McCloskey M 2001 The future of cognitive neuropsychology. In: Rapp B (ed.) *The Handbook of Cognitive Neuropsychology*. Psychology Press, Philadelphia, pp. 593–610

Milner B 1958 Psychological deficits produced by temporal-lobe excision. *Research Publications, Association for Research in Nervous and Mental Disease* 36: 244–57

Moore C J, Price C J 1999 A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain* 122: 943–62

Mozer M C 1991 *The Perception of Multiple Objects*. MIT Press, Cambridge, MA

Mozer M C, Behrmann M 1990 On the interaction of selective attention and lexical knowledge: A connectionist account of neglect dyslexia. *Journal of Cognitive Neuroscience* 2: 96–123

Nielson J M 1946 *Agnosia, Apraxia, Aphasia: Their Value in Cerebral Localization*. Hoeber, New York

Patterson K E, Kay J 1982 Letter-by-letter reading: Psychological descriptions of a neurological syndrome. *Quarterly Journal of Experimental Psychology, Series A* 34: 411–41

Plaut D C 1995 Double dissociation without modularity: Evidence from connectionist neuropsychology. *Journal of Clinical and Experimental Psychology* 17: 291–321

Plaut D C, Shallice T 1993 Deep dyslexia: A case study of connectionist neuropsychology. *Cognitive Neuropsychology* 10: 377–500

Posner M I 1978 *Chronometric Explorations of Mind*. Erlbaum, Hillsdale, NJ

Ruml W, Caramazza A 2000 An evaluation of a computational model of lexical access: Comment on Dell et al. 1997 *Psychological Review* 107: 609–34

Saffran E M, Coslett B 1996 Attentional dyslexia in Alzheimer's disease: A case study. *Cognitive Neuropsychlogy* 13: 205–28

Shallice T 1988 *From Neuropsychology to Mental Structure*. Cambridge University Press, Cambridge, UK

Shallice T, Warrington E K 1970 Independent functioning of the verbal memory stores: A neuropsychological study. *Quarterly Journal of Experimental Psychology* 22: 261–73

Shallice T, Rumiati R I, Zadini A 2000 The selective impairment of the phonological output buffer. *Cognitive Neuropsychology* 17: 517–46

Stuss D T, Benson D F 1984 Neuropsychological studies of the frontal lobes. *Psychological Bulletin* 95: 3–28

Stuss D T, Alexander M P, Hamer L, Palumbo C, Dempster R, Binns M, Levine B, Izuakawa D 1998 The effects of focal anterior and posterior brain lesions on verbal fluency. *Journal of the International Neuropsychological Society* 4: 265–78

Warrington E K, McCarthy R 1983 Category specific access dysphasia. *Brain* 106: 859–78

Warrington E K, Shallice T 1984 Category specific semantic memory impairment. *Brain* 107: 829–54

T. Shallice

Cognitive Neuroscience

The discipline has emerged in the 1990s at the interface between the neural sciences and the cognitive and computational sciences. On one side, it grows out of the traditions of cognitive psychology and neuropsychology, which use behavioral experiments to uncover the processes and mechanisms lying behind human cognitive functions, and of computational approaches within cognitive psychology, which rely on computational models to develop explicit mechanistic accounts of these functions. On the other side, it grows out of the traditions of behavioral, functional, and systems neuroscience, which use neurophysiological and neuroanatomical methods to explore the mechanisms underlying complex functions. It draws on findings and principles of cellular and molecular neuroscience. It joins these approaches with the use of new functional brain imaging methods, such as functional magnetic imaging (fMRI), positron emission tomography (PET), as well as other methods including electroencephalography (EEG) and magnetoencephalography (MEG), and with a growing research tradition in computational neuroscience.

1. The Microstructure of Cognition

1.1 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 an individual has when holding, sniffing, and viewing a rose is a complex pattern of neural activity, distributed over many brain regions, including the participation of neurons in visual, somatosensory, and olfactory, and possibly extending to language areas participating in representing the sound of the word 'rose' and/or other areas where activity represents the content of an associated memory that may be evoked by the experience.

These patterns of activation arise from excitatory and inhibitory interactions among the participating neurons, mediated by connections called synapses. The inputs neurons receive cause them to 'fire' or emit impulses called spikes or action potentials, which travel down their axons to synaptic terminals where they cause the release of chemicals 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 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 3×3 mm) are indicated. While the computations performed by individual neurons should not be underestimated (see *Neurons and Dendrites: Integration of Information*), 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) and of the density of
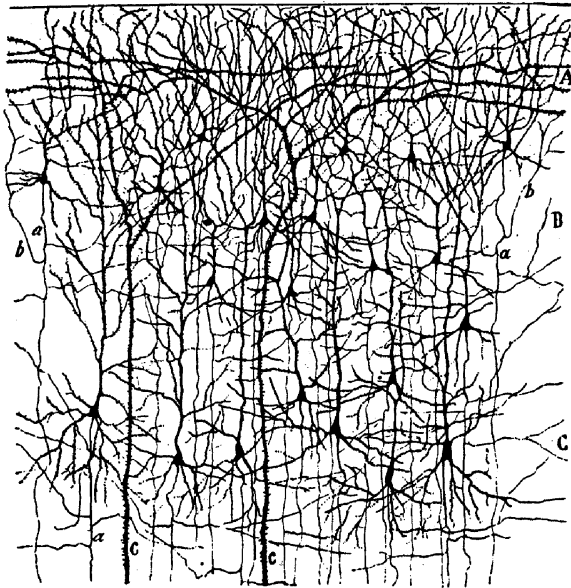
Figure 1
An early camera lucida drawing of the circuitry of the neocortex, based on the Golgi stain method, which impregnates just one out of every 100 cortical neurons. The diagram depicts the rich dendritic branching structure of the individual neurons present, whose cell bodies appear as small, pyramid-shaped 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

connections among them (typical cortical neurons receive between 10,000 and 100,000 individual synapses from other neurons).

1.2 Distributed Representations

A great deal of research has concerned the nature of the active representations the brain uses for objects of perception or cognition, such as the rose discussed above. There is now a great deal of support for the view that the brain's representations typically consist of patterns of activity involving fairly large ensembles 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 the representation of the direction of arm movements in the motor cortex. It appears that the representation of a particular direction of reaching is a pattern 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 in performing different tasks (Markus et al. 1995).

1.3 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 basis 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 likely also 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.

2. System-level Organization: The Macrostructure of Cognition in the Brain

2.1 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, or representation of one's location in extra-personal 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 other systems in the thalamus, lymbic system, and cerebellum.
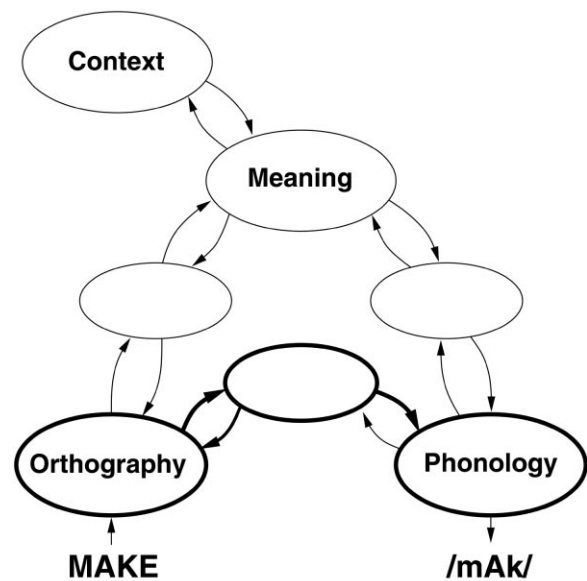

Figure 2
The interactive, distributed framework for modeling individual word reading of Seidenberg and McClelland 1989. All of the relevant processing pathways are assumed to be bidirectional

2.2 Modular vs. Interactive Approaches to the Organization of Function

The above provides only the starting place for the formulation of an understanding of how cognitive processes arise from neural activity. There are two contrasting views: (a) The modular approach, championed by David Marr for vision and Noam Chomsky for language, and systematized as a general approach 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 is thought to be governed by the operation of a system of structure sensitive rules. The module that carries out this assignment is thought 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

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primary and secondary cortical areas and their sub-cortical 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 by 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 Fig. 2. As the figure suggests, the formation of the sound of a word from a visual input specifying its spelling 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 specialized for representing different types of information. Where they differ is in the extent and the role of bidirectional interactions among participating brain areas.

2.3 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.

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 (Hup 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 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.

3. 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.

3.1 Lesion and Behavior Approaches (Cognitive Neuropsychology and Behavioral Neuroscience)

These research approaches within the field 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*; *Aphasia*; *Dyslexia (Acquired) and Agraphia*). The subdiscipline of cognitive neuropsychology has arisen specifically around the study of the effects of brain lesions (see *Cognitive Neuropsychology, Methodology of*). A complementary 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 (see *Lesion and Behavior Approaches in Neuroscience*). 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*). However, the approach is not without its pitfalls, since a lesion may have unintended and unobserved effects in other brain regions; the refinement and extension of experimental lesion techniques is ongoing.

3.2 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, some of which have been discussed above. These studies indicate, among other things, that the brain relies on distributed representations, that neurons participate dynamically and interactively in the construction of representations of external inputs, and that the representational significance of the firing of a particular neuron can vary as a function of context. 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 the 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 they will be after the upcoming eye movement (Duhamel et al. 1992).

An important recent development is the ability to record from up to 100 individual neurons at a time (see *Perception and Cognition, Single-/Multi-neuronal Recording Studies of*). 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). Such methods are in their infancy, but their potential 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.

3.3 Functional Brain Imaging

Cognitive neuroscience has arisen as a separate discipline in tandem with the emergence of functional brain imaging methods (PET and fMRI) as major tools for the analysis of human cognition, and it may be that the prospect of visualizing specifically human cognitive activity has been a major catalyst. First used to analyze cognitive functions by the St. Louis group (Petersen et al. 1988; see *Functional Brain Imaging*), these methods are now coming into widespread use. While these methods currently 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.

To date the observations arising from functional imaging studies have tended to corroborate findings from other methods, and/or to explore commonalities and differences in human and animal brain organization. As one recent example, it has now been possible to visualize the alternating strips in visual cortex reflecting what are known as ocular dominance stripes. Beyond corroboration, a great deal of new information has also been provided by functional brain imaging studies. For example, in a fairly early PET study, investigators found that an area of the cerebellum became active when subjects were required to generate the action that goes along with a concrete object (e.g., the word HAMMER requires a response such as 'pound'). Subsequent investigation of an individual with damage to this region of the cerebellum indicated that the patient had considerable difficulty with the generation task, confirming the importance of this area in the task.

Brain imaging studies, like lesion studies, have often been used to try to determine the loci in the brain associated with particular cognitive functions. However, 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). Imaging is also being used in search of distributed networks in the brain that contribute to particular cognitive functions. For example, Just et al. (1996) have shown that as sentences become more complex, there is an increase in neural activity in an ensemble of brain regions, including Broca's and Wernicke's area on both the left and to a lesser degree the right side of the brain. As another example, investigators have begun to use covariation in neural activity in different brain regions in an effort to determine which brain regions are influencing each other's activation (Maguire et al. 2000) in different task situations.

Imaging methods (including magneto and electro-encephalography, as well as fMRI and PET) are likely to improve dramatically over time, allowing far higher spatial and temporal resolution. The potential for this to bring us closer to the goal of understanding the

details of information processing in the human brain will be discussed below.

3.4 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.

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 form or 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 two separate lesions, one affecting visual processing and the other affecting semantic processing. 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).

4. 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.

4.1 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.

4.2 What Makes an Experience Conscious?

Although some considerable progress has been made in characterizing the concomittants 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.

4.3 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 which 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.

5. 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 *Memory: Genetic Approaches*). 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: Animal Cognition; Brain, Evolution of; Cerebral Cortex: Organization and Function; Cognitive Control (Executive Functions): Role of Prefrontal Cortex; Cognitive Neuropsychology, Methodology of; Cognitive Psychology: History; Cognitive Psychology: Overview; Cognitive Science: History; Cognitive Science: Overview; Cognitive Science: Philosophical Aspects; Comparative Neuroscience; Computational Neuroscience; Evolutionary Social Psychology; Human Cognition, Evolution of

Bibliography

Broca P 1861 Remarques sur le siege de la faculte de la parole articulee, suives d'une observation d'aphemie (perte de parole). *Bulletin de la Societe d'Anatomie* **36**: 330–57

Callan D E, Callan A M, Kroos C, Vatikiotis-Bateson E 2000 Multimodal contribution to speech perception. *Cognitive Brain Research*

Damasio A R 1989 Time-locked multiregional retroactivation: A system-level proposal for the neural substrates of recall and recognition. *Cognition* **33**: 25–62

Duhamel J-R, Colby C L, Goldberg M E 1991 Congruent representations of visual and somatosensory space in single neurons of monkey ventral intraparietal cortex (area VIP). In: Paillard J (ed.) *Brain and Space*. Oxford University Press, Oxford, UK, pp. 223–6

Duhamel J-R, Colby C L, Goldberg M E 1992 The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* **255**: 90–2

Fodor J A 1983 *Modularity of Mind: An Essay on Faculty Psychology*. MIT Press, Cambridge, MA

Georgopoulos A P, Schwartz A B, Kettner R E 1986 Neuronal population encoding of movement direction. *Science* **233**: 1416–9

Graziano M S A, Gross C G 1993 A bimodal map of space: Somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Experimental Brain Research* **97**: 96–109

Hebb D O 1949 *The Organization of Behavior*. Wiley, New York

Hinton G E, Shallice T 1991 Lesioning an attractor network: Investigations of acquired dyslexia. *Psychological Review* **98**(1): 74–95

Hubel D H, Weisel T 1962 Receptive fields, binocular orientation and functional architecture in the cat's visual cortex. *Journal of Physiology* **166**: 106–54

Hup J M, James A C, Girard P, Lomber S G, Payne B R, Bullier J 2001 Feedback connections act on the early part of the responses in monkey visual cortex. *Journal of Neurophysiology* **85**: 134–45

Just M A, Carpenter P A, Keller T A, Eddy W F, Thulborn K R 1996 Brain activation modulated by sentence comprehension. *Science* **274**(5284): 114–6

Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams M M, Turner R, Ungerleider L G 1998 The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Science USA* **95**(3): 861–8

Lee T S, Mumford D, Romero R, Lamme V A F 1998 The role of primary visual cortex in higher level vision. *Vision Research* **38**: 2429–54

Lee T S, Nguyen M 2001 Dynamics of subjective contour formation in early visual cortex. *Proceedings of the National Academy of Science USA*

Linsker R 1986 From basic network principles to neural architecture, I: Emergence of orientation columns. *Proceedings of the National Academy of Sciences USA* **83**: 7508–12

Luria A R 1966 *Higher Cortical Functions in Man*. Basic Books, New York

Maguire E A, Mummery C J, Buchel C 2000 Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. *Hippocampus* **10**(4): 475–82

Markus E J, Qin Y, Leonard B, Skaggs W E, McNaughton B L, Barnes C A 1995 Interactions between location and task affect the spatial and directional firing of hippocampal neurons. *Journal of Neuroscience* **15**: 7079–94

Mesulam M M 2000 *Principles of Behavioral and Cognitive Neurology*. Oxford University Press, New York

Moody S L, Wise S P, di Pellegrino G, Zipser D 1998 A model that accounts for activity in primate frontal cortex during a delayed matching-to-sample task. *Journal of Neuroscience* **18**(1): 399–410

Olson C R, Gettner N 1995 Object-centered direction selectivity in the supplementary eye field of the macaque monkey. *Science* **269**: 985–8

Petersen S E, Fox P T, Posner M I, Mintun M, Raichle M E 1988 Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* **331**: 585–9

Pouget A, Deneve S, Sejnowski T J 1999 Frames of reference in hemineglect: A computational approach. *Progress in Brain Research* **121**: 81–97

Rumelhart D E, McClelland J L, the PDP Research Group 1986 *Parallel Distributed Processing: Explorations in the Microstructure of Cognition. Vol. 1: Foundations*. MIT Press, Cambridge, MA

Seidenberg M S, McClelland J L 1989 A distributed, developmental model of word recognition and naming. *Psychological Review* **96**: 523–68

Tanaka K 1996 Inferotemporal cortex and object vision. *Annual Review Neuroscience* **19**: 109–39

Ungerleider L G, Mishkin M 1982 Two cortical visual systems. In: Ingle D J, Goodale M A, Mansfield R J W (eds.) *Analysis of Visual Behavior*. MIT Press, Cambridge, MA

Wilson M A, McNaughton B L 1994 Reactivation of hippocampal ensemble memories during sleep. *Science* **265**: 676–9

Zipser D, Andersen R A 1988 A back propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* **331**: 679–84

J. L. McClelland

Cognitive Psychology: History

Since the beginning of experimental psychology in the nineteenth century, there had been interest in the study of higher mental processes. But something discontinuous happened in the late 1950s, something so dramatic that it is now referred to as the 'cognitive revolution,' and the view of mental processes that it spawned is called 'cognitive psychology.' What happened was that American psychologists rejected behaviorism and adopted a model of mind based on the computer. The brief history that follows (adapted in part from Hilgard (1987) and Kessel and Bevan (1985)) chronicles mainstream cognitive psychology from the onset of the cognitive revolution to the beginning of the twenty-first century.

1. Beginnings

From roughly the 1920s through the 1950s, American psychology was dominated by behaviorism. Behavior-ism was concerned primarily with the learning of associations, particularly in nonhuman species, and it constrained theorizing to stimulus–response notions. The overthrow of behaviorism came not so much from ideas within psychology as from three research approaches external to the field.

1.1 Communications Research and the Information Processing Approach

During World War II, new concepts and theories were developed about signal processing and communication, and these ideas had a profound impact on psychologists active during the war years. One important work was Shannon's 1948 paper about *Information Theory*. It proposed that information was communicated by sending a signal through a sequence of stages or transformations. This suggested that human perception and memory might be conceptualized in a similar way: sensory information enters the receptors, then is fed into perceptual analyzers, whose outputs in turn are input to memory systems. This was the start of the 'information processing' approach—the idea that cognition could be understood as a flow of information within the organism, an idea that continues to dominate cognitive psychology.

Perhaps the first major theoretical effort in information processing psychology was Donald Broadbent's *Perception and Communication* (Broadbent 1958). According to Broadbent's model, information output from the perceptual system encountered a filter, which passed only information to which people were attending. Although this notion of an all-or-none filter would prove too strong (Treisman 1960), it offered a mechanistic account of selective attention, a concept that had been banished during behaviorism. Information that passed Broadbent's filter then moved on to a 'limited capacity decision channel,' a system that has some of the properties of short-term memory, and from there on to long-term memory. This last part of Broadbent's model—the transfer of information from short- to long-term memory—became the salient point of the dual-memory models developed in the 1970s.

Another aspect of Information theory that attracted psychologist's interest was a quantitative measure of information in terms of 'bits' (roughly, the logarithm to the base 2 of the number of possible alternatives). In a still widely cited paper, George Miller (1956) showed that the limits of short-term memory had little to do with bits. But along the way, Miller's and others' interest in the technical aspects of information theory and related work had fostered mathematical psychology, a subfield that was being fueled by other sources as well (e.g., Estes and Burke 1953, Luce 1959, Garner 1962). Over the years, mathematical psychology has frequently joined forces with the information