further exhibits neural correlates of long-known behavioral signatures of perception (28), including disproportionate inversion effects (36) and sensitivity to holistic information in upright but not inverted faces (37). Despite these initial insights, important open questions about the FFA remain to be addressed, including a more precise characterization of the representations that it extracts and the computations that it performs, whether it plays some (albeit lesser) role in the perception of any nonface objects, whether it is cytoarchitectonically distinct from its neighbors, what other regions it is connected to, whether and how interactions with other regions modulate or participate in the computations conducted in the FFA and whether it constitutes a single contiguous region on the cortical surface.

PPA. The PPA is defined functionally as the region adjacent to the collateral sulcus in parahippocampal cortex that responds significantly more strongly to images of scenes than objects (6). The PPA responds to a wide variety of scenes, including indoor and outdoor scenes, familiar and unfamiliar scenes, and even abstract scenes made of Legos (38, 39). The PPA is primarily responsive to the spatial layout of one's surroundings: its response is not reduced when all of the objects are removed from an indoor scene, leaving just the floor and walls (6). This response profile is tantalizingly reminiscent of the geometric module (40, 41), inferred from behavioral data in which rats and human infants (and adults whose language system is tied up by a concurrent verbal task) rely exclusively on the layout of space, not on objects or landmarks, to reorient themselves in an environment after they are disoriented. Evidence that the PPA is not only activated when information about spatial layout is processed, but that it is further necessary for this function, comes from patients with damage in or near the PPA, who have difficulty encoding information about spatial layout and more generally, in knowing where they are (42, 43). The precise role of the PPA in place perception and navigation is a topic of ongoing investigation (38, 39).

EBA. The EBA is a region on the lateral surface of the brain adjacent to (and sometimes partly overlapping with) visual motion area MT, which responds significantly more strongly to images of bodies and body parts than to images of objects or faces. This region responds equally to visually very different images of bodies and body parts, from a photograph of a hand to a photograph of a body (human or animal) to a schematic stick figure of a person. Evidence that this region is not only activated during but is also necessary for the perception of bodies comes from studies in which disruption of the EBA by a brain lesion (44) or transcranial magnetic stimulation (TMS) (45, 46) impairs the perception of body form but not the perception of faces or object shape (45). Further, current evidence indicates that the EBA is more involved in perceiving other people's bodies than one's own (47, 48) and that it is more engaged in the perception of the form/identity of bodies than in the actions they are carrying out (44, 49–51).

Ovals, Gradients, or Archipelagoes? For simplicity, I have discussed functionally specific regions in the cortex as if they are discrete entities with sharp, well-delineated edges, like the kidney, liver, and heart. Indeed, some functional divisions in the cortex are remarkably sharp, such as the border between retinotopic visual areas V1 and V2. However, there is no reason to assume all functional distinctions in the brain have perfectly sharp edges. Similarly, there should be no requirement that these regions must be simple convex shapes. Irregular-shaped regions with long tendrils or even multiple nonadjacent but nearby (and presumably connected) subregions might be expected. If it becomes clear at higher resolutions that the FFA is in fact a set of distinct noncontiguous regions (a "fusiform face archipelago"?), that will strain the organ analogy but still leave viable a meaningful sense in which these noncontiguous patches constitute a functionally distinct system, much as Maui and Lanai share deep geological, biological, and cultural similarities in virtue of being part of the Hawaiian islands, despite the channel of water between them. However, the more a region turns out to be extensively interdigitated with other functionally distinct entities and the more its borders resemble an arbitrary cutoff point on a gradual functional change across the cortex (52), the less this case will follow the classic idea of a functionally distinct brain region. Most questions about biological systems are matters of degree, and so too is the question of functional specialization in the cortex. Currently available evidence suggests an impressive degree of compartmentalization in at least a few cortical regions (53). Further experiments using new tasks and higher resolution will provide more precise quantitative tests of the anatomical distinctness of these regions.

In sum, evidence is now strong that each of at least three cortical regions in humans are selectively (perhaps even exclusively) engaged in specific cognitive functions: the FFA in representing the appearance of faces, the PPA in representing the appearance of places, and the EBA in representing the appearance of bodies. (See *SI Text* for my reply to an important challenge to the functional specificity of these regions.) Although I have emphasized the role of each of these regions in visual perception, their response is not determined solely by the stimulus that the subject is viewing. The activity of these regions can be strongly modulated by visual attention (54), and they can even be activated when no stimulus is present at all. Simply imagining a face (with eyes closed) selectively activates the FFA and imagining a place activates the PPA (55).

Of course, no complex cognitive process is accomplished in a single brain area, and arguments for the specificity of these regions by no means imply that other brain regions play no role. Earlier cortical regions such as primary visual cortex are obviously crucial in the perception of faces, places, and bodies, and higher areas (e.g., in parietal and frontal regions) are also probably necessary for information in the FFA, PPA, and EBA to be used by other cognitive systems and to reach awareness (56–58). Further, none of these regions is the only one with its defining selectivity. For faces, selective responses are found not only in the FFA but also in a nearby but more posterior occipital face area, as well as other regions in the superior temporal sulcus (34, 59), and anterior temporal pole (60). For bodies, selective responses are found not only in the EBA but also in the fusiform body area (FBA). For scenes, selective responses are found not only in the PPA but also in retrosplenial cortex (RSC) and the transverse occipital sulcus (TOS). These other selective regions have not been studied in the same detail as the FFA, PPA, and EBA, so their functions are less clear. Still, the existence of multiple selective regions for each of these three stimulus classes raises the exciting possibility that we may ultimately understand how the percept of a face, for example, emerges from the joint activity of a number of functionally distinct regions, each conducting a different aspect of the analysis of the face stimulus. In the subsequent sections of this article, I discuss four major questions raised by the work on the FFA, EBA, and PPA concerning their specificity, generality, origins, and computational significance.

Generality: How Much of the Brain Is Composed of Functionally Specific Regions?

The evidence for functional specificity within several brain regions (FFA, PPA, EBA) invites a return to the broader questions raised by Gall, Fourens, and Broca: how much of the brain is composed of regions that are selectively engaged in specific cognitive functions? We consider this question by asking whether other specialized brain regions exist for (*i*) other object categories in the ventral visual pathway and (*ii*) components of high-level thought.

Other Category-Selective Regions? Do we have cortical regions selectively involved in the perception of snakes? Weapons? Vegetables? As Pinker asks in *The Language Instinct*, does the brain have a produce section (61)? What about categories of objects that may not have been crucial to the survival of our ancestors but that play central roles in modern daily lives, like cars and cell phones? There hardly seems room in the brain for all of these categories, or even all of the important ones, and it is not clear what would be accomplished computationally by such extreme compartmentalization anyway. Happily, we are not restricted to mere speculation; we can simply test empirically for other specialized brain regions. Downing and I did just that (62), screening broadly for 20 different categories of objects selected for their (arguable) evolutionary importance (spiders and snakes, predators, prey, tools, food), their experiential frequency in modern life (cars, chairs), or their implication from prior studies of patients with focal brain damage (fruits and vegetables, musical instruments). Despite replicating the existence of cortical regions selective for faces, places, and bodies in each subject, we found no evidence of cortical specialization for any of the other object categories tested. The previously reported selectivity for tools (63) was not evident in our data, and any partial dissociations between responses to living and nonliving things (or animate versus inanimate objects) were restricted to the already documented properties of the face, place, and body areas. Although null results can always be trumped by later discoveries made with higher spatial resolution or greater statistical power, the resolution and power that was sufficient for robust replication of the FFA, PPA, and EBA did not turn up any new category-specific regions.

A central conceptual puzzle arises, however, in the search for brain regions selective for new object categories: how do we decide which categories to test? If we proceed by testing only the categories that seem plausible to us, then we risk getting trapped within the confines of our own theoretical preconceptions. This concern is underscored by the fact that the brain specializations already described for faces, places, and bodies are reminiscent of two of the mental faculties proposed by Gall: the sense of people, and the sense of place. Given that Gall arrived at these categories without real evidence, the fact that we have arrived at the same categories is worrisome. Are we, like the phrenologists, allowing our cultural biases to determine what we find in the brain? Are specializations we discover in the brain a kind of high-tech projective test?

With rigorous experimental methods, we can reduce the chance that the outcomes of our experiments are determined by our cultural/theoretical predispositions. However, how can we ever prevent our conceptual baggage from biasing the space of hypotheses that we consider? My colleagues and I are developing methods to circumvent these biases by searching for structure in the functional responses of the ventral visual cortex in a hypothesis-neutral fashion (64–66). This method searches large datasets composed of the response of each voxel to a large number of stimuli and discovers dominant response profiles in that dataset. Importantly, the method knows nothing about the location of each voxel, so it makes no assumption that functionally related voxels are adjacent. Even more importantly, the method does not look only for selectivity for single-object categories but instead, for any profile of response across the stimuli that best characterizes a large number of voxels (e.g., a high response to all categories except one or a high response to one-half of the categories and a low response to the other one-half, etc.).

For our first test of this method, we scanned subjects while they viewed eight different categories of stimuli. Remarkably, the method spontaneously identified face-, place-, and body-selective response profiles among the top five most robust profiles (Fig. S1 and *SI Text*). Even more impressively, when we split the data in half to produce 16 different conditions (two per category), without telling the algorithm which pairs of conditions belonged to the same category, the algorithm discovered response profiles characterized by high responses to both face conditions compared with everything else, although these conditions were not labeled as the same category. We found the same for scenes and bodies. These results suggest that face, place, and body selectivity are not simply our own cultural projections onto the brain but are actually inherent in the brain's response to visual stimuli. Also, they suggest that we do not have similar specificity in the brain for lots of other categories; face, place, and body selectivity are probably special cases. We are now conducting a stronger test of this hypothesis by generating a larger set of stimuli more representative of human visual experience and asking whether face, place, and body selectivity still emerge from the data, even when no stimulus categories are presumed in advance and even when we do not start by constructing a stimulus set that contains a sizable proportion of faces, places, and bodies. It will be most exciting if this new test not only (re)discovers face, place, and body selectivity but also discovers new, previously unknown, response profiles.

Selective Cortical Regions for Aspects of Thought? Perhaps it is not surprising that discrete cortical regions can be found that are selectively engaged in processing specific aspects of high-level vision. After all, we are highly visual animals who allocate one-third of our cortex to various aspects of vision, and some division of computational labor within this broad expanse of cortex would seem to make sense. But what about the rest of cognition? Do we have specialized brain machinery for specific components of thought?

Indeed, we do. Several years ago, Rebecca Saxe made the astonishing discovery of a region at the junction of the temporal and parietal lobes of the right hemisphere that is selectively engaged when one thinks about what another person is thinking (67, 68). Using the ROI method, Saxe and colleagues (67, 68) have identified this region (known as the rTPJ) in hundreds of subjects and measured its response to a wide array of tasks. These data show that the rTPJ responds strongly when people read scenarios that describe what a person knows or thinks but not when people read scenarios describing physical, as opposed to mental, representations (e.g., in maps or photographs) or vivid descriptions of a person's physical appearance that do not refer to the contents of the person's mind. This region is so selective that it does not even respond when people think about another person's bodily sensations (e.g., thirst, hunger, pleasure), which are mental states but which do not have propositional content like thoughts and beliefs. Most impressively, this region is more strongly activated when people make decisions about what another person knows than when they make the identical response to the identical stimuli but do not construe the task as pertaining to another person's thoughts (69). The rTPJ is the most functionally selective high-level cortical region yet described in humans.

The discovery of the rTPJ, and the characterization of its functional specificity, serves as an existence proof that functionally specific cortical regions are not restricted to primary sensory and motor areas, or high-level perceptual regions, but can be found for at least one very abstract and high-level aspect of human cognition. This finding invites the question of whether other aspects of high-level cognition may also be computed in specialized cortical regions. Perhaps the most obvious case here is the one proposed by Gall and Broca: language. Surprisingly, despite two centuries of investigation, no consensus has emerged on the question of whether any brain regions are specialized for language (or components thereof). The problem arises in part from a conflict between the findings from studies of patients with focal brain lesions, which suggest considerable functional specificity of some cortical regions for some aspects of language, versus the findings from the large neuroimaging literature on language, which suggest considerable overlap between linguistic and nonlinguistic processing.

Evelina Fedorenko and I have argued that one possible explanation of the conflict between these two types of studies is that the methods that have been used in virtually all prior neuroimaging studies of language (group analyses) are not well-suited for detecting functional specificity. Group analyses underestimate functional specificity, because different individuals' brains are anatomically quite different from each other, so alignment across brains is necessarily imperfect. As a result, functionally different regions will sometimes be aligned to the same location in the group space (70, 71). Fedorenko and I are now revisiting the question of functional specificity of the language system using the same individual–subject ROI method that has enabled us to discover the functional specificity of the other regions described above.

Note that the failure to discover functionally specific brain regions for a given cognitive process can also be informative. Suppose, for example, that we discover that no brain region is selectively engaged in any aspect of language processing but rather that all regions that support language processing also contribute substantially to nonlinguistic functions. Such a discovery would offer powerful clues into what language is all about. Specifically, we would want to know: what are those nonlinguistic functions that overlap with (say) syntactic processing? What would it tell us about syntax, if it shares neural machinery with (say) music perception, social cognition, or arithmetic? Such possibilities illustrate the exciting prospect of discovering components of mind and brain defined not by the content of the information they operate on, but rather by the computational structure of the problems they solve. Indeed, evidence of domains of cognition that are not computed in cortical tissue selective for that function would offer clues about the broader questions of which mental functions get their own private patch of real estate in the brain, which do not, why some do and others do not, and what the computational advantages might be of functional specialization in the first place (discussed further in *SI Text*).

In some sense, the discovery and characterization of components of the mind and brain that are uniquely human are the most exciting. The fact that our minds and brains have a special circuit just for figuring out what another person is thinking tells us something deep about what it means to be a human being. If we are lucky enough to discover brain machinery specialized for other uniquely human cognitive abilities, such as syntax or a component thereof, it will provide a similarly thrilling insight into human nature. Further, such discoveries might enable us to trace the evolutionary origins of the function in question. For example, if we discover cytoarchitectonic or gene-expression markers for the brain region for understanding other minds, we could then look for the homologous region in primates and investigate its function.

Discovering functionally specific components of mind and brain that are not uniquely human, but that are shared with other animals, offers different scientific opportunities. Most current methods available with humans do not enable us to determine precisely the time course of engagement, the causal role, or the connectivity of a given cortical area. (Important exceptions are studies using TMS in normal subjects and electrodes implanted for surgical purposes in humans.) We cannot study in humans the development of a given region under controlled rearing conditions, and we have no good tools for studying the actual neural circuits that implement the cognitive ability in question. However, methods exist to answer all of these questions in nonhuman primates. Therefore, the discovery of functionally specific brain regions that are present in both humans and macaques, such as face- and body-selective regions, opens up fantastic opportunities to address the biological mechanisms of cognition in a way that is nearly impossible in humans. The discoveries (72) of face- and body-selective regions in macaque cortex and the investigation of these regions using the powerful tools of systems neuroscience (73–75) provide a stunning illustration of the insights that can be gleaned from work in primates on the neural machinery of high-level vision.

Origins: How Do Functionally Specific Regions Arise Developmentally?

Although it is obvious that genes and experience both play crucial roles in the development of all brain structures, it is less clear which of the precise details of the circuitry of each brain region are specified in the genome and which are derived from experience. At first glance, the existence of brain regions selective for faces, places, and bodies would seem to fit nicely with the view held by many of the most prominent advocates of modularity of mind and brain—from Gall to Chomsky, Fodor, and Pinker—that organs of mind and brain are innate (i.e., the products of natural selection). Indeed, it seems plausible that the rapid and accurate recognition of faces, places, and bodies had such survival value to our ancestors that detailed instructions for wiring up the specific neural circuitry of the FFA, PPA, and EBA may have become specified in the genome. However, alternative accounts are also plausible. Quite apart from the experience of our ancestors, each of us modern-day humans probably looks at (and attends to) faces, places, and bodies more frequently than almost any other stimulus class. Given that cortical organization can be affected by experience, the existence of regions specialized for processing these visual categories could result from the extensive experience each of us has with these categories during our lifetime, without any specific genetic predilection for these categories per se. Recent evidence, discussed next, suggests that the cortical machinery of face perception may be primarily genetically specified, whereas the selectivity of another nearby cortical region may be primarily determined by the individual's experience.

Specific Role of Genes in Face Perception. Until very recently, we had almost no relevant data on the degree to which the existence, location, and fine-grained circuit details of the FFA were genetically specified versus derived from experience, leaving the topic wide open for passion and polemic. In just the last few years, however, several new lines of evidence point to a specific role of genes in determining the neural machinery of face perception. First, a congenital disorder in face perception, developmental prosopagnosia, has been shown to run in families (76, 77). Second, face-perception ability is heritable (i.e., more strongly correlated for identical than fraternal twins), and this effect is independent of the heritability of domain-general abilities like IQ or global attention (78, 79). Third, the spatial distribution of fMRI responses across the ventral visual pathway to faces is more similar between monozygotic than dizygotic twins; the same is true for scenes but not for chairs or words (80). Although all three findings implicate genes in face-specific processing, they do not tell us which genes are involved or by what causal pathway they affect face perception. Perhaps these genes simply increase social interest and hence, experience with face perception, enhancing ability through training. Or perhaps they directly specify the detailed wiring of the neural circuits for face perception. Evidence that genes may be largely responsible for wiring up much of the face system, with little or no role of experience with faces, comes from recent reports that impressive face discrimination abilities are present in human newborns (81) and even in baby monkeys reared for up to 2 years without ever seeing faces (82). These findings support the hypothesis that the specific instructions for constructing the critical circuits for face perception are in the genome.

Note that despite this recent evidence that the face system can develop with little or no experience with faces (81, 82), it is nonetheless clear that experience with faces does affect the face-perception system. First, in the other race effect, psychophysical studies have demonstrated what most people know from daily life: we are better able to distinguish individuals from a more familiar than less familiar race (aka "they all look alike"). Second, in perceptual narrowing, face-discrimination abilities that are initially effective on face stimuli of all races or primate species become restricted within a few months of life to only the race/species that the subject has experienced (82–84). This tuning is entirely consistent with the view that the basic face-perception system can arise with virtually no face experience, even if it is subsequently fine tuned by experience, a phenomenon paralleled in language development (85, 86).

What do developmental studies in humans tell us about the origins of the face system? A long-standing view has held that face perception develops very slowly in humans, not reaching adult levels until adolescence or later (87, 88). Consistent with this view, several imaging papers (89, 90) have argued that the FFA increases in size through and even beyond adolescence. Some have suggested that this slow development implies that experience plays a critical role in constructing the face-perception system (89, 90). This conclusion does not follow, however, because some developmental changes that occur long after birth are primarily genetically, not experientially, determined (as in the case of puberty). Further, more recent behavioral results show that every aspect of face-specific perceptual processing tested so far (inversion effects, measures of holistic processing, etc.) is present at the earliest ages ever tested; several signatures of face processing are present within the first 3 days of life (91). Ongoing studies in our lab and others are finding adult-sized FFAs in the majority of children scanned at age 5 and 6 years. Thus, despite the widespread claims to the contrary, current developmental data do not argue for slow development of face-specific perceptual mechanisms.

In sum, although the precise roles of genes and experience in the construction of category-selective regions of cortex are not yet clear, several studies suggest that the face system may be largely innate: experience with faces may not be necessary for the initial development of the face-perception system, although experience apparently fine tunes it. Still, if new evidence strengthens this view, it would not necessarily imply that all functionally specific regions of cortex are constructed in the same way. Indeed, the functional selectivity of at least one region of the brain, the visual word form area, is derived from the individual's experience, not their genes, as discussed next.

At Least One Functionally Specific Cortical Region Derives Its Specificity from Experience. Visual word recognition provides a powerful test case of the origins of cortical selectivity. Everyone in our study population has extensive experience looking at visually presented words, so if experience is ever sufficient to specify the selectivity of a cortical region for a particular class of stimuli, we would expect to find one for visual words. However, crucially, human beings have only been reading for a few thousand years, which is not thought to be long enough for the evolution of a complex structure. Thus, if a brain region is found that responds selectively to visually presented words, that would suggest that cortical selectivity can be specified by experience (92). What does the evidence show?

A number of studies going back almost two decades have argued for the existence of a visual word form area. However, many of these studies contrasted the cortical response to visually presented words with the response to very simple baseline tasks (93, 94), leaving unanswered the question of whether the region is specific to visual word recognition or whether it plays a more general role in the recognition of any complex visual stimuli. We searched for several years for a brain region that responded more strongly to visually presented words than to line drawings of familiar objects. Although we failed initially to find such a region in many studies, when technical advances enabled us to scan at higher resolution, we then found it in the majority of subjects (95). This region is tiny, about one-tenth the volume of the FFA, which explains why we did not see it with standard imaging resolutions (Fig. S2 and *SI Text*).

To further test the selectivity of this region, we used the same localize-and-test procedure that was effective in characterizing the FFA, PPA, and EBA. In independent tests of the response of the region, we replicated the fact that it responded severalfold higher to words than to line drawings (Fig. S2*A*). Further, we showed that the response was low, in this region, to stimuli that shared many of the visual properties of words: strings of digits and letters in an orthography unfamiliar to the subject (Hebrew). The response to consonant strings was the same as that to words, which suggests that meaning and orthographic regularity are not required to activate this region. In contrast, when we scanned subjects who read both English and Hebrew, we found a high response to words written in both languages (and orthographies) in this region (Fig. S2*B*). Thus, the response of this region is determined by the individual's experience. An even stronger demonstration of the experience dependence of this region comes from a before-and-after study of Chinese illiterates, who showed a character-selective response in this region after being trained for several months to read but not before (96).

Many important questions about this cortical region remain to be answered, such as whether it can develop in an alternate location if damage to this region occurs in childhood (97) or adulthood (98, 99) and whether it reflects a discrete, functionally homogeneous module or a gradient of selectivity (52). Whatever the answers to these questions, the current evidence indicates that the particular selectivity of this region depends on the specific experience of the individual and not the experience of his or her ancestors.

In sum, recent studies are beginning to shed light on the roles of genes and experience in the origins of cortical regions selectively engaged in specific cognitive functions. Multiple lines of evidence indicate a specific role for genes in wiring up the face system, yet at least one other region derives its selectivity from experience. Much remains to be understood about how exactly genes and experience shape neural circuits.

Conclusions

What a great privilege it is to have access to technology that Gall and Broca never dreamed of, technology that enables us to discover fundamental components of the human brain. Already, the evidence is strong for cortical regions that are selectively engaged in the perception of faces, places, bodies, and words and another region for thinking about what other people are thinking. Possible cortical specializations for other domains, including aspects of number (100), music (101), and language (70), are under active investigation. The possibility is within reach of obtaining a cognitively precise parts list for the human brain. The most exciting aspect of this enterprise is not where each component is found in the brain but which functions get their own brain region and ultimately, why some do and others apparently do not. But even a complete parts list, exciting as it would be, is only a first step.

A wide landscape of exciting new questions has opened up. What are the exact neural circuits that enable each region to conduct its signature function? Why do these regions arise so systematically where they do in the brain, and are there ever circumstances in which a region arises in a different locus or moves over after damage to its original locus? Is there some hardware constraint (cytoarchitecture, connectivity, proximity to other areas, etc.) that forces these regions to arise where they do? How do these regions work with each other—and with more general-purpose brain regions (102)—to support complex real-world cognition? How did these regions evolve, and what functions did they conduct in our primate ancestors? Can each region be recruited to perform new tasks? For example, can the neural machinery of social cognition be used to think about the mood of a financial market or to understand why a computer program fails to understand what we want it to do, and can the PPA be used to understand maps, architectural diagrams, or graphs depicting 3D landscapes of data?

But what psychologists like me most want to do is discover fundamental components not just of the brain but also of the mind. For the discoveries of functionally specific brain regions to be useful in this enterprise, we need much richer understandings of the role of each of these regions in cognition. We need not just loose descriptions of the function of a region (e.g., face perception) but precise characterization of the computations and representations conducted in each region. Does the face area extract qualitatively different kinds of representations from those extracted in the place area, as suggested by extensive research on the perception of faces and spatial layouts? Is it involved only in the representation of the physical characteristics of a face, or does it contain information about the sex, age, race, mood, or identity of the person? Methods such as fMRI adaptation and fMRI pattern analysis have started to answer these questions, although each method has limitations and progress to date has been modest. Satisfyingly precise characterizations of the mental functions implemented in each region will require extensive further work using not only fMRI and other brain-based methods but also increased efforts to relate these findings to behavioral and computational work on the representations and algorithms entailed in different aspects of cognition.

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