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# COGNITIVE MODULARITY IN THE LIGHT OF THE LANGUAGE FACULTY

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Ever since Chomsky, language has become the paradigmatic example of an innate capacity. Infants of only a few months old are aware of the phonetic structure of their mother tongue, such as stress-patterns and phonemes. They can already discriminate words from non-words and acquire a feel for the grammatical structure months before they voice their first word (Hespos, 2007). Language reliably develops not only in the face of poor linguistic input, but even without it. For instance, within a community of Israeli Bedouins, a group of people with hereditary deafness have developed their own sign language which has a grammatical structure that does not resemble that of the surrounding speaking community (Sandler, Meir, Padden, & Aronoff, 2005). In recent years, several scholars have extended this uncontroversial view into the stronger claim that natural language is a human-specific adaptation. As I shall point out, this position is more problematic because of a lack of conceptual clarity over what human-specific cognitive adaptations are, and how they relate to modularity, the notion that mental phenomena arise from several domain-specific cognitive structures. The main aim of this paper is not to discuss whether or not language is an adaptation, but rather, to examine the concept of modularity with respect to the evolution and development of natural language.

### 1. Which cognitive capacities are specific to language?

The scientific study of cognitive modularity and of natural language as a specialized human capacity share common roots. During the later decades of the 19th century, Broca and Wernicke noticed that a selective impairment of two cortical areas in the left hemisphere could lead to two kinds of language impairment. Patients with damage to the inferior frontal gyrus — Broca's area — suffered from an inability to understand and formulate grammatical sentences, whereas those with damage to the posterior part of the superior

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temporal gyrus — Wernicke's area — suffered from an inability to understand the meanings of words. It seemed a perfect dissociation: grammar processed by one area of the brain, vocabulary by another (Fig. 1a).

However, a growing body of evidence from neuroimaging studies, developmental psychology and neuropsychology indicates that this classical model of the neural correlates of language is fundamentally wrong (see Poeppel & Hickok, 2004, for a review). Most neuroscientists today agree that Broca's and Wernicke's areas are involved in a larger and as yet poorly understood neural network that also involves other temporoparietal prefrontal areas, as well as subcortical areas, such as striatum, basal ganglia, thalamus and cerebellum (Fig. 1b). Moreover, Broca's area is not uniquely involved in grammar, but also plays a role in the comprehension of musical structure (Maess, Koelsch, Gunter, & Friederici, 2001) and nonvocal imitation (Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003). The functional specialization of Broca's area has precursors in nonhuman animals: a recent neuroimaging study indicates that a homolog of Broca's area is active when chimpanzees produce communicative gestures and vocal signals (Taglialatela, Russell, Schaeffer, & Hopkins, 2008). Similarly, anatomical observations indicate that the left planum temporale, a portion of Wernicke's area that serves linguistic functions in humans, is also enlarged in nonhuman apes (Hopkins, Marino, Rilling, & MacGregor, 1998).



Figure 1. (a) Location of Broca's and Wernicke's areas in the human brain; (b) Brain areas currently known to be involved in language processing.

To add to the confusion, language relies on cognitive capacities that are not specialized for language and that are not uniquely human either. Consider word learning. A necessary condition for word learning is the capacity to isolate words within a stream of continuous speech. Saffran, Aslin, and Newport (1996) demonstrated that eight-month-old infants rely on probabilistic information to detect words: they discern strings of syllables that occur with

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greater statistical frequency (e.g., 'bida' in the string bidakupagodibidaku ...) as words. Since many animals can detect statistical regularities in their environment, it is perhaps unsurprising that this capacity is also found in nonhuman animals: cotton-top tamarins, a New World monkey species, can also perceive words in this way (Hauser, Newport, & Aslin, 2001). Fast mapping, the ability of children to learn a word after just hearing it once, was first proposed as a capacity special to word learning, but turns out to be a more domain general cognitive capacity. Markson and Bloom (1997) found that three-year-olds can also fast map facts (e.g., this object is called 'feb' versus this object was given to the experimenter by her uncle). Moreover, domestic dogs are also able to learn words through fast mapping. In a series of experiments (Kaminski, Call, & Fischer, 2004), a border collie was presented with an array of objects, all of which he knew by name except one. When requested to fetch x (with x the name of the unknown object), the dog correctly learned this word by exclusion, and still remembered it four weeks later. The arbitrary linking of vocal calls with concepts has been found in several non-human species, such as vervet monkeys, which have three distinct alarm calls for three kinds of predators, leopard, eagle and snake (Seyfarth, Cheney, & Marler, 1980), and dolphins (Janik, Sayigh, & Wells, 2006), which rely on signature whistles to discriminate between conspecifics. Even the fine discrimination of speech sounds (such as /b/ and /p/ or /d/ and /t/), once thought to be a hallmark of the human language faculty, is present in a variety of species, including chinchillas (Kuhl & Miller, 1975).

It turns out that many features of human cognition are necessary for the production and comprehension of grammatical language. Language exhibits intentionality — linguistic expressions are 'about something'. In order to have its semantic content, language relies on a pre-linguistic conceptual capacity, i.e., the capacity to make mental representations of objects such as DOG or WATER, and more abstract objects like SOLITUDE and HUNGER. Selective impairment of brain areas involved in specific domains of semantic knowledge leads to impairments in the ability to learn the meanings of the corresponding words, e.g., some patients cannot answer simple questions about animals or plants, like 'do eagles lay eggs', but perform well in other domains of knowledge, such as artefacts (Caramazza & Mahon, 2003). Some features of language, although stable across human cultures, may not even be innate at all. Because languages are limited by extrinsic factors like intelligibility, these features probably come about through the dynamics of group interactions rather than innate tendencies. Linguistic categories usually have a small number of members, for instance, although humans can discriminate about 10 million different colours, all known natural languages have fewer than 15 basic colour terms. This economy might have to do more with communicative efficacy or memory constraints.

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## 2. Language and modularity

The past years have witnessed a lively debate on the question of whether language is a byproduct (e.g., Hauser, Chomsky, & Fitch, 2002) or an adaptation (e.g., Pinker & Jackendoff, 2005). One way to approach this question is to examine language from the perspective of cognitive modularity. Although not all cognitive modules are evolutionary adaptations (e.g., reading), there is a growing tendency to see modularity as a necessary condition for evolvability, i.e., the ability of a system (biological or artificial) to evolve. The evolvability argument (e.g., Sterelny, 2004) holds that unless cognition is to some important degree modular, it is incapable of evolving away from its current organization: a change in one component will be connected to many others changes, and even the slightest modification can have disastrous effects for the organism. The importance of modularity for evolvability has been demonstrated in disparate disciplines, such as evolutionary biology (Lewontin, 1978) and computer science (Wagner & Altenberg, 1996).

The view that there are good evolutionary reasons to expect some degree of modularity in human and other animal brains has been taken up by evolutionary psychologists. Indeed, they argue that brains must be modular because they perform a variety of tasks that are better achieved by separate systems than by one holistic processor (Cosmides & Tooby, 1994). Mind, since natural selection is a tinkerer, not an engineer (Jacob, 1977), it is not inconceivable that it would shape suboptimal non-modular brains. Nevertheless, even without invoking optimality, modularity remains plausible because any reasonably complex nervous system is faced with multiple tasks that are functionally incompatible. For instance, marsh tits sing and cache food, activities that require distinct memory systems (Sherry & Schacter, 1987). Food-caching requires memory that is flexible and can be updated regularly as the birds cache food at different locations each year, and must sometimes relocate food from caches that have been pilfered, whereas song-learning relies on a critical learning period in which the birds learn a particular repertoire that will not change during their lifetime. Since both types of memory are functionally incompatible, marsh tits should have at least two distinct memory systems.

If we take a relatively broad definition of modularity, which specifies that modules are domain-specific computational devices, dedicated to solving specific tasks, and associated with specific brain structures, then language is non-modular. Given that most aspects of human cognition are involved in language, and given that brain structures most commonly associated with language do not appear to be uniquely specialized for language, it is difficult to term language modular without eroding the very concept of modularity. Some evolutionary psychologists further argue that modularity should be grounded in *functional specialization*, i.e., modules should be defined by

their function, both from a proximate and an ultimate point of view (Barrett & Kurzban, 2006). Whereas the proximate function of language is uncontroversial (it is used for communication), there is much disagreement over the question why ultimately language evolved. Explanations range widely: amongst others kin selection, communication during hunting, facilitating cultural transmission, enhancing social bonds through gossip. In sum, evolutionary accounts of language face several problems: there is no well-defined language module, many disparate domains of cognition are important to it, and its ultimate function remains unclear.

# 3. How did language evolve?

# 3.1. The FLB/FLN distinction

Hauser et al. (2002) argue that language is modular, but that it is not an adaptation. They differentiate between two aspects of language. The faculty of language in the broad sense (FLB) consists of capacities that are necessary for language, but that are not restricted to it. The faculty of language in the narrow sense (FLN) comprises capacities that are unique to language. If FLN is sufficiently small, it is not inconceivable that language evolved through non-selective processes, such as genetic drift. Hauser et al. (2002) identify recursion as the only thing that is specific to language and that is uniquely human — two properties that are logically independent, but that they systematically conflate. A recursion specifies a class of objects by defining a few simple base cases or methods, and defining rules to break down complex cases into simpler ones, e.g., my parents are my ancestors; my parents' parents are also my ancestors and so on. In language, recursion allows one to generate an infinite number of expressions from a finite vocabulary and a limited set of rules. Thus, expressions like 'to thine own self be true' can be embedded into larger frames like 'Shakespeare first coined "to thine own self be true" and many other expressions'. If recursion were indeed the only evolutionary novel aspect of natural language, its emergence through nonselective processes seems parsimonious.

However, recursion is not unique to language, as exemplified by three agrammatic patients who were able to solve mathematical tasks that require recursion (Varley, Klessinger, Romanowski, & Siegal, 2005). All three had suffered severe damage in the left hemisphere and were incapable of producing and understanding grammatical speech. Still, they were able to work out complex bracket operations that can only be solved if recursive rules are adopted, and they could even come up with numbers bigger than 1 but smaller than 2, using a simple recursive rule (1.9, 1.99, 1.999, ...) Moreover, recursion does not occur in all natural languages. Based on more than 20

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years of fieldwork, Everett (2005) has argued that the language of the Pirahã, a Native American culture from Brazil, is not recursive: it does not have self-embedded structures that can be expanded at will. Recursion is not a uniquely human capacity either. Gentner, Fenn, Margoliash, and Nusbaum (2006) successfully taught starlings to recognize recursive strings of sounds. So FLN does not do the conceptual work it is supposed to do: it is not unique to language, and it is not even necessary for language.

A more fundamental problem with the FLB/FLN distinction is that it is not biologically relevant. Hauser et al. (2002) take all traits that can be found in at least one nonhuman species as FLB, i.e. not uniquely human traits. This confuses the notion of uniquely human and derived traits. A plesiomorphic or ancestral trait is present in an ancestral species (or clade) and its descendants. For example, the spinal chord is plesiomorphic with respect to goldfish and cats, because both species have inherited this trait from a common ancestral vertebrate species that possessed it. A derived trait is a specialization found in one species (or clade) but not in closely related others. For example, the elephant trunk is a derived trait for elephants compared to other mammals, since no other extant species of mammal has this trait. For the same reason, wings of bats are derived with respect to other mammal clades, even though wings are not unique for bats. Hauser et al. (2002), however, mistakenly claim that all capacities that are not uniquely human are plesiomorphic. For example, they argue that the ability for vocal imitation is not a uniquely human trait because cetaceans and some species of birds also possess this capacity - this view is mistaken because our closest living relatives (the great apes) are not able to imitate vocalizations, as is aptly illustrated by decades of experiments in which chimpanzees were in vain taught to speak. Hence, human speech and a parrot's ability to imitate a wide range of sounds are similar, but not because they share a recent common ancestor. Humans only imitate human language and a limited array of other sounds, finches only imitate conspecifics, and mynahs and parrots imitate a wide range of sounds, including all sorts of natural (streaming water, barking dogs) and artificial (telephone ringing, creaking doors) sounds. In everyday loose language all these are deceptively referred to as vocal imitation, but actually they are three distinct biological phenomena. The fact that humans are relatively poor at imitating non-vocal sounds such as whinnying horses or flying helicopters, whereas mynahs and parrots are good at it, bears testimony to this fact.

# 3.2. The evolution of traits specific to language

Pinker and Jackendoff (2005) rightly remark that traits that are special to language need not be uniquely human, and conversely, that not all uniquely human traits are specific to language. Nevertheless, they do accept the

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FLB/FLN distinction as a useful way to look at language. Using inference to the best explanation, they claim that some anatomical and cognitive adaptations have arisen to meet the demands of vocal communication. Enhanced human hearing due to upregulations (mutations that indicate positive selection) in auditory genes can be plausibly explained as a result of selective pressures brought about by the elaborate vocal communication in humans; the lowering of the human larynx can likewise be interpreted as an adaptation that facilitates the production of speech sounds — although both also serve other adaptive functions (e.g., voice timbre in males as a sexually selected trait). If a distinction between traits 'specific to language' and those 'not special to language' can be made, then it is not difficult to envisage that natural selection honed human anatomical and cognitive traits in such a way as to facilitate vocal communication. However, the inference from current function to adaptive origin cannot be thus made: it is not because the human auditory system, larynx and other traits have adapted to language, that language itself started as an adaptation in the past.

The distinction between what is special to language and what is not sometimes looks arbitrary. Pinker and Jackendoff (2005) argue that some capacities for conceptual thought are uniquely human, but not specific to language. For example, they write that humans are able to represent false beliefs, whereas chimpanzees and other great apes are not. It remains equivocal, however, whether the capacity for reasoning about false beliefs is languagespecific or not. In one experiment, Newton and de Villiers (2007) asked adults to solve a simple false belief task while concurrently either shadowing (repeat with some delay) a pre-recorded dialogue or tapping along with a rhythmic soundtrack. The dialogue, but not the tapping, resulted in a serious disruption in the false belief reasoning. Might one not be tempted to conclude that false belief reasoning is language-dependent, and hence specific to language, especially since the ability is seriously compromised in those who cannot speak, and delayed in deaf children raised by hearing parents (these children also experience a delay in language development). A similar argument could be made for natural numbers, which can only be accurately represented by humans. Whereas infants and nonhuman animals can only distinguish very small numbers up to three precisely, and larger numerosities only when the difference between them is large enough (e.g., 6 and 12, but not 10 and 12), more educated children and adults can discriminate large numbers accurately. Speakers of languages with very few number words represent numerosities as imprecisely as infants. Although it needs much more support to claim that this difference is caused by language, maybe as a cognitive tool to guide exact representations (Frank, Everett, Fedorenko, & Gibson, 2008), such uniquely human concepts might turn out to be languagespecific.

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Proponents of language as a modular adaptation argue that our linguistic capacities can be selectively impaired or spared. Williams syndrome (WS), a rare genetic disorder due to a deletion of about 25 genes in the 7ql1.23 region, affects many domains of cognition, especially social abilities and visuospatial skills. People affected by WS find it difficult to infer other people's mental states; they also have difficulties finding their way and performing mundane motor-tasks such as tying their shoes. In comparison to this, their linguistic skills seem to remain relatively spared. Some authors even suggest that WS patients are 'hyperlinguistic': in their spontaneous speech, they choose markedly more unusual and sophisticated words, like 'sauté', 'alleviate', and 'mince'. When asked to name a number of animals, a normal eight-year-old will come up with prototypical barnyard and pet animals like 'cat', 'dog', 'sheep' and 'pig'; WS children typically respond with more exotic examples like 'ibex', 'koala', 'yak' and 'chihuahua'. This has led several researchers (e.g., Pinker, 1994, 44-46) to claim that the language faculty can be considered as a modular computational system, which can be selectively impaired or spared. Yet the atypical word choice reveals that at the semantic level, their language is disrupted. Their word learning relies more on the phonological properties of words than on their meanings. This may explain why vocabulary learning is severely delayed in young children with WS: only at about 28 months they reach the lexicon of a typical one-yearold. Older children and adults with WS have difficulties with placing words into different categories, e.g., both Spiderman and Mozart are 'not alive', but WS subjects fail to see that in this case 'not alive' belongs to two different categories, i.e., fictional character and dead (Bellugi, Lichtenberger, Jones, Lai, & St. George, 2000). Semantics is indisputably one of the core features of language — language has intentionality, it refers to objects. The disrupted semantics of WS patients speaks against the claim that their language faculty as a whole would be selectively spared.

# 3.3. Deep homologies and FoxP2

Over the past decade, the discovery of *FoxP2*, a gene critically involved in the development of language has given an exciting new perspective on the evolution and modularity of language. People with mutations in this gene have serious impairments in many areas of speech, including effortful, slow speech, problems with phonology, and difficulties in grammar comprehension. *FoxP2* expression is not specific to the human brain; it is also expressed in the lungs, gut and heart. It is also not unique to humans, occurring in clades as divergent as mice, songbirds, and yeast. Enard et al. (2002) noted that there were only three amino-acid substitutions separating human and mouse *FoxP2*, two of which were evolutionary very recent, occurring after the human-chimpanzee divergence, and therefore human-specific.

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Remarkably, FoxP2 also plays a key role in vocal communication in nonhuman species. Inhibiting FoxP2 expression in the basal ganglia (a brain area critical to the development of song repertoire) in young songbirds hampers their capacity to learn songs (Haesler et al., 2007). A disruption in one copy of the FoxP2 gene in mice pups yields a substantial reduction in ultrasonic vocalizations that are normally elicited when they are separated from their mothers (Shu et al., 2005). Language, birdsong and mouse vocalizations may be examples of deep homologies, traits that look like examples of convergent evolution, but that nevertheless share a deep genetic ancestry. The paradigmatic example of this is Pax-6, a gene that stands at the top of a developmental cascade involved in eye-development (it can even generate an eye on the antenna of a fruit fly if it is artificially expressed there). Pax-6 initiates the building of light-sensitive cells in a variety of species, even those where eyes are anatomically analogous, such as frogs and flies: these clades did not inherit their eyes from a common sighted ancestor. Apparently, Pax-6 can be easily modified to produce light-sensitive cells, and natural selection has hit upon this solution several times independently. If FoxP2 acts as a 'master control gene' for language development, one can see how slight evolutionary changes in this gene might have shaped the evolution of human language (and birdsong and mouse vocalizations). As Marcus and Fisher (2003, 261) point out: 'The genetic mechanisms involved in speech and language development are likely to involve recruitment and modification of preexisting genetic cascades, much in the way that the development of the wing began with the development of the basic design of a vertebrate forelimb.' Deep homologies show that natural selection often recycles ancient structures. Although birdsong and human speech evolved independently due to different kinds of evolutionary pressures, FoxP2 is critically involved in the development of both kinds of communication, because across species the gene seems to be co-opted for tasks involving complex facial muscular motions and vocal communication. Unfortunately, the causal role of genes in shaping cognition is still poorly understood. As a mutation in FoxP2 does not altogether abolish the ability to speak, but merely compromises it, more genes must be at work in the development of language. Similarly, inhibiting the expression of the gene in songbirds does not eliminate their capacity for song learning entirely.

# 4. Towards a more fundamental solution

The view that natural selection is a tinkerer is not just useful for looking at language evolution at the molecular level, it can also be applied to the anatomical level. An advantage of this is that we have a much better (albeit still fragmentary) understanding of language from the anatomical than

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from the genetic-developmental point of view. To understand how something as highly specialized as the language faculty emerged, evolutionary thinkers might have to reconsider their notion of modularity. As mentioned earlier, evolutionary psychologists have a relatively coarse-grained view of modularity: to them, modules are domain-specific units, dealing with evolutionarily salient tasks like inferring mental states or vocal communication. On the other hand, cognitive neuroscientists have a more fine-grained idea of modularity: they take modules to be specified units with a narrow function that are connected in larger, distributed networks. Particular modules can be co-opted for several tasks. For example, cognitive neuroscientists have demonstrated that theory of mind (inferring mental states) is not subserved by a single module, but by several neural structures involved with narrow domains like eye-direction detection and detection of biological motion (Castelli, Happé, Frith, & Frith, 2000). The module for detecting biological motion is not only used for inferring mental states, it also appears in a network involved in semantic knowledge about animals (Chao, Haxby, & Martin, 1999) — arguably, an important part of our semantic knowledge about animals is how they move.

There are no theoretical reasons why modules should correspond to domains humans find intuitively appealing, such as language, theory of mind or number, rather, the grain of modularity is something to be empirically discovered. For example, traditionally theory of mind was seen as a single module that could be selectively impaired, and that was engaged in inferring the mental states of others (Baron-Cohen, 1995). But recent studies with nonhuman primates have challenged this monolithic view: in a topical review paper, Call and Tomasello (2008) argue that chimpanzees know what others can and cannot see, that they understand the goals and intentions of others, but that they cannot understand false beliefs. Hence the seemingly straightforward question 'does the chimpanzee have a theory of mind?' cannot be answered by a simple yes or no. Nine-month-old human infants are already able to understand other agents' goals and intentions (Csibra, Gergely, Biró, Koós, & Brockbank, 1999), but likewise show no capacity to understand false beliefs. It may therefore be useful to abandon investigating theory of mind as a whole, but rather to concentrate on more basic, finer-grained capacities (like detecting goal-directed behaviour) that together constitute the ability to understand the minds of others.

As we have just seen, current neuroanatomical and neuroimaging studies point towards a fine-grained modularity, where elementary modules are recruited in diverse larger, distributed networks. A useful metaphor to capture how this might work is a large set of hundreds of lego blocks, which can be recombined to make larger, meaningful objects. In isolation, each of these blocks may not be evolutionary significant, but the role each of them carries

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out in the larger wholes (the distributed networks) allows that natural selection can fine-tune them to better accomplish these roles. For example, the module for edge detection alone cannot do much, but the role it fulfils in the visual system as a whole makes that natural selection can improve the detection of edges. Similarly, phoneme detection by itself does not do much, but its role in communication and other auditory tasks can fine-tune its ability. The view outlined here has some affinities with Carruthers' (2006) concept of massive modularity that proposes that most of our cognitive processes are subserved by dedicated modules, the input of which can be flexibly combined by the language module to produce creative thought. An important difference is that the present model does not conceptualize of language as a module in itself, but rather as an interplay of several fine-grained modules that can be combined with others.

As an aside, we may ask whether natural selection can also detect the networks, i.e., enhance or facilitate the connections between modules. Perhaps this could be meaningfully answered in a 100,000 years or so, if by that time *Homo sapiens* has developed a distributed network specialized in reading and writing. Currently, learning how to read and write is a tedious and difficult task, because we have to co-opt a variety of modules used for other purposes. Young children struggle to connect sounds with arbitrary signs, whereas they have no problems to learn how to speak, i.e., connecting arbitrary sounds to concepts, such as objects and mental states.

Returning to Broca's area, the fact that it is a relatively large neural structure that seems to serve several not always compatible functions probably means that it contains several fine-grained modules, involved in amongst others nonvocal imitation, analyzing auditory structures (musical and grammatical) and social communication. Each of these modules can be subject to selective pressures resulting from the role they play in diverse distributed networks. For example, it is conceivable that the structure-analyzing neurons located within Broca's area can be fine-tuned to meet the demands of comprehending complex grammatical language. Similarly, the ability to link concepts with arbitrary signs, although not uniquely human, could have been selectively enhanced because doing so facilitates cognition and communication. As mentioned earlier, several studies indicate that language is a cognitive technology, enabling us to denote cardinal numbers or keep track of the beliefs of others. According to Jackendoff (1996), the reason for this is that language allows us to hold thoughts longer in attention, enabling us to pay attention to relational and abstract aspects of thought. The human brain, when compared to other primate brains (Rilling & Insel, 1999), shows indications that Wernicke's area has been under strong selective pressure during human evolution. Interestingly, neurons within this area facilitate the forging of such arbitrary links.

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In this paper, I have provided several lines of research from comparative psychology, developmental psychology and cognitive neuroscience that give reasons to doubt that the language faculty is subserved by a domain-specific cognitive module. This perspective has an important advantage for evolutionary accounts of language: if language is composed of numerous modules, many of which also figure in other distributed networks, no single evolutionary reason for why or how language evolved is needed. Rather, research can focus on more contained, more modest hypotheses about the evolution of the specific neural structures that underlie the language faculty and other cognitive capacities. For instance, comparing Broca's area and its homologs in different primate species may indicate which evolutionary pressures shaped this brain structure. Whereas the inferior frontal cortex (area F5, a homolog of Broca's area) in rhesus monkeys is a seat of mirror neurons, concerned with understanding actions, it is involved in social communication in chimpanzees, and in language comprehension, nonvocal imitation and grammar in humans. Asking why this homolog evolved differently in rhesus monkeys, chimpanzees and humans presents a more constrained and perhaps more interesting question than why language evolved in humans, but not in other species.

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