Cognitive Neuroscience

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Abstract

Cognitive neuroscience explores the neural basis of cognition, including perception, attention, language understanding, memory, problem solving, and decision-making. The field draws on findings on how neurons process and represent information, and on ideas about how learning may occur through the modification of properties of neurons and their connections. It is clear that there is specialization of function in the brain, yet brain areas appear to work together, interactively, to support emergent cognitive functions. The article discusses these points, reviews research methods used in this field, and touches on open questions, as well as the future of cognitive neuroscience.

What is the neural basis of cognition? How do our thoughts, perceptions, beliefs, and intentions arise from the activity of the vast numbers of neurons in the brain? The discipline of cognitive neuroscience emerged in the 1990s at the interface between neurobiological, cognitive, and computational sciences to answer these questions. On one side, the discipline grows out of the traditions of both cognitive psychology and neuropsychology, which use behavioral experiments to uncover the processes and mechanisms underlying normal and impaired human cognitive processes, linking work of this kind to computational modeling approaches to develop explicit mechanistic accounts of these functions and dysfunctions. On the other side, it emerges from the traditions of neuroscience, which use neurophysiological and neuroanatomical methods to explore the mechanisms underlying complex functions and draws on findings and principles of cellular and molecular neuroscience. It joins these approaches with the use of both structural and functional brain imaging methods, and the application of formal mathematical models (computational neuroscience) to explore how neural processes give rise to cognitive outcomes.

The Microstructure of Cognition

Patterns of Activity Arising in Ensembles of Simple Elements

A starting point for cognitive neuroscience is the idea that a cognitive or mental state consists of a pattern of activity distributed over many neurons. For example, the experience of holding, sniffing, and viewing a rose is reflected in a complex pattern of neural activity, distributed over many brain regions, including the participation of neurons in somatosensory, olfactory, and visual regions, and possibly extending to language areas (that represent the words we use and hear in relation to this object) and other neural regions that code information associated with the experience.

These patterns of activation arise from excitatory and inhibitory interactions among the participating neurons, mediated by connections called synapses. The inputs that neurons receive cause them to 'fire' or emit electrical pulses, called spikes or action potentials, which travel down their axons to synaptic terminals where they cause the release of chemicals (neurotransmitters) that then have excitatory or inhibitory influences on the neurons on the other side of the synapse. The combined effect of the incoming signals to each neuron, together with its recent history, determines whether it will fire at a particular moment. Figure 1 indicates something
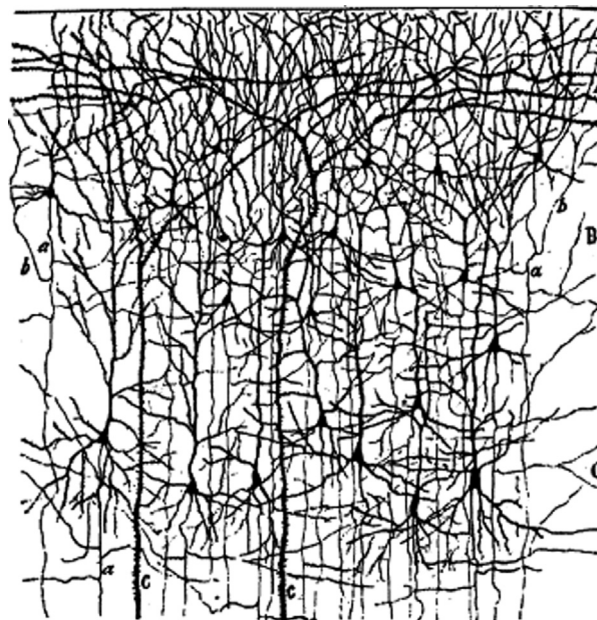
Figure 1 An early camera lucida drawing of the circuitry of the neocortex, based on the Golgi stain method, which impregnates just one out of every 100 cortical neurons. The diagram depicts the rich dendritic branching structure of the individual neurons present, whose cell bodies appear as small, pyramid-shaped blobs. The dendrites (and the little spines visible on the surfaces of some of the larger dendrites) are the structures on which the neurons receive most of their inputs from other neurons. This figure comes from a book by the Spanish neuroscientist Santiago Ramon y Cajal. I recently retrieved it from Wikimedia Commons on 2009-11-20. It was originally published in Santiago Ramon y Cajal 'Comparative study of the sensory areas of the human cortex' published 1899, ISBN 9781458821898. I believe it is in the public domain.

of the fundamental circuitry involved, though it should be noted that only one out of 100 of the neurons in the tiny region shown (about 1×1 mm) are indicated, and the synaptic connections onto the neurons illustrated are not visible. While the computations performed by individual neurons should not be underestimated (*see* Neurons and Dendrites, Integration of Information in), it seems likely that what gives the system its power and complexity is the number of neurons involved (most estimates place the number in the human brain between 10 and 100 billion) plus the density and pattern of connections among them (typical cortical neurons receive between 10 000 and 100 000 individual synapses from other neurons).

Distributed Representations

A great deal of research has concerned the nature of the active representations that the brain uses (cf rose example above). There is now a great deal of support for the view that the brain's representations typically consist of activity patterns involving many thousands or millions of neurons. Individual neurons are often described as 'detectors' for particular stimulus or situational features or conjunctions of features (e.g., the 'edge detectors' introduced by Hubel and Weisel (1962) in their seminal studies in visual cortex), but most such neurons are fairly broadly tuned, so that they will also be partially activated by a wide range of stimuli overlapping in one way or another with the optimal stimulus, and thus will participate at least partially in the representation of many different inputs.

A prime example of distributed representation is that of the direction of arm movements in the motor cortex. It appears that the representation of a particular direction of reaching reflects a pattern of distributed activity over a large population of neurons, each of which responds maximally to a particular preferred direction, but responds to a lesser degree to neighboring directions, and thus participates partially in the representation of many different directions of reaching (Georgopoulos et al., 1986). There are other types of distributed representations used in the brain, in which a neuron can participate in two different representations, without there being a clear shared feature or other similarity between the situations that cause the neuron to fire. For example, in the hippocampus, individual neurons participate in distributed representations of the animals' location in external space and other aspects of the current behavioral situation. Interestingly, the same neurons may participate in different ways in the representation of different environments, or even of two distinct representations of the same environment when the animal performs different tasks (Markus et al., 1995). Some studies suggest that there may be neurons specialized for items or persons who are highly familiar (e.g., a current actress frequently described in the popular media, Quiroga et al., 2005).

Knowledge and Learning in the Strengths of Connections

The particular pattern of activation that arises in experiencing an input (or in reconstructing a memory or formulating an imagined experience) is determined by the connections among the neurons. A key issue, then, is to understand the processes that lead to the formation of the specific excitatory and inhibitory connections that shape the processes of perception, cognition, and action. Generally, it is thought that largely activity-independent processes establish an initial skeleton framework of connectivity early in development, for example, causing connections to form between neurons in the retina of the eye and other neurons in the lateral geniculate nucleus, a way station for visual information on the way to the cortex. Then, activity-dependent processes selectively refine and stabilize some of the connections, and perhaps cause new ones to form, while other connections are pruned away.

Activity-dependent processes continue throughout life, at least in many parts of the brain, and appear to provide the basis of both explicit and implicit learning. They have been the subject of intense scrutiny in neuroscience. Donald Hebb, the mid-twentieth-century neuropsychologist, proposed that if one neuron participates in firing another, the connection from the first to the second will be strengthened (Hebb, 1949). Hebb's idea has been encapsulated in the phrase 'cells that fire together wire together.' While there is no direct proof that this is a principle of learning in the brain, the idea has received a great deal of experimental support in experiments that have been carried out in slices of brain tissue (*see* Neural Plasticity). It should be understood that there may also be plasticity at the level of the whole neuron (in some specialized brain areas, neurons are continually created and incorporated into circuits while others are continually being lost). There is also likely to be some plasticity at the level of the branches of axons and/or dendrites, which provide the scaffolding underlying the formation and loss of synaptic connections.

System-Level Organization: The Macrostructure of Cognition in the Brain

Specialization of Brain Regions

A central and important fact about the organization of cognition in the brain is that individual brain regions are specialized. The cerebral cortex can be partitioned conceptually into primary, secondary, and tertiary cortical zones (Luria, 1966). According to this conception, the primary areas contain neurons whose responses can be largely characterized as reflecting relatively simple, local properties of inputs or outputs within a given modality, such as the presence of an oriented line segment at a particular position on the retina of the eye, the presence of acoustic energy in a particular frequency band, or the presence of a tactile stimulus at a particular point on the skin surface. Corresponding motor areas contain neurons whose responses may correspond to the activation of specific muscles or elementary movement elements. Secondary areas contain neurons whose responses represent higher order stimulus attributes within a given modality, such as conjunctions of features, and the representations in these areas may be relatively invariant over some lower level properties, such as position of the stimulus containing the feature on the sensory surface (Tanaka, 1996). Tertiary areas are responsible for representations that transcend individual modalities, such as representations of the current task context, representation of one's location in extrapersonal space, or representation of semantic content. It should be noted that this picture is only a very crude approximation, and many so-called primary areas appear to participate in the representation of the global

structure of a stimulus or response situation, and many areas that are treated as modality-specific can be modulated by influences from other modalities (see below). It should also be noted that structures outside the neocortex also play very important roles in cognitive functions. Among these are the diffuse neuromodulatory systems that regulate behavioral/cognitive states such as alertness, wakefulness, and mood; and subcortical systems in the thalamus, basal ganglia, and cerebellum that play important roles in sensory motor processes, skills and habit formation, and motor learning. The amygdala plays a central role in emotion and its influence on cognition, and the hippocampus plays a crucial role in the formation of new memories.

Modular versus Interactive Approaches to the Organization of Function

The mechanisms and processes noted above provide only the starting place for the formulation of an understanding of how cognitive processes arise from neural activity. There are two contrasting views: (1) The modular approach, championed by David Marr for vision and Noam Chomsky for language, and systematized as a general approach to understanding brain organization by Fodor (1983), holds that the brain consists of many separate modules that are informationally encapsulated in that their operation is informed only by a very limited range of constraining sources of information. The modular view also holds that the principles of function are specific to each domain, and that distinct and individualized mechanisms are used to subserve each distinct function. For example, the initial assignment of the basic grammatical structure to a sentence is thought to be based only on the syntactic classification of words and their order, and to be governed by the operation of a system of structure-sensitive rules. The module that carries out this assignment is considered to be structured specifically so that it will acquire and implement structure-sensitive rules, and to contrast in the principles that it employs internally with other modules that carry out other tasks, including other aspects of language processing, such as the assignment of meanings to the words in a sentence. In Fodor's view, there are many specialized modules (corresponding approximately to primary and secondary cortical areas and their subcortical inputs and outputs). These are complemented by a general-purpose cognitive system that is completely open-ended in the computations that it can undertake and in the range of informational sources that it can take into consideration.

The alternative, interactive approach, has its seeds in the ideas of Luria (1966), and has been championed by Mesulam (2000) and Rumelhart et al. (1986), and overlaps with the ideas of Damasio (1989). On this view, cognitive outcomes, such as the assignment of an interpretation to a sentence, arise from mutual, bidirectional interactions among neurons in populations representing different types of information. An example of a system addressing the representations and interactions involved in reading individual words aloud is shown in Figure 2. As the Figure suggests, the formation of the pronunciation from a visual orthographic input arises from an interactive process involving orthographic (i.e., letter identity), semantic, phonological, and contextual information. Both the modular and the interactive view are consistent with the idea that neurons in the brain are organized into populations
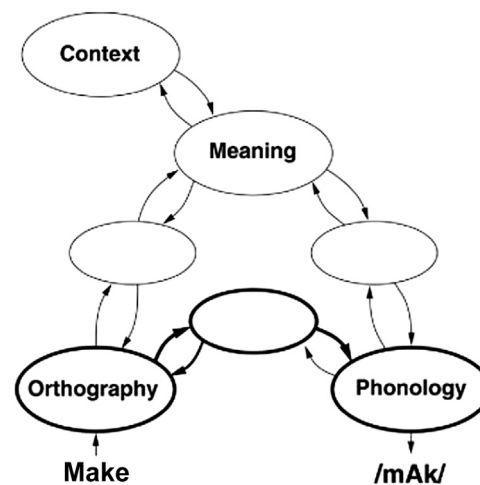
Figure 2   The interactive, distributed framework for modeling individual word reading of Seidenberg and McClelland, 1989. All of the relevant processing pathways are assumed to be bidirectional. Figure 2 comes from Figure 1, p. 526, of Seidenberg, M.S., McClelland, J.L. 1989. A Distributed, Developmental Model of Word Recognition and Naming. Psychological Review 96, 523–568. Copyright 1989 American Psychological Association. Reprinted with permission (automatically granted by APA for a single figure).

specialized for representing different types of information (though the degree of specialization remains hotly debated; see Kanwisher, 2010). Where they differ is in the extent and the role of bidirectional interactions among participating brain areas and in the extent to which the principles governing computation in each area are domain-general or domain-specific.

Evidence of Interactive Processes in the Brain

The debate between modular and interactive approaches is a long-standing one, and can be seen as the modern legacy of a history of diverse views on the localization of functions within the brain (Luria, 1966). While the debate is likely to continue to evolve with additional empirical evidence, it may be worth considering a few elements of evidence that support the idea that processing may be interactive. One relevant anatomical point is the fact that connectivity within and between brain areas is generally reciprocal: when there are connections from region A to region B, there are nearly always return connections (Maunsell and van Essen, 1983).

While there is no consensus on the function of reciprocal connections, there is some evidence that they subserve distributed, interactive computations, at least in particular cases. For example, there is evidence that interactive processes influence the activation of individual neurons in primary visual cortex (Area V1). Traditionally, individual neurons in this area have been seen as encoding the presence of segments of oriented edges at particular positions in a visual display. Recent evidence suggests, however, that primary visual cortex participates in a distributed and interactive process that contributes to the representation of global stimulus properties such as figure-ground organization. The firing of neurons in primary visual

cortex is strongly affected by temporary inactivation of corresponding portions of secondary visual cortex, suggesting that reciprocal interactions between these areas shape neuronal responses in V1 (Hupe et al., 2001). Although the initial response of neurons in V1 is determined by appropriate oriented line segments at a specific location, by about 80 ms their firing is heavily dependent on the global structure of the display (Lee et al., 1998). Furthermore, neurons in V1 respond to illusory contours (contours that are not present in the image but are implied by other contours and perceived by the viewer) that fall in their receptive field. The response occurs at a lag of about 80 ms, suggesting an indirect source, perhaps arising from feedback from higher cortical areas (Lee and Nguyen, 2001). There is also considerable evidence of between-modality interactions. For example, activity in auditory processing areas associated with speech perception is enhanced by visible speech (Callan et al., 2001). There are many corresponding examples of cross-modal influences in single neuron recording studies in animals.

Methods and Approaches in Cognitive Neuroscience

Cognitive neuroscience is a highly interdisciplinary endeavor and draws on a wide range of research methods and approaches, each with its own history and underlying theoretical frame of reference. One important challenge for the field is to find ways of integrating the insights gained from the different methods to allow the field as a whole to converge on a common theoretical framework. Here the predominant research approaches are briefly described, and some of the prospects for integration are considered.

Lesion and Behavior Approaches (Cognitive Neuropsychology, Behavioral Neuroscience, and Transcranial Magnetic Stimulation)

These research approaches have the oldest historical roots, based as they often are in the assessment of the effects of naturally occurring brain damage on cognitive function. A seminal case study was the report by Broca (1861) of a man with a severe disturbance of language arising from a large brain lesion in the posterior portion of the left frontal lobe. Since Broca's day, neurologists and neuropsychologists have investigated the effects of accidental or therapeutic brain lesions in humans, and many key insights have arisen from these studies (see Agnosia; Amnesia: General; Aphasia; Dyslexias, Acquired and Agraphia). The subdiscipline of cognitive neuropsychology arose specifically around the study of the effects of brain lesions (see Cognitive Neuropsychology, Methods of). A complementary endeavor has grown up around the use of brain lesions in animals carried out with specific experimental intent. This tradition is relevant to human cognitive neuroscience in view of the very close homology between many structures in the human brain and corresponding structures in the primate and rodent brains. This work has obvious advantages in that lesions can be carefully targeted to particular brain areas to test specific

hypotheses. Many key insights have emerged from this work, including the discovery of complementary processing streams in the visual system (Ungerleider and Mishkin, 1982; see Neural Plasticity). A third technique, which shares many of the same features, is transcranial magnetic stimulation (TMS). TMS utilizes a high magnetic field to generate stimulation in the cortex immediately below the coil. When combined with careful behavioral experiments, TMS can be used to test the role of targeted (human) brain regions. Unlike human neuropsychology, of course, the transiently stimulated brain regions are under experimental control not only in terms of location but also the timing of the interference. Consequently, both the function and the chronometry of brain regions can be probed (Walsh and Cowey, 2000). While all three techniques have provided important and fundamental insights about brain function, the approaches are not without their pitfalls, since lesions or localized stimulation may have unintended and unobserved effects in other brain regions; the refinement and extension of experimental lesion techniques is ongoing (including the combination with functional neuroimaging).

Neuronal Recording Studies

Studies relying on microelectrodes to record from neurons in the brains of behaving animals can allow researchers to study the representations that the brain uses to encode information and the evolution of these representations over time. Several fundamental observations have been made using this technique. As discussed above, these studies indicate, among other things, that the brain relies on distributed representations and that neurons participate dynamically and interactively in the construction of representations of external inputs. As one example, neuronal recording studies have had a profound impact on our understanding of the nature of representations of extrapersonal space. There are neurons in the brain that encode the location of objects in extrapersonal space simultaneously in relation to many different parts of the body, including the limbs and head (Duhamel et al., 1991; Graziano and Gross, 1993) and other neurons that encode the locations of objects in relation to other objects (Olson and Gettner, 1995). Furthermore, recordings from neurons in parietal cortex suggest that when we move our eyes from one location to another, we update our internal representations of the locations of important objects in space, based on where we anticipate that they will be after the upcoming eye movement (Duhamel et al., 1992).

An important recent development is the ability to record from hundreds or thousands of individual neurons at a time. A key finding that has come out of this work is the confirmation in studies with rodents that the simultaneous and successive patterns of activity acquired during behavior may be reactivated in the brain during subsequent sleep (Wilson and McNaughton, 1994). The potential of such methods to shed light on the moment-by-moment relations between activations of different neurons and between distributed brain representations and specific inputs and outputs makes them essential to the future of cognitive neuroscience.

Although primarily utilized in nonhuman situations, some important findings have arisen from the rare opportunity to measure directly from the human cortex. As a part of preoperative neurosurgical investigations, some patients have subdural grid or depth electrodes inserted. In addition to providing key clinical information (e.g., localizing important language and motor functions, or epileptic foci), these studies have generated direct insights about the location of human cognitive functions (including language), and about the timing of the underlying neural activity and interactivity between regions. For example, although often considered to be a high-order component of the visual 'ventral stream,' these methods have shown that the anterior fusiform/inferior temporal gyrus region is important in human language function (the 'basal temporal language area': Lüders et al., 1991) and can probe the presence and timing of cortico-cortical connectivity (Matsumoto et al., 2004).

Functional and Structural Brain Imaging

Cognitive neuroscience arose as a distinct discipline at the same time as the emergence of functional brain imaging methods (PET, fMRI, EEG, and MEG) as major tools for the analysis of human cognition. Indeed, the prospect of visualizing human cognitive activity has been a major catalyst for the field. First used to analyze cognitive functions by the St Louis group (Petersen et al., 1988; see Functional Brain Imaging), these methods have come into widespread use. While these methods have low temporal and spatial resolution compared to neuronal recording studies, they still provide our best opportunity to explore the neural mechanisms underlying distinctly human cognitive functions.

The broad adoption of functional neuroimaging techniques since 1988 means that a vast array of methods and findings has emerged from this part of cognitive neuroscience (Bandettini, 2012). The full range of cognitive functions spanning from perception to higher cognitive functions including language, social interaction, and consciousness have been explored using these methods. The first and still very common use of functional neuroimaging is to localize function often with an aim to corroborate findings from other methods, and/or to explore commonalities and differences in human and animal brain organization. As an obvious extension to classical neuropsychology, such approaches have the advantages that, depending on the imaging technique, function can be probed across the entire brain simultaneously and for 'normal' function. Consequently, studies are not confined either to the limited number of recording locations offered with single cell recording or to the neural locations implicated by neurological disease or TMS. In addition to this, brain imaging has begun to reveal a great deal about the plasticity of the brain, since patterns of brain activation can change dramatically with practice (Karni et al., 1998) or after brain damage (Saur et al., 2006). The counterpoint limitation of functional neuroimaging, however, is the method does not identify which region(s) are necessary for that function – something that can only be derived from neuropsychology and TMS (Price and Friston, 2002).

As noted above, at the heart of cognitive neuroscience has been a debate between modular and distributed approaches to understanding human cognition. These same themes are apparent within functional neuroimaging. Thus, the early and still common use of the 'subtraction method' in neuroimaging (where brain activity for a specific cognitive component is identified by contrasting target and control activities that utilize the same assumed cognitive elements minus the key cognitive component) is based, at least implicitly, on a version of a modular view of brain function, which may be incorrect for a variety of reasons (Price and Friston, 2002). Functional neuroimaging, however, has tended to support a more distributed approach given that studies of cognitive function almost never elicit a single region but rather a broadly distributed 'network' of cortical and subcortical areas. Thus, more recently, alternative acquisition and analysis methods have been adopted, which consider cognitive function to be inherently distributed in nature either at whole brain or local levels. At the whole-brain systems level, many studies explore or extract the pattern of correlated activity across a set of regions from either spontaneous ('resting state') or task-based brain activity (referred to as 'functional connectivity') or investigate how the relationship between brain regions changes with respect to task- or stimulus-related factors ('effective connectivity'). At the local level, other approaches have adopted the principle that representations are likely to be distributed and may generate only small variations in local activity (i.e., within $\sim$1 mm^2 voxels) in keeping with multielectrode neurophysiological studies (see above). Accordingly, multivoxel pattern analyses investigate the pattern of activity observed across a patch of cortex in order to reveal how different types and levels of information for a set of stimuli are neurally coded (Kriegeskorte, 2011).

In addition to the investigations of neural function, neuroimaging techniques also provide important information about the anatomy of the brain. Indeed, before the advent of neuroimaging, attempts to relate patients' impairments to the pattern of underlying damage (neuropsychology) or investigations of the white-matter connectivity of the human brain were limited to postmortem studies. Modern structural neuroimaging has provided a method for investigating neuroanatomy in ever-increasing detail such that with high-field scanning and analysis methods, it is now becoming possible, for example, to image the layered structure of cortex in the living human brain (in vivo). This technological shift provides multiple novel opportunities for cognitive neuroscience including: (1) the ability to relate function and dysfunction (after brain damage or in neurodevelopmental disorders) to brain structure not only in vivo for each individual but across a much larger sample of individuals than is practically possible for postmortem studies, licensing correlational as well as intergroup comparisons (e.g., voxel-based lesion-symptom mapping: Bates et al., 2003); (2) the opportunity to map the white-matter connectivity between neural regions including the major long-distance neural pathways or fasciculi, and relate these to function and dysfunction; and (3) emerging possibilities to map subtle anatomical features of different brain areas in vivo.

Computational and Mathematical Modeling Approaches

While investigations relying on lesion and behavior approaches, neuronal recording studies, and functional brain

imaging have provided and will continue to provide the empirical evidence on which to build our understanding of the basis of cognitive functions in the brain, these approaches, even when used in a convergent way, may still fail to provide a complete understanding of how cognitive functions emerge from underlying neural activity. This may require the use of additional tools provided by mathematical modeling and computer simulation. These approaches allow researchers to formulate possible accounts of specific processes in the form of explicit models that can be analyzed mathematically or simulated using computers to determine whether they can account for all of the relevant neural and behavioral evidence. In short – like other sciences – purely analytical techniques are insufficient to build a true understanding, instead it is important to test and refine theories through synthesis.

Three examples of cases in which computational models have already led to new thinking will be briefly considered. First, a number of computational modeling studies have shown that many aspects of the receptive field properties of neurons and their spatial organization in the brain can arise through the operation of very simple activity-dependent processes shaped by experience and a few rather simple additional constraints (Linsker, 1986; Miller et al., 1989; see Neural Development: Mechanisms and Models). Second, models may aid in the understanding of the pattern of deficits seen in patients with brain lesions. Certain patients with an acquired dyslexic syndrome known as deep dyslexia make a striking type of error known as semantic errors; for example, the patient may misread apricot as 'peach.' In addition, all such patients also make visual errors, for example, reading sympathy and 'symphony.' Early, noncomputational accounts postulated that there must be multiple lesions underlying this disorder. However, computational models of the reading process (Hinton and Shallice 1991; see Cognitive Functions (Normal) and Neuropsychological Deficits, Models of) have shown that a single lesion affecting either the visual or the semantic part of an interactive neural network will lead to errors of both types. Thus, the coexistence of these errors may be an intrinsic property of the underlying processing architecture rather than a reflection of multiple distinct lesions. A third area where computational models have shed considerable light is in the interpretation of the receptive field properties of individual neurons (Zipser and Andersen, 1988). While initial interpretations were based on verbally describable features such as oriented bars or edges, such properties are not always apparent, and even when they are, a more detailed characterization may be possible in computational terms (Pouget et al., 1999). A further area of fertile research is in the use of computational models to explain and catalog the ways in which neuronal activation changes dynamically in the course of task performance (Moody et al., 1998).

Like all single methodologies in cognitive neuroscience, an important future step will be the fusion of computational and mathematical models with complementary neuroscience methods. Computational models have the capacity to include and test the implications of new findings at different levels of analysis, ranging from cellular/molecular influences on neuronal assemblies through to the question of how sophisticated high-order human cognition arises from interactions between widely distributed, interconnected cortical and subcortical regions. Perhaps even more excitingly, computational models may offer a formal mechanism to bridge between these different levels of analytical neuroscience (Ueno et al., 2011), ultimately offering a tangible link between brain and mind, which is the central, essential goal of cognitive neuroscience.

Open Issues in Cognitive Neuroscience

Cognitive neuroscience is young, and there is a great deal of work to be done. No aspect of cognition is fully understood, and in general, the more abstract or advanced the cognitive function, the less is known about its neural basis. A few of the most important and interesting issues that remain to be addressed are considered briefly here.

How Does the Brain Learn?

There is a great deal known about the basic mechanisms of synaptic plasticity, but typically these are studied in highly reduced preparations, such as brain slices. The basic processes that are studied in slices surely play a role in the shaping of neural connections in the whole, living brain, but they are also undoubtedly modulated by processes that are usually eliminated in slices. We know that attention and engagement in processing is essential for learning, and there is good reason to believe that learning is gated by various neuromodulatory mechanisms in the brain, but the details of the modulation and gating processes are only beginning to be explored.

What Makes an Experience Conscious?

Although some considerable progress has been made in characterizing the concomitants of consciousness (see Consciousness, Neural Basis of), there is no overall understanding of exactly what it is about the activity of the brain that gives it the attribute of consciousness. It appears likely that consciousness will not be localizable; although it may be highly dependent on specific brain structures (e.g., those that regulate sleep vs wakefulness, etc.), it may well depend on the intact functioning of many interacting parts of the brain. Exactly why or how consciousness arises from these interactions is not at all understood.

What Is the Basis for the Unique Cognitive Capacities of the Human Brain, Relative to that of Other, Simpler Organisms?

The issue of what sets humans apart from other organisms remains one of the central unresolved questions. The similarity of the human genome to that of closely related species can be taken in different ways. It can suggest to some that a very small number of specific faculties have been added that differentiate the human from, say, the chimpanzee; or it could suggest that rather than new faculties, the human brain really differs only in the expansion and extension of structures already present to a degree in other organisms. The idea that the highest cognitive functions are emergent functions rather than localizable or

locally encoded in genes remains an attractive, though elusive possibility.

The Future of Cognitive Neuroscience

Nobel laureate Eric Kandel has suggested that cognitive neuroscience will increasingly assume center stage in the neurosciences in the twenty-first century, and it has begun to make dramatic inroads into the field of cognitive psychology, where many leading investigators have redirected their research to exploit ideas and methods from neuroscience. Future research in cognitive neuroscience will address the general issues raised above as well as many other topics. What makes the future of the field so exciting is the prospect of further development of a number of important contributing methodologies. Breakthroughs in functional brain imaging and other related methods are likely to provide far greater spatial and temporal resolution of brain activity. Another, very important area of methodological advance is the ability to create genetically altered brains especially in small mammals and invertebrates, and thereby to explore the consequences of these alterations for function (*see* Genetic Approaches to Memory). These methods have already reached the point where it is possible to allow an organism to develop normally, and then induce a region-specific gene knockout, thereby providing the opportunity to investigate, for example, the effect of the alternation of synaptic plasticity in a specific part of the brain. Breakthroughs should be expected in many other areas of cognitive neuroscience as well, including neuronal recording, functional imaging, and computational modeling approaches. Together, these methods will lead to a deeper understanding of how the highest capabilities of the human mind arise from the underlying physical and chemical processes in the brain.

See also: Brain, Evolution of; Cerebral Cortex; Cognitive Control (Executive Function): Role of Prefrontal Cortex; Cognitive Neuropsychology, Methods of; Computational Neuroscience; Evolutionary Social Psychology; Human Cognition, Evolution of; Lesbian, Gay, Bisexual, Transgender, Queer: Bear and Leather Subcultures.

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