Introduction to Brain mechanisms of selective perception and action. Proceedings of a Discussion Meeting held at the Royal Society of London on 19 and 20 November 1997.

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Introduction

The world is full of objects. Some may be static, others not. Some may be partially occluded, others standing alone. Some may emit sounds, others not. Some we may be touching (hands resting on a table), others out of reach. At a sensory level, the means by which the world comes to be organized into objects is a far from trivial problem, since stimulus information is typically ambiguous as to which local parts of a scene 'belong' together. It is also unclear how different forms of sensory information combine—does each sense operate independently, or is information integrated in forms of multi-modal representation (Driver, this issue)? Furthermore, the behavioural responses we are equipped to make are inherently limited. We may only name one object at a time; we can reach at most to two objects. The information available to our senses needs to be selected, so that only relevant parts of the world are represented for action. In this way, action may interact in important ways with perceptual processing. Scenes may be parsed in different ways according to our intended behaviour. Perception and action may be linked through processes of selective attention (Milner, this issue; Tipper *et al.*, this issue).

These are exciting times in the study of selective attention. For many years, the topic has been studied primarily at a psychological level. More recently, however, progress has been made by linking theories and experimental procedures from psychology to the techniques of neuroscience. This has allowed us to begin to understand how perceptual processing in the brain is modulated by selective attention, and how selective perceptual processing relates to action. This issue brings together papers capturing this recent progress, as presented to a Discussion Meeting of the Royal Society on 'Brain mechanisms of selective perception and action'.

What can be gained by inter-disciplinary research in this field? We suggest that there is much. Psychology launched the scientific study of attention, making seminal contributions to both theoretical issues and methodology, but we suggest that progress has accelerated since the findings and ideas developed through behavioural techniques have been complemented by contributions from cognitive neuroscience.

(a) *Contribution from psychology*

(i) *Research questions*

Psychology has made, and continues to make, a large contribution to our understanding. Many of the research questions were posed by work in psychology. Examples include: is selection early (affecting perceptual processes), or late (post-perceptual processing)? Is selection constrained by limited processing resources or by the need for coherence of action? Is there a single, central processing limit (the 'bottleneck'), or many, separable limitations? Does selection use either excitatory or inhibitory processes? What factors control attention—bottom-up (exogenous) signals or top-down (endogenous) cues? Can attention be split? Can it be spread? Is selection location-based or object-based? What is the relation between selective attention and consciousness?

(ii) *Paradigms*

Experimental psychology has also led the way in terms of designing many of the basic paradigms, and demonstrating basic phenomena, that have been used to study selective attention, typically using controlled situations that limit the variables affecting performance. Thus, paradigms such as dichotic listening, dual task interference, spatial cueing, task switching and visual search have provided tests of when selective processing is required (and how efficiently it operates). Phenomena such as flanker interference, inhibition of return, negative priming, and visual marking provide measures of attentional effects which can then be subject to further manipulation, to enable us to understand better the underlying mechanisms. Using these paradigms and phenomena, psychologists discovered (not without pain!) the necessary controls that must be imposed to gain uncontaminated measures of selection (to minimize order effects, effects of change with practice and/or strategy, effects of context, range effects etc.).

Of course, much remains open in this behavioural-level research. At the same time, we increasingly see agreement over broad principles, and the systematic use of these to provide accurate, sometimes quantitative, theoretical accounts covering a wide range of attentional phenomena (see Bundesen, this issue). This broad understanding at the behavioural level provides a general framework guiding the next level of neuroscientific analysis. In this respect, indeed, the problem of attention has proved well suited to the new multidisciplinary attack of current cognitive neuroscience. With new techniques for measuring and localizing the activity of the human brain, coupled with more established neuropsychological and neurophysiological methods, we see convergence between questions at a psychological and physiological level.

(b) *Contribution from neuroscience*

(i) *Temporal ordering and localization of function*

Event-related brain potentials (ERPs) and magnetoencephalogram recordings allow us to probe the fine time course of mental operations, to tap intervening stages between the physical stimulus and the behavioural response. One example is in the use of visual evoked potentials to address the question of early versus late selection. By showing at what point in time the neural responses are first modulated by attentional instructions, and how this differs across tasks, we can test competing theories of selection (see Hillyard, this issue). Measures of visual evoked potentials can also provide an assessment of the brain regions that modulate attentional effects. Results using these methods can then be coupled with those derived from more traditional localization techniques (e.g. from studies of single cell recordings or from the effects of lesions), which indicate the functional properties of brain regions. In this way we gain converging (new) evidence on the mechanisms by which selection is achieved.

A similar point can be made from studies of functional imaging. For example, Rees & Frith (this issue) report on evidence using functional magnetic resonance imaging (fMRI) to show that activity in the human equivalent of cortical area V5, driven by motion signals, is modulated by the processing load imposed in a task performed to fixated stimuli. Under high load conditions, activity in V5 is reduced. The evidence suggests that processing load can modulate perceptual processing in the brain.

These methods are also important in showing that the same brain areas are recruited in tasks that involve particular psychological processes. From this it may be inferred that a common operation is involved in the different tasks. For instance, Corbetta (this issue) reports that the same area of the parietal lobe is implicated in switching attention in space (under conditions of spatial cueing), and in search tasks requiring the detection of conjunction targets, whose features may need to be bound together. This suggests that a common process is involved in these conditions—the requirement to shift attention in space, either to follow spatial cues or to bind features (see Treisman, this issue, for this argument). Of course, the precise process involved remains open to theoretical debate, in neuroscience as in psychology. Neuroscience can add new information to the debates about psychological functions, even if it does not solve them.

(ii) *Dissociative methodology*

Neuropsychological studies can provide additional insights into the functional components of task performance, by demonstrating ways in which behaviour breaks down after selective brain lesion. For example, the now common-place distinction between visual codes specifying ‘what’ visual stimuli are and ‘where’ they are localized arose from lesion studies in monkeys (Ungerleider & Mishkin 1982), and this provides a framework for understanding visual coding and selection in humans (albeit in more elaborated forms; see Humphreys, this issue; Milner, this issue). Attempts to characterize such deficits help link studies back to the world outside the laboratory (since any model would need to be able to fractionate in ways that fit with real-life problems in patients), and in turn they can pose new problems for modelling. Thus, if performance deficits reveal the separate processing of different visual attributes, models need to explain how a coherent representation of the world can then emerge.

(iii) *Theoretical concepts*

One particularly exciting aspect of this field of work is the increasing use of single-unit electrophysiology to constrain theoretical models (see Desimone, this issue; O’Keefe *et al.*, this issue; Sakata *et al.*, this issue). Through this work, our models of attention gain firm grounding in primate sensorimotor physiology, and in such associated concepts as: competing neural populations, synaptic change for associative learning, population coding, and winner-take-all networks. The field is moving towards models in which broad theoretical principles at the level of behaviour are integrated with corresponding accounts at the level of single-neuron physiology (e.g. Desimone, this issue; Duncan, this issue).

One other point to note is the shift away from simple theoretical dichotomies, that tended to be stressed in early psychological accounts, towards accounts that detail the circumstances under which particular processes come into play. Instead of asking whether selection is ‘early’ or ‘late’, we may ask when is selection early, and under what circumstances. Instead of asking whether selection is space- or object-based, we can ask how processes interact to determine the forms of representation that are selected (and how these different forms of representation may be disturbed after brain damage, as in cases of visual neglect; Humphreys, this issue).

(c) *This issue*

The papers in this issue are organized into four broad topic areas covering: visual selective attention; attention and perceptual integration; spatial representation and attention; and visual attention and action.

(i) *Visual selective attention*

This section includes four papers. Desimone begins with an analysis of single-cell recording data showing that the responses of cells in several cortical regions are modulated by attention. According to

Desimone, attention serves to bias competition between cells responding to competing signals in the environment, with one major source of this bias being top-down activation from working memory. Desimone shows how single-cell research can be allied to an over-arching theoretical framework, to provide a functional account of whole-system behaviour. In the following paper, Hillyard uses recordings of ERPs to provide converging evidence for attentional modulation of early visual processing. He suggests that attentional effects are produced by changes in the gain control of activation in extrastriate visual areas. This ERP work also provides information on the time-course of such modulatory effects in the brain. The third paper in this section, by Bundesen, presents a mathematical model of visual attention as a unified account of how people select information from multi-element displays. This model conceptualizes selection in terms of competition between elements in the visual field; elements may group in various ways, and competition is based on the activation of memory templates that specify the criteria for the selection task. This framework is similar to that offered by Desimone and also by Duncan (this issue), but couched at a level abstracted from a physiological mechanism. The fourth paper on visual selective attention is presented by Rees & Frith. They summarize recent data acquired using functional imaging procedures (positron emission tomography (PET) and fMRI), that suggest that selective attention changes the gain control and bias signal mechanisms of sensory processes. They also show how these new neuroscientific techniques can be used to address long-standing psychological questions, such as whether there are early effects of attention on visual processing.

(ii) *Attention and perceptual integration*

In the first paper, Treisman presents her feature integration theory, which holds that attention is required in order to bind together the features of objects. She uses converging evidence from neuropsychology to show that feature binding can be disrupted following damage to the parietal cortex, a brain region implicated in shifts of visual attention (Corbetta, this issue). A rather different view of attention is presented in the following paper by Duncan. Duncan proposes an 'integrated competition' hypothesis, in which stimuli compete for neural representation in multiple separated brain systems (see also Desimone, this issue; Bundesen, this issue). Integration of this competition across systems produces a unified state of 'attention' to the same, dominant object with its multiple properties and implications for action. This integration process operates over a relatively long time-course. Clearly, it will be important for future work to address whether selective attention is a function of a particular brain region or an emergent property of many regions, and to assess the time-course over which attentional selection operates in different circumstances. The third paper in this section, by Driver, is concerned with how stimuli from different modalities interact in perception and action. He uses evidence from audition and touch, as well as vision, to illustrate the important role of cross-modal interactions in attention.

(iii) *Spatial representation and attention*

This section includes three papers. The first, by O'Keefe *et al.*, begins with single-cell recording work that assesses the forms of spatial representation used for navigation by the rat. This illustrates not only the particular types of information used to represent space, but also the involvement of the hippocampus in this process. This is supported by converging data on activation of the hippocampus in humans during spatial navigation tasks, using functional imaging techniques. The second paper, by Humphreys, addresses the ways in which information about objects and information about space interacts in human vision. He uses neuropsychological data as well as evidence from experimental psychology to argue for the existence of different forms of spatial representation, some concerned with the relations between parts within objects and some with the relations between independent visual objects. These different forms of spatial representation are linked to different constraints on visual selection. Corbetta finally uses PET evidence to argue for a form of interaction between spatial vision (in the dorsal cortex) and object vision (in the ventral cortex) in which visual processing is biased by attention to areas of the visual field containing objects. He proposes that this biasing operation involves regions of parietal and frontal cortex that are closely related to oculomotor processes. These results mesh with those of Treisman (this issue), who argues for feature binding via attention to space.

Over the past ten years, there has been a growth in the realization that one important role for attention is to enable actions to be made in a coherent manner when there are many objects in the environment. The final section of this volume deals with the relations between 'visual attention and action'. Sakata *et al.* first report evidence on cells in the parietal association cortex that respond to the sight of three-dimensional objects. Though this area of cortex has classically been linked to coding object location, these results indicate that it also mediates the visual guidance of hand actions to three-dimensional object features. Neuropsychological evidence on the ways in which visual information is used for perception and action is reviewed by Milner in the following article. Milner documents the case of patient D.F., who was unable to use visual information for perceptual judgements, but who could use the same information for immediate, prehensile action (e.g. grasping). Similar dissociations in using visual information for perceptual judgements and for action are also noted in cases of visual neglect. The work indicates that visual processing for perception and for action can be functionally separated in the brain. The final paper, by Tipper *et al.*

deals with how visual information is selected when actions are made towards objects. These authors argue for a role of action-based representations which can be selectively activated or inhibited according to task demands and the presence of other stimuli in the environment.

Overall, the papers provide examples of the broad yet converging set of techniques that characterize current cognitive neuroscience. Many issues remain to be debated concerning the nature of attentional processes within the brain, but the papers presented here offer the promise of a future convergence, a convergence helped no doubt by research pitched at different levels of analysis.

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References

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