

Cognitive neuroscience

Editorial overview: Beyond images

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Abbreviations

EEG electroencephalogram
REM rapid eye movement

Introduction

When we first edited an issue of this journal in 1994 [1], the ability to image the human brain dominated the field. Topics such as ‘integrating human brain maps’ [2] and ‘what and where in the human brain’ [3] reflected the interest in localizing cognitive operations within the human brain. The current issue fully reflects the continuing importance of imaging the brain’s functional anatomy (see, for example, the review by Fox, Parsons and Lancaster, pp 178–187), but more emphasis is now placed upon characterizing the interactions between various brain areas as they carry out cognitive functions in real time (see Hillyard, Teder-Sälejärvi and Münte, pp 202–210, and Treisman and Kanwisher, pp 218–226). In addition, it is now becoming possible to relate regional brain areas found active during imaging studies in humans with potential homologous areas in other animals, which may compute the same or related function (see Schall and Bichot, pp 211–217). Connecting human and animal work in this way makes it possible to relate computations of individual cells (see Wiggs and Martin, pp 227–233, and Baddeley, pp 234–238) or their genetic precursors (see Hobson *et al.*, pp 239–244) to the regional brain activity found in imaging studies. One might say that the focus of the brain imaging field is shifting from asking ‘where’ cognitive operations take place to asking ‘how’ they take place.

We have divided this overview into three sections. First, we discuss the reviews concerning interaction of brain areas in performing cognitive functions. Second, we consider the analysis of brain states, such as sleep, attention, and development. Finally, we examine pathologies attributable to brain injury, genetic abnormality or psychopathology, and the possibility of methods to aid their remediation.

Interaction of brain areas

The first achievement of brain imaging was to show that circumscribed brain areas have increased or reduced activity during cognitive tasks. Generally, networks of specific areas were found to be active in tasks ranging from obtaining the use of a word to acquiring a new sequence of spatial locations. Metanalysis has proven an important vehicle for summarizing the almost overwhelming number of brain areas that have been described over the past ten years. The logic of combining data from different studies about brain regions that display changes in activity during similar tasks is thoroughly described by Fox *et al.* Their review raises many of the statistical problems and biases in selection that are problems for this field. Despite the many difficulties that are raised in their review, one must nevertheless be impressed with the general degree of convergence across laboratories, methods and modalities.

The problem of combining results from different studies, different techniques, and even different primate species has recently been made much easier in the sensory processing areas of the cortex as a result of advances in brain mapping techniques (see the review by Sereno, pp 188–194). The combination of phase-encoded visual stimulation, brain flattening algorithms, and the high spatial resolution of functional magnetic resonance imaging (fMRI) has led to retinotopic maps of human visual areas thought to be homologous to areas V1, V2, V3, V3a, MT/V5, VP, and V4v in macaque monkeys. When retinotopic mapping is combined with functional activation studies of motion, color, shape, and other object features in human cortex, it becomes possible to directly link the properties of human cortical areas to the properties of neurons in their monkey counterparts.

Although spatial maps exist in several cortical regions beyond the early sensory processing areas, these higher-order maps appear to bridge the gap between maps of the sensory surfaces, on the one hand, and the maps of the final motor output, on the other (see the review by Graziano and Gross, pp 195–201). In the ventral premotor cortex, for example, neurons have visual receptive fields closely tied to body parts, such as the hand, and these visual fields move with the body part rather than with the retina. The information to construct these body-centered maps of space is probably relayed through the anatomical projections to premotor cortex from the parietal cortex, where visual, tactile, proprioceptive, and efference copy inputs converge to create several different spatial coordinate frames for representing both incoming

stimuli and body parts. Behavioral analyses coupled with imaging and electrophysiological measures are beginning to reveal the temporal dynamics of the sensory–motor transformation.

In the 1960s, cognitive psychologists showed that a wide variety of tasks could be described in terms of mental operations (subroutines) that took place over tens to hundreds of milliseconds. Sometimes, the timing is constrained by the nature of the task. For example, a skilled reader averages only about 275 ms for an individual fixation. There is clear evidence that the length of the saccade that follows the fixation is influenced by the meaning of the fixated word. Thus, 275 ms sets an upper bound to achieve the word meaning sufficiently to convey appropriate information to the saccadic eye movement system. In this case, and in the study of faces and scenes, the constraints of natural behavior set a strong upper bound on the time course of mental operations.

For several decades, event-related electrical potentials recorded from EEGs in humans have been important for tracing the real-time activity of cognitive processes. However, with the advent of imaging techniques, it is now possible to relate the scalp activity to generators obtained from blood flow measures in humans (see the review by Hillyard *et al.*) and neurophysiological measures in animals (see the review by Schall and Bichot). While the earliest parts of the event-related potential are primarily driven from the sensory event, top-down attentional influences are clearly evident in human cortex within 100 ms (see Hillyard *et al.*). Likewise, neurophysiological studies in animals indicate that the sensory representation of all objects present in the visual field rapidly evolves into a more exclusive representation of behaviorally relevant objects, one of which may eventually become the target of an eye movement (see Schall and Bichot). As even quite early extrastriate visual areas can show top-down influences, it has become very important to document the time course of activity in neural substrates in the millisecond range to distinguish pure sensory from top-down influences. The importance of these time-course measures is well documented in processes involved in the perception of objects (see the reviews by Treisman and Kanwisher and by Schall and Bichot). Several types of representation are constructed by the visual system, allowing subjects to recognize, prepare actions and construct preferences toward sensory events. These separate pathways become active in parallel and allow for recognition of up to eight objects per second, showing clearly that awareness of the object is critically dependent upon the first 100 ms following input. The difference between the activation caused by novel and familiar objects can be shown in ventral visual areas within 170 ms after input (see the review by Treisman and Kanwisher).

Neurophysiological studies in animals that present the same item on successive occasions (repetition priming)

show that a single repetition of an object can lead to dropping out of many of the neurons active during its first presentation (see the review by Wiggs and Martin). Behaviorally, as repetitions allow faster reaction times to identify the primed item, the degree of attention given the item may be reduced. Reductions in blood flow indicate tuning or selection of the neural activity needed to process the items. The discovery of how priming takes place in ensembles of neurons fits well with the automatic priming results postulated from cognitive studies of the 1970s. Priming can occur without awareness and improves the efficiency of reaction time. These results contrast with improvements in reaction time that can be produced by attending to an event. In cognitive studies, attention to the prime serves to improve processing of a related target, but slows processing of items unrelated to the prime. Correspondingly, attention has usually been shown to produce a marked increase in blood flow, for example, within extrastriate areas encoding color, form or motion. An understanding of the relation of improvements due to priming and due to attention can, according to Wiggs and Martin “be expected to play a pivotal role in memory research”.

Priming is a form of memory that can be completely implicit or that can be attended. Once attended, such items can be held briefly in working memory (see the review by Baddeley). The anatomy of verbal, spatial and object working memory has been greatly clarified by imaging studies. Each domain appears to involve both frontal and posterior areas. Recent imaging studies suggest that the frontal and posterior components are not involved in the same operations. For example, rehearsal of verbal information appears to involve frontal areas, while the posterior areas hold rehearsed information in a temporary store. The idea of a phonological loop appears directly supported by the anatomical connectivity between anterior and posterior areas. A number of the recent papers reviewed by Baddeley have attempted to examine how these domain-specific memory systems relate to a central executive controller.

Brain states

The brain changes remarkably as we shift from sleep to wake, from slow wave sleep to REM (rapid eye movement) sleep and even from inattentive to focal attention within the waking state. The changes in brain activity that accompany some of these states has recently been clarified by a number of functional imaging studies (see the review by Hobson *et al.*). Slow wave sleep produces an overall reduction in metabolism within the thalamus, orbitofrontal and cingulate areas. There is also increased synchrony in thalamo-cortical loops recorded by EEG. Activation during positron emission tomography (PET) studies of slow wave sleep contrasts markedly with the increases in brain activity in the same areas during REM dreaming. These new findings may allow us to understand much more about the mental processes during

the dream state and to connect them with studies of attention in the awake state. The cingulate activity found during REM sleep, for example, has also been shown to be an area of high activity during the focused attention state when awake.

Even within the waking state, there are clear differences in brain activity as we shift from general alertness toward the world around us to focal concentration on one (or more) modality. Much of what we know about attention comes from concentration upon a single modality, but there is nothing more common in our daily experience than objects or events that represent combined sensory experiences (see the review by Driver and Spence, pp 245–253). Careful cognitive and imaging studies can begin to tease apart the mechanisms by which the separate sensory modalities become integrated in our experience. In waking as in sleep, many of these mechanisms arise automatically and allow us to bring to mind already integrated representations of our external environment. Just as studies of vision have shown that parallel pathways can be integrated into unified perceptual objects (see the review by Treisman and Kanwisher), similar mechanisms appear to be involved in crossmodal integration.

The first few years of life bring about the most radical changes in the brain. Perhaps the most striking of all these changes is the development of language. The anatomy of language has been known in a general way for about a 100 years, but imaging modalities have pinpointed key areas of auditory, phonological, semantic and grammatical information. By comparing English with American Sign Language, it is possible to show how vast a difference there can be in the anatomy of languages when they differ in their input and output modes (see the review by Neville and Bavelier, pp 254–258). Sign language is usually learned by people without auditory experience, but the contrast between hearing and deaf native signers provides a window for viewing how both sensory and language experience organize our brains. We will need to know much more about how brains at different ages acquire skills and how that acquisition influences their future development.

Pathology

Disorders of mood, including depression, anxiety and panic, are the growing mental illnesses of our generation. Schizophrenia combines emotional and cognitive abnormalities. Imaging studies (see the review by Frith and Dolan, pp 259–262) have provided a new perspective of some of these disorders. Imaging can be used to connect neurochemical views (e.g. dopamine theories of schizophrenia) to particular brain areas (such as the dorsolateral prefrontal cortex and anterior cingulate). In so far as the disorders show different cognitive and emotional symptoms, one would expect different computations and thus different brain areas to be involved. The imaging approach could be used to group patients with common

symptoms, or phenotype, in order to determine sources of the pathology.

It may seem ironic that attention deficit disorder, which has been one of the most controversial of illnesses, has been among the first forms of developmental disorder to engender an analysis at levels from the gene to the behavior (see the review by Swanson *et al.*, pp 263–271). Only in the past few years has it become clear that the prevalence of the disorder, and the extent to which it has a genetic precursor, depends so critically on constraining the diagnosis to avoid many types of related disorders. Once this is done and there is more consistency across cultures, the possibility of understanding the neural systems, transmitters and genes involved improves. The story of recent developments in this area, well laid out in the review by Swanson *et al.*, and the role of attentional networks in forming a link between normal function (see the review by Driver and Spence) and pathology, suggests that our understanding of other pathologies will improve as we are better able to understand normal function of the networks related to them.

Genetic approaches in animals are opening up new avenues of understanding, not only of many different pathological states that affect cognition, but also of the circuitry that underlies normal cognition (see Lipp and Wolfer, pp 272–280). The bulk of the cognitive work in genetically modified mice has been directed at long-term potentiation (LTP), spatial memory, and the hippocampus, although many of the basic cellular mechanisms of memory in the hippocampus are probably shared in every brain structure. Careful behavioral and neurophysiological analyses of genetically modified animals indicate that even single-gene mutations typically do not have all-or-none effects on spatial memory but affect cognitive abilities and strategies in ways that are often complex and subtle.

Traumatic brain injury changes the organization of the brain in a swift and dramatic way. Difficulties in attending and remembering are frequent consequences of this change (see the review by Wilson, pp 281–287). Imaging methods open up the possibility of an improvement in therapies by allowing empirical investigation of the brain changes that relate to the improvement in behavior. The increasing evidence that rehabilitation can improve functioning documented by Wilson needs to be accompanied by an effort to view the changes in structures, circuits or strategies that might form the basis of successful remediation.

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