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Editorial

Beyond the decade of the brain: towards a functional neuroanatomy of the mind

1. Introduction

The 1990s was called “the decade of the brain”. The amount of knowledge gained from investigating the neural basis of behaviour and cognition was unprecedented. As a result, a new interdisciplinary field emerged, the cognitive neurosciences, specifically devoted to understanding brain–mind relationships. Tremendous progress has been made: five years after the first monumental edition of *The Cognitive Neurosciences* (Gazzaniga, 1995, MIT Press), a second equally monumental (and almost completely new) edition was published, titled *The New Cognitive Neurosciences* (Gazzaniga, 2000, MIT Press). Some fainthearted will be daunted by so much newly accumulated knowledge in such a short time span and would want to give up attempting to follow that progress. But then others would happily take over. In fact, some neuroscientists have already been so enthusiastic about this progress that they forget that there is more to understanding behaviour and cognition than tracing the neural activities alone. For example, in his *Principles of Neural Science* the most recent Nobel laureate in medicine, Eric Kandel, states that “the goal of neural science is to understand the mind – how we perceive, move, think, and remember” (Kandel, Schwartz, & Jessell, 2000, p. xxxv). Some psychologists will be shocked by this kind of statement because understanding the mind was supposed to be the traditional territory of psychologists.

In reaction perhaps, the American Psychological Association declared the new decade “the decade of behaviour”, but simply replacing the “brain” with “behaviour” will not help much. Instead, it is better for psychologists to maintain and extend their contributions to this newly emerged field of science. In stronger words, it is necessary that scientists, who are highly educated in asking questions about mental functions and conducting well-controlled experiments to try to answer them, keep track of what is going on. We believe there are many important aspects to know about mental processes in addition to identifying correlated activities in the brain. Although brain mapping has sparked a lot of interest in the broad scientific community (as testified by the large number of functional localisation studies published in *Nature* and *Science*), many psychologists have retained a healthy dose of scepticism. In addition to the serious methodological problems, which some cognitive

neuroscientists pretend not to matter much, the question must be asked what insight in the mental processes themselves is gained by knowing its localisation in the brain.

The editors of *Acta Psychologica* found the time ripe to look back on the achievements of the decade of the brain, and to encourage psychologists to go beyond pure localisation, in the direction of a detailed functional understanding of mental processes. Insight in the neural basis of these mental processes is then simply part of a deep and multi-leveled understanding of one of the final frontiers of science: the mind. This is a quite different enterprise than the neuroreductionist one, which is often taken for granted in the cognitive neurosciences.

In an attempt to convince our readership of the role which experimental psychology has to play in this endeavour, the board of editors has taken the initiative for two special issues. The first one of these, "Brain activity and cognitive processes" (vol. 105, no. 2–3), edited by Wolters and Nyberg, was mainly focussed on memory. The second one, which you currently have before your eyes, consists of 13 papers on a variety of issues within the general context sketched above. Some review the progresses made regarding specific mental functions (e.g., motion perception, speech production). Others introduce new techniques that help circumvent some of the problems with conventional neuroimaging methods (e.g., transcranial magnetic stimulation, functional magnetic resonance adaptation, pathway analysis of brain activity). Some authors attempt to sketch new theoretical frameworks to understand age-old problems like awareness and face perception. And many if not all of the papers argue for converging evidence from a large number of different approaches: neuropsychological studies with brain-damaged patients, single-cell recordings from awake monkeys, functional neuroimaging with high spatial resolution as well as high temporal resolution, etc.

Below are the previews of the major contributions from the individual papers included in this special issue. These papers were written on invitation from the editors, after a screening of proposed summaries, and they have been reviewed by at least two expert reviewers and by one of the editors. To preserve the anonymity of the reviewers, their assistance will be acknowledged in the list of reviewers published at the end of 2001.

2. Overview

Savoy sets the stage for this special issue. He presents a thorough review of the history of human brain mapping and functional neuroimaging. More specifically, he starts by sketching early attempts to localise mental functions in the human brain such as case studies of brain damaged patients and direct cortical stimulation. He then discusses the whole range of modern techniques: transcranial stimulation techniques (magnetic and electrical), electromagnetic recording techniques (EEG and MEG), and techniques based on hemodynamic responses (PET, fMRI, and optical imaging). He describes the physical and biological basis of these techniques as well as their implications for experimental design and their limitations. In a final section on current research, *Savoy* discusses a number of interesting future direc-

tions, including an increased role of behavioural data and new attempts to go beyond local activations. The whole article is pervaded with a great concern for methodology and a plea for better functional models. It is worth reading this paper twice: once as an introduction to the special issue and once as a conclusion after you have read all the other articles.

Creem and Proffitt deal with the issue of how to partition the visual system into structurally and functionally distinct subsystems, a central topic in the cognitive neurosciences known as functional neuroanatomy. They start from Ungerleider and Mishkin's well-known division between a ventral "what" stream for object information and a dorsal "where" stream for spatial information. They then discuss Goodale and Milner's alternative view of the dorsal stream as a "how" system for transforming the information in preparation for direct action. In the third and final part of their paper, Creem and Proffitt outline their own proposal for a structural and functional organisation of both a "where" and a "how" system within the posterior parietal lobe. This paper exemplifies the multi-method approach in the current cognitive neurosciences: their review draws from psychophysics, neurophysiology (single-cell recordings and ablation studies), neuropsychology, and neuroimaging. A diverse set of findings is integrated into a coherent theoretical framework, which will hopefully inspire future work on this topic too.

Culham, He, Dukelow and Verstraten review the contributions from neuroimaging studies to our understanding of visual motion perception in the human brain. They too focus on the complementarity of neuroimaging in relation to the more traditional techniques of psychophysics, neurophysiology and neuropsychology. Neuroimaging has verified and extended findings from other techniques but it has also identified numerous motion-sensitivity areas throughout the brain in addition to the MT/MST complex. Even more interestingly, neuroimaging has examined top-down influences on motion perception and the neural correlates of awareness, all of which are much more difficult to study with other techniques. In addition to providing a solid state-of-the-art review, Culham and her colleagues have also speculated a bit on possible future developments like the improved temporal resolution of single-event designs, the investigation of cell-population relationships, and structural equation modelling of the interactions between the different motion areas.

Munhall's paper is the only paper in this special issue that does not deal with visual perception (or does not even touch upon it) but it takes a very similar approach as some of the other papers. He reviews the contributions of functional imaging to the understanding of speech production. A range of specialised motor and cognitive processes are involved whose underlying neural mechanisms can now be visualised in large numbers of normal and disordered subjects. Like other papers in this special issue, Munhall also deals with the methodological concerns of this research. More specifically, for speech production, one of the challenges is in the measurement of the vocal tract and of the neural activity during overt speech. In addition, fundamental questions about the planning units of speech, the role of feedback during speech and the influence of learning must be addressed, which requires better psychological theories and methods to measure task performance. This

demonstrates that psychologists have a major role to play in the further development of the cognitive neurosciences.

Humphreys and Price also touch upon speech production and speech comprehension, in addition to picture naming, object identification, and visual attention, in the context of a thorough discussion of the relations between functional neuroimaging and cognitive neuropsychology. They make a distinction between accounts of cognitive performance at a neural level and a functional level of description. They then discuss a great number of difficulties in making neural-level arguments from neuropsychological data and they consider how neuroimaging can remediate these problems and complement cognitive neuropsychology. It can reveal the brain systems which are necessary and sufficient for a particular cognitive task and it allows tests of neural-level models of cognition. In addition, Humphreys and Price argue that neuroimaging studies can contribute directly to functional-level theories of cognition. Knowing the neural locus of a functional component of some cognitive process can also inform us about how a cognitive process is performed. Although not all contributors to this special issue are equally optimistic about the achievements of neuroimaging, the views of Humphreys and Price on these issues clearly deserve great attention if one is interested, as many psychologists are, in functional-neuro-anatomical models of cognition.

The same topic is addressed in a parallel paper by *Parsons*, which is also focussed on the relations between cognitive psychology, functional neuroimaging and behavioural neurology (or cognitive neuropsychology). He clearly demonstrates the two-way traffic between the different disciplines dealing with brain–mind relationships, by reviewing two lines of his own research. In the first series of studies on object recognition and mental imagery, the nature of a particular cognitive process is clarified by the use of these three different methodological approaches. In the second series of studies on cutaneous, tactile, and auditory pitch discrimination, the function of a particular brain structure, the cerebellum, is elucidated by the use of the same three methods. These two lines of work clearly show that integration of knowledge about brain structures and mental functions is possible and useful. Based on his own experience and his personal view, Parsons also presents several key issues that must be addressed to facilitate such an integrative approach.

De Gelder and Rouw apply the same integrative approach to a specific hot topic in the cognitive neurosciences, face perception. Face perception has often been described as the prime example of specialisation (or modularisation) of the brain. Single-cell recordings and lesion studies in monkeys as well as cognitive neuropsychological studies in brain-damaged patients with specific problems in face perception (so-called “prosopagnosia”) and recent fMRI studies of a dedicated face area in the fusiform gyrus, all provide strong evidence in support of an area with face specificity. Nevertheless, De Gelder and Rouw review some recent behavioural results with prosopagnosias and neuroimaging results on face and object recognition in normal subjects, which require more complex explanations that go beyond localisation of the face area. They propose a dual-route account of face perception within which the diverse findings can be understood. They make a distinction between a face-specific detection system and a system for identification which is part of the

general object recognition system but which becomes face specific by its interaction with the detection system. The model is applied to the role of configural (or whole-based) versus featural (or part-based) processing of faces.

The next paper, by *Lamme*, is similar in nature in that it offers a new, rather speculative account of a classic and very interesting phenomenon, blindsight. The idea is that visual awareness critically depends on re-entrant cortico-cortical connections, while unconscious visuo-motor transformations like those involved in forced-choice motor commands may be executed in a purely feedforward fashion. *Lamme* provides supporting evidence for this idea from a great number of different studies: neuropsychological case studies, lesion studies in monkeys (including recent anaesthesia and cooling studies), single-cell neurophysiology, psychophysics (e.g., masking studies), TMS and combined EEG/fMRI work. We consider this paper a prime example of the multi-method approach in the new cognitive neurosciences and of the possible benefits of increased integration and speculation, which is afforded in a special issue compared to more standard journal articles.

Morland, Baseler, Hoffmann, Sharpe, and Wandell review classic fMRI research showing retinotopic representations of the visual field in occipital cortex of normal subjects and present three new case studies of patients with abnormal retinotopic representations due to early-stage visual dysfunctions (e.g., a subject with operating rod photoreceptors only, an albino, and a subject with white-matter lesion). These studies demonstrate that the cortex can sometimes modify its representations as a function of abnormal visual input and also what the limitations of this plasticity are. More generally, they show some of the methodological strengths of fMRI compared to other techniques.

Related work on cortical reorganisation is reviewed by *Bennett, Sekuler, McIntosh, and Della-Maggiore* in a paper focussed on the effects of aging on visual short-term memory for the spatial frequency of sine-wave gratings presented at different inter-stimulus intervals. Two experiments in which psychophysics was combined with PET are described. Although memory performance was comparable for young and old participants, the neural systems that correlated with good performance differed for the two age groups. Multivariate partial least squares analyses were used to derive the networks of neural activity across tasks and groups, based on the covariance between the regional cerebral blood flow and the spatial frequency discrimination thresholds. In addition, covariance structural equation modelling was used to distinguish between alternative hypotheses about the mechanisms behind the discovered correlations. In this technique, interregional correlations and anatomical data are combined to construct plausible models of functional neural networks. Compared to the conventional subtraction technique, we consider these advanced techniques a great step forward, beyond mere localisation, in the direction of a detailed functional neuroanatomical understanding of perceptual and cognitive processes.

Another new technique is reviewed by *Stewart, Ellison, Walsh and Cowey*. They describe transcranial magnetic stimulation (TMS) as a virtual lesion technique, which is capable of disrupting cortical activity transiently and reversibly. It thus has the key advantages of an experimental technique, in contrast to the correlational

approach in neuroimaging techniques like PET and fMRI, being able to answer whether a particular brain area is necessary for a given function, rather than merely sufficient. At the same time, with this technique one does not have to wait for “experiments of nature” as they occur with all their peculiarities in specific instances of brain damage. The contributions of TMS are reviewed in the areas of vision, attention, development and plasticity, and speech and language.

Grill-Spector and Malach review several of their own recent studies on the functional properties of human cortical neurons using the so-called “fMRI adaptation”. Whereas conventional fMRI measures the averaged activity of a whole region (with a usual “voxel” from an fMRI scan containing several hundred thousands of neurons), fMRI adaptation enables to tag specific neuronal subpopulations within the larger region by first adapting the neuronal population by repeated stimulus presentation and then assessing recovery from adaptation by varying some stimulus attribute. The logic of this experimental paradigm implies that the neurons are invariant to the changed stimulus attribute if the fMRI signal remains adapted (i.e., reduced) and that they are sensitive to that attribute in case of a recovered fMRI signal. This technique allows research of functional properties of cortical neurons, which are normally beyond the spatial resolution limits of fMRI and would thus require single-cell recordings in monkeys instead. This is illustrated with research about the invariance versus sensitivity of neurons in the lateral occipital complex for changes in object size, location, illumination, and pose.

The final paper in this special issue, by *Op de Beeck, Wagemans and Vogels*, is also concerned with the relevance of indirect measures of population activity to our understanding of what the brain is doing. In principle, neuroimaging techniques like PET and fMRI are quite limited in supporting inferences about computations and representations in the brain but in combination with single-cell recordings in monkeys they can be useful. In parallel to the opening paper by Savoy, the principles and limitations of neuroimaging techniques are discussed and some of their contributions to our understanding of the visual system are then reviewed. In this review, a number of issues, which have been touched upon in several other papers of this special issue, are put in the broader context of a computational understanding of brain and mind. It addresses the question of how relevant localisation studies are to cognitive and experimental psychologists.

3. Conclusion

In general, we are convinced that the selection of papers in this special issue allows a rather balanced evaluation of what has been achieved in the past decade of the brain and how much remains to be done before obtaining a more complete, multi-levelled understanding of behaviour and cognition, including their neural basis. Our hope is that this special issue will help the readership of *Acta Psychologica* to become acquainted with some of the new developments in the field. To our mind at least, they address some of the criticisms, which could be raised against some earlier neuroimaging work, and which made some cognitive and experimental psychologists

turn away from this hype. Converging operations using diverse methodological approaches, as well as detailed functional models of mental operations are what the field needs most and this is precisely what psychonomics can and has to offer.

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