VISION
AND MOVEMENT
mechanisms in the cerebral cortex

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Frank Bremmer (Paris): Andersen, Hoffmann, Goldberg, Sparks
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Emmanuel Guigon (Paris): Sakata, Tanji, Georgopoulos
Claus Hilgetag (Newcastle-upon-Tyne): Young, Logothetis, Mallot, Singer

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## PARTICIPANTS

<table>
<thead>
<tr>
<th>Name</th>
<th>Institution/Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jennifer ALTMAN</td>
<td>Editor of the Proceedings, London, UK</td>
</tr>
<tr>
<td>Richard A. ANDERSEN</td>
<td>Division of Biology, California Institute of Technology, Pasadena, USA</td>
</tr>
<tr>
<td>Alexandra BATTAGLIA-MAYER</td>
<td>Istituto di Fisiologia umana, Università di Roma La Sapienza, Rome, ITALY</td>
</tr>
<tr>
<td>Anneliese BOHN</td>
<td>Director for Fellowships and Workshops, Human Frontier Science Program, Strasbourg, FRANCE</td>
</tr>
<tr>
<td>Frank BREMMER</td>
<td>Lab. de Physiologie de la Perception et de l’Action - CNRS, Paris, FRANCE</td>
</tr>
<tr>
<td></td>
<td>now at: Allgemeine Zoologie und Neurobiologie, Universität Bochum, GERMANY</td>
</tr>
<tr>
<td>Roberto CAMINITI</td>
<td>Istituto di Fisiologia umana, Università di Roma La Sapienza, Rome, ITALY</td>
</tr>
<tr>
<td>Michel CUÑNOD</td>
<td>Secretary-General, Human Frontier Science Program, Strasbourg, FRANCE</td>
</tr>
<tr>
<td>Claudia DISTLER</td>
<td>Allgemeine Zoologie und Neurobiologie, Universität Bochum, GERMANY</td>
</tr>
<tr>
<td>Apostolos P. GEORGOPOULOS</td>
<td>Brain Sciences Center, VA Medical Center, Minneapolis, USA</td>
</tr>
<tr>
<td>Michael E. GOLDBERG</td>
<td>Laboratory of Sensorimotor Research, NIH, Bethesda, USA</td>
</tr>
<tr>
<td>Patricia S. GOLDMAN-RAKIC</td>
<td>Section of Neurobiology, Yale University School of Medicine, New Haven, USA</td>
</tr>
<tr>
<td>Emmanuel GUIGON</td>
<td>INSERM CREARE, Neurosciences et Modélisation, Université P. et M. Curie, Paris, FRANCE</td>
</tr>
<tr>
<td>Claus HILGETAG</td>
<td>Dept. of Psychology, University of Newcastle, UK</td>
</tr>
<tr>
<td>Klaas-Peter HOFFMANN</td>
<td>Allgemeine Zoologie und Neurobiologie, Universität Bochum, GERMANY</td>
</tr>
<tr>
<td>Marc JEANNEROD</td>
<td>Vision et Motricité, INSERM U 94, Bron, FRANCE</td>
</tr>
<tr>
<td>Jacob KRAICER</td>
<td>Director for Research Grants, Human Frontier Science Program, Strasbourg, FRANCE</td>
</tr>
<tr>
<td>Francesco LACQUANITI</td>
<td>IRCS S. Lucia, Rome, ITALY</td>
</tr>
</tbody>
</table>
Nikos LOGOTHETIS  
Division of Neuroscience,  
Baylor College of Medicine,  
Texas Medical Center,  
Houston, USA

Hanspeter A. MALLOT  
MPI für Biologische Kybernetik,  
Tübingen, GERMANY  
now at:  
Wissenschaftskolleg zu Berlin,  
GERMANY

David PERRETT  
Psychological Laboratory,  
University of St. Andrews,  
SCOTLAND, UK

Jean ROSSIER  
Member of the HFSP Council of Scientists  
Neurobiologie de la Diversité Cellulaire,  
Ecole Supérieure de Physique et Chimie Industrielles,  
Paris, FRANCE

Hideo SAKATA  
Dept. of Physiology,  
School of Medicine,  
Nihon University,  
Tokyo, JAPAN

Hideaki TANAKA  
Director for Research Grants,  
Human Frontier Science Program,  
Strasbourg, FRANCE

Wolf SINGER  
MPI for Brain Research,  
Frankfurt, GERMANY

David L. SPARKS  
Dept. of Psychology,  
University of Pennsylvania,  
Philadelphia, USA

Keiji TANAKA  
The Institute of Physical & Chemical Research (RIKEN),  
Frontier Research Program,  
Saitama, JAPAN

Jun TANJI  
Dept. of Physiology,  
Tohoku University School of Medicine,  
Sendai, JAPAN

Leslie G. UNGERLEIDER  
Lab. of Neuropsychology,  
NIMH, Bethesda, USA

Malcolm P. YOUNG  
Dept. of Psychology,  
University of Newcastle, UK
Cortical nomenclature

Each hemisphere of the mammalian cortex has four main lobes: occipital posteriorly, parietal dorsolaterally, temporal ventrolaterally and frontal anteriorly. Each of these is further subdivided into many areas. This complexity is further compounded by the use of at least three schemes of nomenclature for the various areas: topographical, based on the gross anatomy of the cortex, e.g., inferior temporal, principal sulcus; cytoarchitectonic, a parcellation into areas determined by neuron distribution, known as Brodmann areas (BA) following the maps produced by Brodmann (1909, 1925; further subdivided by Vogt and Vogt, 1919); and functional, based on the operations carried out in the area, e.g., primary visual cortex, frontal eye fields. Not all terms used in one system have exact equivalents in the others. Furthermore, there are discrepancies in both the topographic and cytoarchitectonic schemes between monkey and human brain.

For these reasons, it has not been possible to use a single nomenclature throughout this report but we have aimed to call each area by the same term throughout. We hope the following list of areas named in the text will help confused readers when referring to the research publications on which the discussion reported here is based.

Orientation
a anterior
c caudal; posterior
d dorsal
l lateral
m medial
p posterior
r rostral; anterior

Cortical landmarks

- **corpus callosum**: band of myelinated axons joining the two cerebral hemispheres
- **longitudinal fissure**: the cleft separating the cerebral hemispheres
- **mesial cortex**: the part of the cortex forming the wall of the longitudinal fissure
sulcus  a groove produced by the folding of the cortical sheet; the sulci provide topographical subdivisions within the four main cortical lobes; many cortical areas lie in the walls (or banks) of the sulci.

The main sulci mentioned here are:
- intraparietal (IPS) in the parietal lobe
- superior temporal (STS) in the temporal lobe
- central, dividing frontal cortex from the more posterior sensory areas
- principal and arcuate in the frontal lobe
- cingulate in the mesial cortex

Occipital cortex
Primary visual cortex visual area 1(V1), striate cortex, BA 17; the main cortical input area for visual information coming from the retina via the lateral geniculate nucleus in the thalamus

Posterior extrastriate prestriate; BA18 = V2 and V3, BA19 = V4 and V5 (MT)

Dorsal occipital dorsal BA 19 = PO and DP (dorsal prelunate)
Ventral occipito-temporal ventral BA19 and BA 37; probably includes visual occipito-temporal (VOT; Felleman and Van Essen, 1991)

Parieto-occipital area PO, V6 (V6a, the dorsal part of V6, is now considered separate from PO)

Middle temporal MT, V5

Parietal cortex
Posterior parietal cortex PPC includes:

Inferior parietal lobule IPL, BA 7a, 7b, which contains:
- AIP anterior intraparietal
- LIP lateral intraparietal
- PIP posterior intraparietal
- VIP ventral intraparietal (part)
- cIPS caudal bank of IPS

Superior parietal lobule SPL, BA 5, BA 7 (part) which contains:
- area 5d dorsal part of BA 5
- area 7m mesial part of BA 7
- MIP medial intraparietal
- VIP ventral intraparietal (part)
- MDP mediodorsal parietal
- rIPS rostral bank of IPS

Temporal cortex
Medial superior temporal MST
Floor of superior temporal FST
Inferotemporal cortex IT, inferior temporal cortex, BA 20 and 21; IT has the following subdivisions:
• posterior PIT; PITv = TEO
• central CIT
• anterior AIT } = TE

Superior temporal polysensory areas
STPa and STPp, parts of the superior temporal cortex, located on the anterior bank of STS

Frontal cortex
The more posterior part of the frontal lobe includes the premotor and motor areas; the prefrontal areas, which are concerned with working memory and social behaviour, are more anterior.

Motor areas
Primary motor cortex M1, BA 4
Premotor cortex PM, BA6; divided into a dorsal part, PMd and a ventral part, PMv

Supplementary motor area
SMA, BA6; divided into a rostral part, pre-SMA (6aβ) and SMA proper (6α)

Cingulate motor areas CMA; located in mesial cortex, also considered to be part of the limbic system; divided into CMAr (24c), CMAd (6c) and CMAv (23c)

Frontal and supplementary eye fields
FEF, BA 8; SEF BA 6aβ; areas involved in the control of saccadic eye movements

Prefrontal areas
Dorsolateral prefrontal area 46 (following Brodmann in human; in macaque monkey, according to Walker, 1940), principal sulcus
Ventral prefrontal BA 12, 45, 47

Glossary of general terms and abbreviations

3-D three-dimensional
BA Brodmann area; cytoarchitectonic map of cortical areas according to Brodmann (1909, 1925)
contralesional the side of the body opposite to a brain lesion
coordinates the projections of a point on to the set of base vectors that define a frame of reference.
Examples of 3-D coordinate systems are Cartesian, spherical (distance, azimuth, elevation), object-centred or world-centred (allocentric)
coronal sections through the human or monkey brain in the plane parallel to the front of the face; because of the orientation of the brain in the skull, this produces bilaterally symmetrical transverse sections through the cortex
EEG electroencephalogram; recording of the electrical activity of the brain with electrodes on the scalp
EMG electromyogram; recording of the electrical activity associated with muscle contraction
frame of reference defined by a given set of base vectors (not necessarily orthogonal) intersecting at an origin; the position of a point with respect to a reference frame is given by the corresponding coordinates; examples of frames of references include eye-centred (retinotopic), head-centred (craniotopic, supraretal) and body-centred, depending on the locus of the origin
fMRI functional magnetic resonance imaging; brain scanning technique detecting intrinsic nuclear magnetic resonance changes used to monitor regional cerebral blood oxygenation levels
fovea central area of the retina where discrimination is greatest
ipsiversive a movement towards the side of the body on which a brain lesion has been made or brain recordings are being made
LGN lateral geniculate nucleus; thalamic nucleus on the main input pathway from the retina to the visual cortex
MRF mesencephalic reticular formation; part of a network of neurons in the brain stem that mediates arousal
NPV neuronal population vector; a method for determining the tuning of a population of neurons (Georgopoulos et al., 1986)
optokinetic nystagmus rolling of the eyeball that stabilizes the gaze during head movements and prevents involuntary slip of the retinal image
PET positron emission tomography; brain scanning technique using emission of positrons from administered radiochemicals to monitor regional cerebral blood flow; also used to measure turnover of neurotransmitters
rCBF regional cerebral blood flow; small task-related changes in rCBF are a reliable indicator of cortical activity; measured by PET or optical imaging of the brain surface
saccade a rapid eye movement that redirects the line of sight
superior colliculus the rostral division of the tectum in the mammalian midbrain; a motor control centre concerned with orienting the body in space
vergence convergent movements of the eyes to align an object on the fovea of both eyes, used as a signal for judging the distance of an object
visual hemifield the part of the visual field that projects directly to the visual cortex in the contralateral cerebral hemisphere
INTRODUCTION

Roberto Caminiti

The cerebral cortex is divided into many areas differing in their connectivity and functional operations. Information processing streams in the cortex are defined by the connections and operations both within and between subsets of these areas. The distributed systems serving vision and movement offer excellent models for studying information processing in domains where hierarchical and parallel operations coexist.

Since the work of Trevarthen (1968) and Schneider (1969), it has been widely accepted that the mammalian visual system is composed of several parallel channels, each subserving a different aspect of visual experience (see Maunsell and Newsome, 1987; De Yoe and Van Essen, 1988; Martin, 1988; Van Essen et al., 1992, for reviews). In 1982, Ungerleider and Mishkin proposed that visual processing in the primate cortex is divided into two main ‘streams’, a ventral one devoted to the fine analysis of the visual scene and to the perception of form, colour and features, and a dorsal one that codes the spatial characteristics of the visual scene and analyses motion (Fig. 1). The current status of this hypothesis is reviewed in Part I of this report.

The ventral stream, which uses mainly foveal signals, processes information relatively slowly but with high resolution. It projects to the inferotemporal cortex and then on to prefrontal areas. In contrast, the dorsal stream is concerned with ambient or peripheral vision (Trevarthen, 1968) and operates rapidly but with coarse resolution. It is the anatomical substrate of the visual control of voluntary movement, with its central node in the parietal cortex (Motter and Mountcastle, 1981). Among other inputs, it receives an exclusive pathway from the visual areas of the occipital cortex that may provide for quick transfer of crucial spatial visual information through to the motor areas of the frontal lobe.
**Figure 1.** Visual information processing in the primate cerebral cortex is separated into two streams. The dorsal stream (black arrows) is concerned with spatial localization of objects of interest and with composing motor commands for movements related to objects. The ventral stream (open arrows) performs detailed analyses of object shape. The streams project into different areas of the prefrontal cortex (grey arrows), the dorsal stream into the dorsolateral area, devoted to short-term storage of spatial locations, and the ventral stream into a ventral area specialized for short-term memory of objects.

This functional organization means that the roles of the two streams are more easily understood when considered not just from the point of view of the input but also from that of the output (Goodale and Milner, 1992; Caminiti et al., 1996). Part II examines the dorsal stream from this angle, particularly its involvement in the spatial analyses relevant to the composition of commands for different visuomotor behaviours, such as eye movements, reaching and grasping. Since multisensory fusion is required for the composition of motor commands, the relevant signals are probably integrated in different reference frames, perceived in relation to our stored image of the body’s form and position in space. The ventral stream, as discussed in Part III, is more involved with perception, i.e., object recognition and memory. Viewing angles are of impor-
tance here, rather than frames of reference. Lastly, how this functional information may be recombined to provide a coherent experience of the visual world is considered in Part IV.

**Questions for debate**

Despite this well-established framework, many questions remain and the purpose of this workshop was to highlight areas of agreement and disagreement on several issues. In the articles and discussion that follow, the work that has led to the development of these concepts is critically reviewed and the way towards resolving outstanding disputes and questions examined.

There is still considerable debate about the nature of the coding mechanisms within each stream. Two examples considered here are the coding of the trajectory of a hand movement when reaching to a visual target, which has been analysed and discussed in terms of both body-centred and hand-centred representations (Caminiti, Lacquaniti, Georgopoulos, Hoffmann), and the eye movements used for target localization in space (Andersen, Goldberg, Sparks) and retinal image stabilization (Hoffmann).

A recent development is the discovery that the streams are subdivided into channels devoted to different aspects of analysis. Those discussed here are the separation of the arm movement and manipulation components of reaching (Jeannerod, Sakata) in the dorsal stream and the recognition of object shapes independent of other attributes in the ventral stream (Tanaka, Perrett).

A central concept is that particular functions are not served by single cortical areas but by overlapping areas at different anatomical levels. Thus, both the visual and the motor cortical systems are seen as a network of interactive areas rather than a cascade of areas each performing a single processing task (Young, Caminiti, Tanji, Logothetis, Goldman-Rakic). It also seems likely that different processing strategies may be used for different operations, depending on whether speed or accuracy is more important (Mallot). Further issues of selection and coordination arise for each strategy.
The problem remains that if various components of a movement are processed separately, there must be some provision for coordinating them. Similarly, different attributes of an object have to be bound together for recognition (Singer). The discovery that the two streams project to separate areas in the frontal lobes involved in temporary memory storage during tasks raises further questions about how the information from the two streams is treated in the frontal cortex and how memories coded in the parietal and temporal lobes differ from those handled by the frontal lobes (Ungerleider, Goldman-Rakic).

The evidence for a slow colour-sensitive motion pathway as well as a fast colour-blind one (see Gegenfurtner and Hawken, 1996) implies interaction between colour and motion, generally considered to be processed separately in the cortex. Throughout the discussion at the workshop ran the awareness of the interactions between the streams that are required for unitary perception and action. In this respect, it is worth stressing that the degree of segregation and thus of parallelism of the two streams has recently been questioned (Merigan and Maunsell, 1993), because of the large number of cortico-cortical connections between dorsal and ventral stream areas. Elucidating the function of this crosstalk remains a crucial task for understanding the interplay between informational domains in the cortex.
PART I

DORSAL AND VENTRAL STREAMS: THE CONCEPT TODAY

The idea that ‘what’ and ‘where’ might be processed separately in the brain dates back to the late 1960s. Marc Jeannerod reviews the development of the concept since then, particularly the establishment of the separation into dorsal and ventral processing streams in primate cortex. He also discusses recent work showing that these two streams may be subdivided into specialized processing channels. Functional imaging is allowing the extension of experimental work from primates to humans, as described by both Jeannerod and Leslie Ungerleider, and the latest developments in functional magnetic resonance imaging (fMRI) are beginning to reveal interindividual differences. Among other things, imaging has confirmed that both dorsal and ventral streams extend from the parietal and temporal cortices into the frontal lobes, where working memory aspects of visual tasks are carried out (Ungerleider). The neuroanatomical tracing techniques on which all this work is based have provided an enormous impetus to collect data within this framework. Malcolm Young emphasizes the need for analytical evaluation of the various claims about connectivity that have been made and validates the main hypothesis of two streams for visual processing in the cortex.

Cortical coding of visual object attributes during object-oriented behaviour

Marc Jeannerod

Interactions with objects make up a large part of everyday behaviour. Tasks such as recognizing, reaching and grasping, although appa-
rently very simple, are underpinned by complex visual processes that code different attributes of objects. Visual function mainly subserves perception, necessary for object recognition, and visuomotor transformations, for object-oriented behaviour. Here I review the history of the concept that these two processes take place in separate pathways in the primate cortex, usually referred to as the dorsal and ventral streams. Imaging studies have recently confirmed this separation in the human cortex and reinforce the necessity to consider interchange between the streams for fully integrated visually guided behaviour.

Two visual systems

The notion that axons from the retina are distributed along parallel visual pathways in the brain was introduced at the beginning of this century. In 1909, Ramon y Cajal assigned a visuomotor function to the subcortical pathway, distinguishing subcortical vision, considered as serving a purely motor function, from the cortical visual pathway for perception. This concept reappeared in a paper by Schneider (1969) who postulated a similar anatomical separation into two visual systems based on studies in the Syrian hamster. He considered the pathway from the retina through the lateral geniculate nucleus to the primary visual cortex (V1) responsible for pattern discrimination, whereas the retinal input to the midbrain tectum (superior colliculus in mammals) generates orienting responses. This anatomical and functional distinction established the well-known duality of systems answering respectively “what is it?” and “where is it?”.

The two-visual-systems hypothesis was reinforced by experiments in primates. From studies of visuomotor behaviour in split-brain monkeys, Trevarthen (1968) concluded that the subcortical visual system subserves ambient, or peripheral, vision whereas the cortical system subserves focal, or foveal, vision. He proposed that ambient vision coordinates interactions between the subject and the external environment during locomotion, whereas focal vision is used for object identification. Experiments such as those of Humphrey and
Weiskrantz (1967) showed the existence of residual visual functions in monkeys with large lesions of striate cortex, who were able to generate motor responses such as reaching, although their ordinary visual behaviour was seriously impaired. All these observations stressed the role of subcortical areas in vision related to limb or body movements.

**Two cortical visual systems**

More recently, the emphasis of research in primates has shifted to the separation of visual processing streams for spatial vision and object recognition within the cerebral cortex, and the subcortical pathway is now thought to have less important functions. Based on lesion and tract-tracing experiments in monkeys, Ungerleider and Mishkin (1982) proposed that the streams both arise from V1 but diverge into a *ventral* pathway projecting to the inferior temporal cortex and a *dorsal* pathway with its central node in the posterior parietal cortex. In their view, the ventral pathway is devoted to object identification, coding for features such as shape and colour, whereas the dorsal stream is aimed at coding the spatial characteristics of visual stimuli.

In the intervening years, the concept of two cortical visual systems has been refined. In their 1982 paper, Ungerleider and Mishkin emphasized perceptual functions but subsequent studies including motor behaviour have shown that the dorsal stream has a major role in coordinating visuomotor transformations. For example, monkeys with lesions in the posterior parietal lobe have difficulties with reaching or grasping food with the hand on the side of the body opposite to the lesion (contralesional) (Faugier-Grimaud et al., 1978). Furthermore, single-unit recording experiments (Taira et al., 1990) have revealed that neurons in Brodmann area (BA) 7a in parietal cortex are selectively activated by certain object shapes or manipulative configurations of the hand. Based on these results, Goodale and Milner (1992) suggested that the dorsal stream is concerned with the spatial analysis that is relevant to
the composition of motor commands for visually guided actions. These are movements directed to objects whose perceptual identification is analysed in the ventral pathway.

There are at least two good reasons to attribute visuomotor control to the dorsal stream. First, the types of information processed in this system, such as visual motion, orientation and the distance of the object, are more concerned with motor commands than static parameters like shape or colour; second, several experiments and clinical cases have shown that visuomotor behaviour is specifically affected by lesions in parietal areas and not by damage in inferior temporal areas. Thus the concept of parallel streams in visual cortex has led to the identification of a crucial role for the posterior parietal cortex in organizing object-oriented action, complementing the role of occipitotemporal areas in object identification.

**Multiple channels in the dorsal stream**

The dorsal stream can itself be subdivided into at least two anatomical subsystems or channels, one for reaching and one for grasping (Fig. 2). The first, which projects to the dorsal part of premotor cortex, codes directions of movements, such as reaching, and includes mechanisms for computing distance and coding localization. The other is specialized for shaping the hand to the object and requires information on intrinsic properties of the object, such as form and size (see Fig. 19b for details of the channels).

This dissociation was demonstrated in monkeys by inactivation of a limited region of the parietal cortex, the anterior intraparietal area (AIP) (Gallese et al., 1994), which produces almost no deficit in transporting the hand to a certain point in space but causes a profound impairment in the grasping phase, especially in the precision grip. The deficit is visuomotor and not purely motor because it is corrected under tactile guidance: as soon as the monkey incorrectly touches the target, the hand is adjusted to the proper configuration.
Figure 2. Pathways involved in visuomotor transformation. Within the dorsal visual stream, the connections between the primary visual cortex (V1) and the primary motor cortex (M1) can be divided into two main processing channels. 

**a**, the connections run via the parieto-occipital extrastriate area (PO) and dorsal premotor cortex (PMd). Some of these connections run directly to PMd, whereas others go through the mediodorsal parietal (MDP) and medial intraparietal (MIP) areas in the intraparietal sulcus. This channel is responsible for directional coding of reaching movements towards objects in extrapersonal space. **b**, the connections run through dorsal extrastriate (ES) areas of the occipital lobe via the anterior intraparietal area (AIP) to ventral premotor cortex (PMv). This channel is responsible for transforming intrinsic visual attributes into motor commands.

**Two visual streams in humans**

The paradigm of two cortical visual systems in its simple space-versus-object version has also been studied in humans, using purely perceptual tasks while monitoring brain activity with positron emission tomography (PET) imaging in normal subjects. When the task involved recognition of visual pattern, cortical activation occurred in the occipitotemporal area, i.e., in the ventral stream, whereas during spatial matching tasks the cortical areas located in the superior parietal lobule were activated (Haxby et al., 1991; see Ungerleider, this volume).
To confirm that the dorsal areas have the same specific functions as in monkeys, visuomotor tasks are required in addition to perceptual tasks. To achieve this, we asked subjects either to grasp an object or to do an object-matching task, in which they had to say which objects are identical in shape without making any arm movements. Activity related only to grasping or to shape discrimination was then extracted using the subtractive paradigm for PET studies (Table 1).

Table 1. Areas of the human brain showing significant activation in PET scans during grasping an object and matching its shape. See text for details. BA, Brodmann area.

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<tr>
<td><strong>GRASPING</strong></td>
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<tr>
<td>Primary motor (hand area)</td>
<td>4</td>
<td>Intraparietal sulcus</td>
<td>7,40</td>
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<tr>
<td>Lateral premotor</td>
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<td>Parietoinsular</td>
<td>2,40</td>
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<tr>
<td>Anterior supramarginal gyrus</td>
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<td><strong>MATCHING</strong></td>
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<td>Inferior temporal cortex</td>
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<tr>
<td>Intraparietal sulcus</td>
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<tr>
<td>Posterior parietal</td>
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Figure 3. Diagrammatic representation of central processes involved in object-oriented behaviour. Objects are classified according to their intrinsic properties (size, shape) in object-centred coordinates and their extrinsic properties (spatial position) in body-centred coordinates. Visuomotor processing is thought to rely on processing in the dorsal stream, with separate channels leading to reaching and grasping (see Table 1). Object recognition, which requires semantic processing, is thought to occur in the ventral stream but semantic knowledge could improve visuomotor performance through the connections between the two pathways. For further explanation, see text. Modified from Jeannerod, 1994.
In the grasping task, most activity was seen in the dorsal stream in the hemisphere contralateral to the active hand, predominantly in parietal and occipitoparietal areas. In the shape-matching task, right inferior temporal cortex was strongly activated. In addition there was a focus of activity common to both tasks in the posterior and dorsal parts of the parietal cortex, corresponding to the junction of BA 7 and 19 (Faillenot et al., in press). These results indicate that object identification requires visual processing in both the dorsal and the ventral streams. The dorsal stream, especially the upper part of the intraparietal sulcus participates in object perception whenever it is required for object-oriented action.

Support for this conclusion comes from extensive studies of reaching and grasping in humans with lesions in the parietal lobes (see Jeannerod, 1988; Jeannerod et al., 1995). Patients with parietal lesions causing optic ataxia not only misreach with the hand contralateral to the lesion but also misshape the hand before grasping and sometimes make errors in hand orientation (see Jeannerod, 1994). In contrast lesions in the ventral pathway produce deficits in recognition but do not affect grasp or hand orientation (Goodale et al., 1991).

These conclusions are formalized in Figure 3. An object can be analysed in terms of two systems of coordinates: extrinsic properties related to its spatial position are registered in body-centred coordinates and used for generating reaching; intrinsic object properties, such as shape or texture, are coded in object-centred coordinates. The processing of intrinsic properties is split into a semantic representation for object identification and recognition, which takes place in the ventral stream, and visuomotor transformation, which is located in the dorsal stream.
What and where in the human brain? Evidence from functional brain imaging studies

L. G. Ungerleider

In monkeys, the concept of two visual processing streams in the cortex (Fig. 1, 4) has been supported by double-dissociation experiments: posterior parietal lesions produce mainly visuomotor impairments and problems with reaching, whereas temporal lesions result in deficits in object recognition (Ungerleider and Mishkin, 1982).

Figure 4. Visual cortical areas in the monkey are organized into two divergent pathways, each consisting of multiple functional areas. One pathway subserving object vision or 'what' is directed ventrally into the temporal lobe. The other subserving spatial vision or 'where' is directed dorsally into the parietal lobe. Both pathways have further projections to sites in prefrontal cortex which serve working memory. For abbreviations, see Glossary. Adapted from Ungerleider, 1995.
Human patients with dorsal or ventral cortical lesions show a similar pattern of impairments, indicating parallels in organization in monkey and human brains (Newcombe et al., 1987). Recently, we have demonstrated that the two pathways can also be separated in the normal human brain, using a double-dissociation task during brain imaging with either PET or fMRI: ventral-stream areas were activated in a face-matching task and dorsal-stream areas in a location-matching task (Haxby et al., 1994; Ungerleider and Haxby, 1994).

Imaging further reveals the involvement of the frontal cortex in visual processing. Both streams extend into the prefrontal cortex, where separate dorsal and ventral areas are activated by working memory procedures for the two tasks. Although the areas in both streams are organized in a functional hierarchy, our results show a considerable distribution of basic visual processing, specific recognition/localization and working memory activities between the lower and higher areas in each stream (Courtney et al., 1996a).

**Double-dissociation studies**

In both the face-matching and location-matching tasks, the sensory stimulus was identical but the two tasks required differently directed attention (Haxby et al., 1994). For face matching, subjects had to indicate which of the test stimuli contained the same face as the sample stimulus, whereas for location matching, they had to identify the test stimulus in which the face-containing box was at the same location as in the sample stimulus. In a sensorimotor control task, the sensory stimulation and the motor action were the same as in the two matching tasks: subjects saw an array of three stimuli in the same configuration as in the other tasks and alternately pressed a button on either left or right. Eye movements were neither controlled nor measured. To exclude learning effects all subjects had experience with the task before the brain scanning session, although different stimuli were presented during
training and scanning sessions. Performance ranged between 81% and 92% correct choices during scanning.

In the PET recording sessions, changes in regional cerebral blood flow (rCBF), which have been established as a reliable indicator of neuronal activity (Fox and Raichle, 1986), were monitored. The data were analysed by averaging across subjects and across the two-minute scan time. The group summary data were statistically compared during matching and control tasks, and during face-matching and location-matching tasks, i.e., data obtained during different tasks were subtracted from each other (Friston et al., 1995).

The results provide strong support for two cortical visual streams in humans (see also Jeannerod, this volume). Both matching tasks produced greater activation than the control task and both produced bilateral activation in primary visual cortex and posterior extrastriate cortex (BA 17, 18, 19). In face matching, activity extended forward from these regions to the fusiform gyrus in the ventral occipitotemporal cortex (ventral BA 19 and BA 37). In contrast, location matching resulted in activation of dorsal occipital cortex (dorsal BA 19) and inferior parietal lobule (BA 7). In addition, a region in dorsal occipitoparietal cortex was activated by both tasks indicating that it contributes to both systems. We also found evidence for links between each system and the frontal cortex. During face matching, a region in right ventral prefrontal cortex (BA 45, 47) was activated, whereas a more dorsal and posterior frontal region (BA 6/8) was activated during location matching.

A second series of experiments using fMRI instead of PET provided a powerful confirmation of these results (Clark et al., 1994). Because of the superior spatial and temporal resolution of fMRI, the data from different tasks could be correlated with different aspects of the task and the much greater anatomical resolution revealed considerable individual variability in the exact location of the active area. Furthermore, although both streams were
active during each task, they were modulated differently: during location matching, the activity was enhanced in dorsal parietal and diminished in ventral temporal areas, and vice versa for face matching.

**Prefrontal cortex and working memory**

As a working hypothesis we assumed that the modulation originates outside the posterior processing areas. To identify its source, it is helpful first to review the anatomy of the two visual streams, as determined in monkeys. Based on anatomical and physiological studies a large number of visual areas have been identified that occupy the entire inferotemporal cortex and large portions of the parietal cortex (Fig. 4; Desimone and Ungerleider, 1989; Felleman and Van Essen, 1991; see also Young, this volume) and their connectivity is well established. V1 projects through the middle temporal area (MT) to multiple regions of parietal cortex and through V4 to regions extending into the temporal lobe. The divergence is the substrate for the separation of information flow into a dorsal ‘where’ and a ventral ‘what’ stream. Numerous anatomical connections provide opportunities for crosstalk between the streams, which finally converge in several areas located in the superior temporal sulcus (see Ungerleider, 1995).

Reciprocal connections exist between most if not all of these areas. The feedforward connections to higher-order areas are obligatory: severing them deaferents the next area. The role of feedback connections from higher to lower order areas is poorly understood, although a top-down role in vision, regulating the processing of new inputs according to the global context, has been proposed (Tononi et al., 1992; see also Singer, this volume). Almost all posterior dorsal and ventral areas project into and receive reciprocal inputs from prefrontal cortex. It is these feedback projections, possibly from areas involved in working memory (see Goldman-Rakic, this volume), that may modulate responses in sensory processing areas (Ungerleider, 1995).
To perform correctly in a working memory task, the subject must hold a representation of the stimulus in mind during a delay. In monkeys, neurons in the inferior convexity of the prefrontal cortex (BA 12) show sustained responses to patterns and faces during the delay interval before the animal has to respond (Wilson et al., 1993; see also Goldman-Rakic, this volume). More dorsal regions, specifically in the principal sulcus, show a sustained response only when the monkey has to retain the spatial location. Thus, the dorsal and ventral pathways seem to extend into prefrontal areas with the memory located ventrally for objects and dorsally for spatial location.

To investigate whether there is a similar dissociation of dorsal and ventral areas in the prefrontal cortex in humans, we used a working memory paradigm in which the subject was shown an array of three pictures forming a memory set (Fig. 5; Courtney et al., 1996a). In the face matching test, the subject had to indicate after a delay whether the face was the same as any in the memory set. For location matching, the subject indicated whether the face appeared at the same location as any face shown earlier.

Consistent with the data from monkeys, PET imaging during these tests provided evidence for separate locations for working memory for faces and for spatial locations in prefrontal cortex in humans (see Frontispiece). During tests of working memory for faces, the bilateral activation of occipitotemporal areas extended anteriorly to include parts of the right parahippocampal gyrus, the hippocampus and at least two regions in ventral prefrontal cortex. One of the prefrontal regions was similar to that activated during face matching (BA 45-47), the other was located on the ventral surface (BA 11). Working memory for spatial locations specifically activated dorsal occipital and parietal cortex (dorsal BA 19 and BA 7) and more anterior regions, including the dorsal posterior frontal cortex at the confluence of BA 6 and 8 in the depth of the superior frontal sulcus.
In this experiment, we could not differentiate areas principally concerned with the perception of faces or spatial locations from areas principally involved in working memory. To accomplish this, we varied the delay interval in the working memory task between 1 s and 9 s (Courtney et al., 1995a). We predicted that the activation in areas primarily involved in perception would decline with longer delay intervals, whereas the activation of working memory areas would be constant or even increase with increasing delays.
With this protocol, working memory for both faces and spatial locations activated posterior extrastriate areas (mainly BA 18, 19) as well as a region in prefrontal cortex (BA 45, 47). The pattern of activation as a function of delay interval indicated, as expected, that the extrastriate areas were principally involved in the perceptual aspect of the task whereas the prefrontal region played a role principally in working memory. The activation of ventral occipitotemporal (BA 37, 36, 20) and prefrontal cortex (BA 45, 46, 47, 9) that was observed specifically during the face working memory task showed, respectively, similar decreasing and sustained responses as a function of delay interval. This pattern of activation is again consistent with a role for posterior cortical areas mainly in face processing and anterior cortical areas in working memory for faces.

Working memory for spatial locations activated a dorsal occipitoparietal region posteriorly (BA 19, 7, 40) and a frontal region anteriorly (BA 6/8). The pattern of activation in the anterior region indicated a contribution mainly to working memory but, unexpectedly, so did that in the dorsal occipitoparietal region. One possible explanation for the apparently greater contribution of this posterior region to working memory than to perception is that subjects maintained their attention during the delay interval to a specific spatial location rather than to an internal representation, as they did in the face working memory task.

**Distributed functions**

Similar results were obtained in an fMRI study designed to test the interaction between perception and working memory for faces (Courtney *et al.*, 1995b). The subjects had to say whether a face shown after a delay was the same as or differed from the test face. The trials were intermingled with control trials using scrambled faces. We distinguished three types of responses. The first was to simple visual stimulation, i.e., faces and scrambled faces, found in the primary and secondary visual cortex (BA 17, 18).
Second, more anteriorly in the fusiform area of the temporal lobe (BA 19, 37), there was transient face-selective activity and less activity during viewing scrambled faces. We cannot exclude the possibility that these areas are sensitive to all meaningful stimuli rather than being face-selective. Third, in three prefrontal sites (BA 44, 46 and 49; 45 and 47; insula and BA 10) we found a sustained response during the memory-delay interval that represented the working memory aspect of the task.

Using a multiple regression analysis revealed a more complex picture (Courtney et al., 1996b). BA 17 and 18 were activated mainly by visual stimuli with some specificity for faces but little contribution from working memory. The activation in the more anterior fusiform area came in part from visual stimulation, with the greatest contribution from faces, but working memory also contributed significantly. The posterior part of the frontal lobe was activated by visual stimulation, by faces and by working memory. In the anterior part of the frontal lobe there was face selectivity and a strong influence from working memory but no response to general visual stimulation.

Thus, working memory for this face recognition task is not mediated exclusively by anterior areas in prefrontal cortex but also involves more posterior areas in extrastriate cortex. General visual responses and face processing are similarly observed in anterior as well as in posterior areas. Despite this distributed representation, there is an additional hierarchical organization, with perception stronger in more posterior extrastriate areas and the more anterior frontal areas increasingly involved in working memory.
Are there two processing streams in the cortical visual system?

Malcolm P. Young

In the past 15 years, the clear picture provided by Ungerleider and Mishkin (1982) has become muddied, mainly due to the great amount of anatomical data that has been collected and the partial way in which some of this information has been analysed. Applying independent statistical methods of analysis to the connectivity of the visual system has enabled us to evaluate the various claims and counter-claims. All the methods we have used support the subdivision of the primate visual system into dorsal and ventral pathways, with constituent structures very similar to those originally proposed by Ungerleider and Mishkin.

The need for analysis

More than 30 areas in the primate cortex are now known to participate in visual processing (see Fig. 4) and over 300 ipsilateral cortico-cortical connections between them have been reported (e.g., Felleman and Van Essen, 1991). This accumulation of information is evidently progress but, instead of revealing the organization of the system more clearly, it has led to increasing confusion. The knowledge of neuroanatomical connectivity has grown so fast that many, perhaps most, neuroscientists have been taken by surprise and there is a tendency to interpret connections between particular areas in isolation from the other connections that define the system. The data are far too complex and numerous for such an approach: they certainly embody information about the organization of the nervous system but this information cannot be accessed simply by intuition. Approaches without systematic analysis have very little predictive power and render neuroanatomy little more than stamp collecting. The practice of drawing conclusions from data without analysing them would not be acceptable in neurophysiology or in any other scientific discipline.
A systematic, formal analysis of connections is required to extract reliable conclusions from the data. Happily, several methods are available (Table 2). The application of those marked * are discussed here for the visual system; all analyse connections between areas revealed by conventional neuroanatomical tracing techniques. Although some neuroanatomical descriptions include the laminar origins and terminations of the connections or give an estimate of relative connection densities, this information is rare. It is possible to deduce important features of system organization only from knowledge of whether or not connections between certain areas exist (see below and Young et al., 1995).

Table 2. Methods for obtaining data about cortical connectivity and function and their respective methods of analysis, on which knowledge of the anatomical organization of the primate cortex is based.

<table>
<thead>
<tr>
<th>Available data</th>
<th>Method of analysis</th>
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<tr>
<td>Behavioural effects of lesions</td>
<td>ANOVA etc.</td>
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<tr>
<td>Quantitative strength of connections</td>
<td>* Modelling of underlying system geometry</td>
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<td>Laminar connection patterns</td>
<td>Hierarchical analysis</td>
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<td>Area-to-area connectivity</td>
<td>* $X^2$ test of stream dissociation</td>
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<td>Seriation analysis (e.g., Travelling Salesman problem)</td>
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<td></td>
<td>* Nonmetric multi-dimensional scaling (NMDS) of raw data</td>
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<td></td>
<td>* NMDS of conditioned data</td>
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<td></td>
<td>Graph theoretical methods</td>
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Methods marked * are explained in the text.

**Significant separation of dorsal and ventral streams**

If we define a stream as a set of areas that have more connections with each other than with structures in other sets, and also have fewer reported non-connections with each other than with structures in other sets, a simpler analysis can be made. This test is an elementary
statistical evaluation of whether there are distinct dorsal and ventral streams in the cortical visual system. It examines whether areas that are conventionally considered to be in the two streams fulfil this definition. For this purpose the dorsal stream is assumed to contain areas MT, MSTd, MSTl, FST, PO, LIP, VIP, DP, 7a; and the ventral stream V4, VOT, PITd, PITv, CITd, CITv, AITd, AITv (area definitions follow Felleman and Van Essen, 1991; for abbreviations see Glossary). A \( \chi^2 \)-square test was used to answer two questions:

- Are the areas in the streams more connected with each other than with structures outside their stream? Simply counting and comparing the number of connections between the respective areas yielded the answer “Yes!” (\( \chi^2 = 17.2, p < 0.0004 \)).
- Are structures in the two streams more disconnected with each other than areas within the streams? Taking into account all the connections that have been looked for and found absent, and comparing their numbers for the respective areas again yielded an affirmative (\( \chi^2 = 18.6, p < 0.0002 \)).

From this test, it follows that the areas listed above do indeed form two streams. It remains possible, though, that individual areas could be re-assigned to the other stream and that the anatomical data might be better represented by more than two streams. This method also does not reveal anything of the processing arrangements in the areas. These questions require fuller analytical techniques.

**Quantitative connectivity of cortical systems**

The quantitative connection strengths for 26 cortico-cortical connections were determined from studies in which the percentage of labelled cells were estimated. Examination of their frequency distribution (Fig. 6) makes it clear that strong connections between areas are rare and most areas are not connected to each other at all. In other words, the visual cortex is only sparsely connected. Assuming that more strongly connected areas are ‘closer’ in their processing relationship, or topology, then this quantitative
Figure 6. Quantitative distribution of neuroanatomical connection strengths in the monkey cortex, derived from data obtained by injecting tracers into 26 areas of cortex and compiled from five quantitative neuroanatomical studies (see Young et al., 1995). The quantitative distribution of connection strengths that is approximated here provides important constraints on the possible organization of visual cortex. The most frequent result was no significant tracer transport, reflecting the sparsity of connections at all levels of the visual system. Modified from Young et al., 1995.

distribution may reveal shapes, or manifolds, in the underlying topology. Models show that the distribution of connection strengths resembles only a few of the possible geometries that could underlie the connectivity of the system. It appears that areas are arranged in an annular or horseshoe-like shape (Young et al., 1995), indicating that the areas are ordered more or less sequentially. This immediately rules out whole classes of possible geometries; e.g., no cortical sensory system can be a diffuse heterarchy (cf. Simmen et al., 1994). The system is thus very likely to contain semi-sequential processing hierarchies in at least two streams that may or may not reconverge. To address these remaining uncertainties, the exact placement of areas in this hierarchy or hierarchies has to be determined by other methods.
Multidimensional scaling analysis

Further details of the connectional topology can be revealed by analysing collections of area-to-area connections using qualitative information on whether particular connections between areas exist (Table 3). One of the data-analysis tools applicable to this question is nonmetric multi-dimensional scaling (NMDS), which interprets the connectivity patterns of the areas as proximity ranks and

Table 3. Matrix of connections between areas of the macaque visual cortex.

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Cortical parcellation and connections are according to Felleman and Van Essen (1991) with a few exceptions (see Young, 1992). 2, reciprocal connections; 1, one-way projections; 0, projections that have either been found absent or connections that are not known. The information represented concerns only the existence of a connection between two areas and is the coarsest and most reliable that can be extracted from neuroanatomical studies.
attempts to find an optimal representation in a small number of dimensions. NMDS places areas with similar patterns of connections closer together and those with dissimilar connectivity patterns further apart.

Before applying NMDS to real anatomical data, we established its accuracy by checking that it can recover test data that are as similar as possible to the real connection data (Young et al., 1995). Metric distances between 30 cities in the United States were transformed into route data with the same proportion of 2s, 1s and 0s as for the visual system data (cf. Table 3). Although the data now consist only of information on whether cities are connected or not, i.e., whether the distance between them is shorter than the threshold value, the original metric configuration can be recovered with an accuracy above 95% (Fig. 7). More extensive simulation studies (Young et al., 1995) show that applying NMDS to connection data can be expected to recover all but a small fraction of the variability in the data.

Applying this technique to the data shown in Table 3 revealed some characteristic features of the visual system’s topology (Fig. 8). With V1 placed at the left, the two dimensions of the diagram roughly correspond to the orientation of the cortex, indicating that the spatial position of an area in the brain is a predictor of the other structures to which it is connected (Young, 1992; Cherniak, 1994). Starting with the cluster containing V1, the visual areas are clearly segregated into dorsal and ventral streams, each consisting of the areas previously assigned to them. Within the streams, areas seem to be arranged in semi-sequential hierarchies, i.e., a sequential order rather than a diffuse, non-ordered network, although with many possible routes through the sequence (Van Essen et al., 1992; Hilgetag et al., 1996). Cross-talk between the two streams is limited but this representation illustrates the opportunities for reconvergence, particularly in the rostral part of the temporal lobe.
**Figure 7.** Examples of output from successful methods of recovering metric parameters from matrices at the same level of measurement as anatomical connection data. Above, the metric structure for distance data between 30 US cities and a regular hexagonal grid. Below, the ordinal solutions for matrices derived using a data-conditioning method termed weighted dissimilarity transform 1 (wdsm1; Young et al., 1995). The positions of the cities have been recovered almost perfectly by this method: the fit between the conditioned data and the metric data solutions for the cities is 0.99 (left). The solution for data treated by wdsm1 from the regular hexagonal grid (right) also shows a fit of 0.99. Modified from Young et al., 1995.
Figure 8. The topological organization of one hemisphere of the macaque visual cortex determined by nonmetric multi-dimensional scaling (NMDS). A total of 301 connections is included, of which 62 are one-way. This non-arbitrary representation is a best fit in two dimensions of the connectional topology of this system: areas are given positions specified by the minimum distance between connected areas and maximum distances between areas that are not connected. The derived structure has an organization similar to that of the cortex, with dorsal (top) - ventral (bottom) and posterior (left) - anterior (right) axes. The analysis provides a spatial framework for the organizational network of connections in the visual cortex. Some connections exist between areas that are widely separated in the structure, indicating that these areas are topologically close in solutions of higher dimensionality. Red, reciprocal connections; blue, one-way projections from left to right (posterior to anterior); green, one-way projections from right to left (anterior to posterior).
Figure 9. The organization of the entire macaque cortical system as presently known. Mainly visual areas cluster on the left side of the diagram, auditory areas at top right and somatosensory bottom right. The central position of the amygdala is notable, reflecting its role as a gateway between the sensory cortices and the subcortical limbic system. A total of 834 connections between 79 areas is represented, of which 136 (18%) are one-way. This connectivity represents 15% of the possible connections between these areas.

Considering all 834 connections reported between 79 areas in the whole cortex (Fig. 9), three hierarchically organized sensory systems emerge: the visual, the auditory and the somatosensory–motor system. In monkeys, a dichotomy of streams within a sensory
system is clearly indicated only in the visual system and not in any other sensory system; in cats, there is little evidence for a separation into two visual streams (Young et al., 1994; but see Lomber et al., 1995). The central position of the amygdala, which sends inputs to many cortical areas and receives outputs from higher cortical areas, points to its importance as a gateway for information from the limbic system to the cortex.

**Implications for visual processing**

The particular characteristics that this architecture confers on visual processing in primates is a matter for further research. Anatomical connectivity is far from the whole story; it provides only the basic framework in which processing can occur. The flexibility of visual behaviour in primates implies that the system cannot be completely hard-wired. If it were, there would be a large number of simple regularities between stimulation and behaviour but these seem to be the exception rather than the rule. Although there may seem to be a simple linkage between stimuli and the animal’s learnt response during an experiment, this depends on the animal’s cooperation and it disappears as soon as the animal loses interest. Rather, visual behaviour in primates seems to be determined by dynamic interactions among large ensembles of neurons and systems, only some of which we are beginning to understand.
As discussed above, the dorsal stream has its node in the parietal cortex, which has two main divisions receiving different visual inputs. Information reaches the inferior parietal lobule through V3, V4 and medial superior temporal cortex, whereas inputs to the superior parietal lobule come from V2 and V3 through the parieto-occipital area. Areas in the superior parietal lobule are specialized for processing different sources of information related to the visual and kinaesthetic guidance of reaching, those in the inferior parietal to movements of the head and eyes. Outputs from both divisions project to the motor areas of the frontal cortex and to subcortical motor structures, such as the striatum in the basal ganglia and the superior colliculus in the midbrain.

**Reaching and grasping**

Visually guided reaching requires the integration of target, eye and head position to evaluate the direction and distance the arm must move to intercept the target. Roberto Caminiti considers the areas processing this information as a network and compares the results of physiological investigations with the performance of neural network models. The frame of reference in which the coordinates of the target and the hand are coded are examined by Francesco Lacquaniti, who reports separate populations of neurons in the superior parietal lobule coding for the main spatial parameters of distance, azimuth and elevation. Before the hand arrives at the target, it has to be shaped to grasp the object. Hideo Sakata describes neurons in the anterior intraparietal area, in the intraparietal sulcus, that show both visual and hand movement-related activity in a manipulation task. Reaching and grasping requires
a sequence of movements that have to be performed in the correct
temporal order and Jun Tanji reviews recent data that implicate the
supplementary motor area in such sequencing. The final output
from the cortex to the spinal cord is from primary motor cortex
(M1), where Apostolos Georgopoulos demonstrates that direction
of movement is coded as a vector by populations of neurons and
illustrates how this can be used as a tool for assessing implicit
transformations of motor commands.

**From vision to movement: combinatorial computations in the dorsal stream**

*Roberto Caminiti*

When a visual stimulus serves as target for a reaching movement,
different sources of information must be combined to bring the hand
successfully to the target. As a reflection of this requirement,
reaching to visual targets is subserved by a distributed cortical
network that includes several areas of the parieto-frontal cortex
(*Fig. 10*). To help with defining the key issues underlying spatial
motor behaviour, it seems useful to make a critical evaluation of
the information available about this network. Such an overview of
the cortical mechanisms leading from target localization to
generation of the arm movement provides a basis for discussing
these mechanisms within the frame of neural network studies.

**Anatomy and physiology**

The anatomical substratum through which visual information
influences the motor circuits in frontal cortex underlying reaching
is shown in Figure 11. In the past 15 years, much has been learned
about some of the parieto-frontal areas, such as the dorsal part
of BA 5 (5d), dorsal premotor cortex (PMd) and M1, and concepts
about their functions have been developed. Little or nothing
Figure 10. Approximate location and boundaries of the cortical areas discussed in the text. **a**, mesial aspect of the cerebral hemisphere. Visual areas PO (=V6) and V6a lie in the rostral bank of the parieto-occipital sulcus. MDP, medial dorsal parietal area; 7m, medial division of area 7. **b**, lateral aspect, with the intraparietal sulcus (IPS) opened out to display the lateral (LIP) and medial (MIP) intraparietal areas, which are located in the lateral and medial banks of the sulcus. M1, primary motor cortex; PMdc, caudal dorsal premotor cortex; PMdr, rostral dorsal premotor cortex; 5d, dorsal part of BA 5; 7a,b, lateral divisions of BA 7. Modified from Caminiti et al., 1996.
**Figure 11.** Tentative scheme of the organization of the parieto-frontal network for reaching, showing the origins and terminations of ipsilateral forward association pathways; reciprocal connections are not shown. **a,** mesial aspect; **b,** lateral aspect. Abbreviations as in Figure 10 and see Glossary. Modified from Caminiti et al., 1996, adapted from Johnson et al., 1993, 1996.
is known, however, about the medial intraparietal (MIP) area, the medial part of the inferior parietal lobule (BA 7m) and the parieto-occipital area PO (= V6) (Caminiti et al., 1996).

The cortex lying in the rostral bank of the parieto-occipital sulcus has recently been parcellated into a ventral area, PO, and a dorsal area, V6A (Galletti et al., 1996). Area PO seems to be the only visual area of the primate brain that lacks an expanded representation of the fovea while containing a large representation of the peripheral visual field. Most neurons in PO have large receptive fields (Colby et al., 1988), whose visual activity is modulated by the angle of gaze; a few, however, are gaze-independent. Both types of neurons could code for target location in craniotopic coordinates (Galletti et al., 1996).

The cortico-cortical connections of PO include both direct and indirect projections to BA 7m and MIP and to PMd (Fig. 11; Johnson et al., 1993, 1996; Tanné et al., 1995). Both its connectivity and the coding properties of its neurons indicate PO has a role in the control of reaching. We are currently using a variety of behavioural tasks aimed at temporal dissociation of the command for eye movements from that for hand movements, i.e., eye-position signals from hand-position and movement-related signals. Although the work is still in progress, it is indicating that neural activity in PO reflects not only visual parameters but also information related to arm movement and position, which often interacts with information about eye position.

Visually driven neurons in area V6A have larger and more scattered receptive fields than those of PO, with more complex properties, such as tuning to slow-motion stimuli; they are also influenced by attentional signals. Unlike PO, a large proportion of the neurons do not respond to visual input (Galletti et al., 1996) but the properties of these cells have not yet been characterized. We have recently found neurons with activity related to hand reaching, resulting from interaction between eye-position, hand-position and hand-movement signals. Thus, even at an early stage
in the pathway leading from vision to movement, information about the position of the target on the retina is probably combined with information related to eye and hand position.

BA 7m receives cortico-cortical connections from several related areas with visual functions, including PO, V3A, V4, MST, MT, the dorsal parietal area and TEO in the inferior temporal lobule. It projects to PMd, the supplementary motor area and other prefrontal regions (see Cavada and Goldman-Rakic, 1989; Johnson et al., 1993, 1996; Tanné et al., 1995). These connections indicate that BA 7m has a role in the visual guidance of movement but no neurophysiological studies in this area have previously been made. We are rectifying this by characterizing the functional properties of neurons in BA 7m in monkeys that have been trained in a variety of reaching tasks. Our preliminary data indicate that visual, eye-position, hand-position and hand-movement-related signals all influence neural activity in this area. As individual neurons in BA 7m receive combinations of these signals, it seems likely that they use retinal error signals to encode the difference between the desired and the actual position of the hand, in other words, between target and hand position.

Qualitative observations have shown that neurons in MIP combine visual and somatosensory information (Colby and Duhamel, 1991). Its anatomical connections, however, indicate that MIP could be crucial for visual control of movement (Johnson et al., 1993, 1996). This has been confirmed by recent behavioural neurophysiology studies and the best explanation for the neuronal activity recorded in this area is that it combines visually derived signals with arm-position and movement-related signals during reaching (Johnson et al., 1996). The input–output relationships dictated by cortico-cortical connectivity also indicate that neural activity in MIP can be influenced by the angle of gaze (see Caminiti et al., 1996 for discussion).
Neural networks for reaching

It is instructive to compare this data with the restrictions imposed by the operations occurring in current network models of the visual control of reaching. One type of network model uses information about retinal target position, angle of gaze, vergence angles (signalling distance of object) and head angles to learn a representation of target location in three-dimensional (3-D) space. Combining this with information about arm position and configuration produces a movement-direction vector and a motor command (Guenther et al., 1994). Another approach uses a visually derived movement-direction vector that is encoded relative to the fixation point (Burnod et al., 1992).

Despite their differences, these models have certain features in common: a combinatorial layer of units, where visually derived information about target location is combined with the somatic information about arm position and configuration; and an output layer, where the motor command is refined and issued. In the cortical network, areas PO, V6A, BA 7m, and MIP are clearly part of the combinatorial layer as they have access to visual, somatosensory and motor information and are anatomically connected with the output layer, the motor areas of the frontal cortex. The pattern of cortico-cortical connectivity of these areas indicates that sources of hand-movement and position-related information in these parieto-occipital areas, which are far removed from the peripheral motor apparatus, are probably represented by re-entrant signals originating in the frontal lobe.

Another requirement arising from network models is that there is no obligatory linkage between neural activity in the parietal lobe and movement. Recent experimental data obtained in BA 5d in the superior parietal lobule show that neuronal activity reflects movements that might be made during ‘No-go’ trials in a ‘Go/No-go’ task (Kalaska and Crammond, 1995), which fits this requirement.

Frontal cortical areas represent the output layer of the network. The frontal fields of importance for reaching are mainly PMd and
M1 but their exact roles in this task still have to be defined precisely. For PMd to be considered as part of the output layer, its neural activity should be similar to that in M1. The available physiological evidence indicates this is the case only during simple behavioural tasks (Georgopoulos et al., 1986; Caminiti et al., 1990, 1991). The two differ, however, in a predominance of target-related signals in PMd and of direction-related signals in M1 (Fu et al., 1995; Crammond and Kalaska, 1996). A clearer functional difference between the two areas emerges when more complex behavioural tasks are used, such as those involving novel spatial conversions and transformations of non-spatial information into spatial motor commands. Activity in PMd is also influenced by gaze and attentional signals (see Boussaoud et al., 1996, for a review) but this has not so far been demonstrated for M1.

PMd could thus be considered as a ‘pre-output’ layer inserted between parietal and motor cortices, as its properties are only partly similar to those of the output layer and it has a less obligatory relationship to the motor periphery than M1. It is interesting to note that Kalaska and Crammond (1995), in their recent Go/No-go study, found that activity in PMd was not modulated so intensely during No-go trials as that in BA 5d.

A new view of cortical connectivity

Another question relates to the distribution in the cortex of visuospatial and movement-related activity and how these correspond to the pattern of cortico-cortical connectivity. In other words, how does the network use different types of information? The answer may deeply influence the understanding of cortical coding mechanisms for reaching. We have recently been studying this problem in frontal (PMd and M1) and parietal (BA 5d and MIP) cortices with a combination of behavioural neurophysiology and neuroanatomy (Johnson et al., 1996).

We used an instructed-delay reaching task, in which a cue signal instructs the monkey about the direction of the next reaching
This task dissociates the early event of target presentation from the later events involved in movement generation. Signal-related activity is believed to reflect the visuo-spatial process linked to target localization; instructed-delay activity probably expresses the combination of visually derived information about target location with signals about the position of the arm in space. Arm movement-related activity is linked to the execution of the motor command and position-related activity across the cortex to the arm position in space. In both frontal and parietal cortices, the distribution of these different types of activity across the cortex is non-uniform and overlapping. Furthermore, parietal and frontal areas displaying similar patterns of activity are structurally linked by intracortical projections.

These data point to a functional architecture of the cortical network that differs from the models described above. The combinatorial and the output operations do not form distinct layers but are a continuum within a single functional layer that spans many cortical regions. In such a network, the computation from vision to movement consists of progressive matching of different information domains. As information ‘percolates’ through the network, the motor command emerges gradually and is refined. Whether this or other strategies are used by the cerebral cortex for computing a motor command for reaching will be a subject of intense research in the coming years.

**Coding spatial information for visuomotor coordination**

*Francesco Lacquaniti*

How the movements of the arm and hand are matched to the target during reaching is not understood, although it is most likely that a vector of desired hand movement is derived from the difference
between final and initial hand positions. Psychophysical experiments and behavioural neurobiology studies indicate that this matching is coded in terms of a body-centred or egocentric frame of reference. We have found a neural substrate for this coding in monkeys in the superior parietal lobule (SPL; BA 5).

**Psychophysics**

The location of a visual target, and to some extent of the hand, is encoded in eye-centred coordinates whereas psychophysical studies indicate that reaching movements are specified in an egocentric frame of reference (Jeannerod and Biguer, 1987; Soechting and Flanders, 1989; Paillard, 1991; Lacquaniti, in press). That is, a coordinate transformation of sensory information about target and hand position is required for the generation of the required motor commands. A spherical coordinate system may be appropriate to describe endpoint position relative to the body (Soechting and Flanders, 1989).

The spatial parameters of distance, azimuth (horizontal position) and elevation (vertical position) of reaching may not be dealt with as a single unit but may be processed in parallel, largely independently of each other (Soechting and Flanders, 1989). For example, misreaching in distance is generally much greater than misreaching in direction and the information transmitted by the movement is accordingly higher for direction than for distance (Gordon et al., 1994; Soechting and Flanders, 1989). In addition, chronometric studies have indicated that the central processing time involved in programming direction is longer than that involved in programming distance (Rosenbaum, 1980). Work in progress in our laboratory with humans indicates that direction and distance may be stored in separate channels in the buffer of visuospatial working memory, because the rate of decay of directional information is faster than that of distance information as the delay after target extinction increases.
Egocentric coordinates in SPL

We recently gathered evidence that SPL might represent a substrate for egocentric representations of reaching in the monkey (Lacquaniti et al., 1995). Monkeys were trained to make arm movements directed to visual targets placed in different parts of 3-D space in a reaction-time task. We found that the activity of most neurons in dorsal SPL during the movement is related to the position of either the target or the hand with respect to the body (Fig. 12). Moreover, many neurons coded specifically for either azimuth or elevation or distance. In these experiments, the origin of the frame could not be determined precisely because the head was fixed and the motion of the torso and shoulder was limited. Head-centred coordinates on average yielded a slightly better fit than shoulder-centred coordinates.

Four classes of neurons with distinct functional properties were identified in SPL (Lacquaniti et al., 1995):

- initial position neurons, with activity related most prominently to the starting point of the movement;
- via-point neurons, related to positions along the direction of movement;
- final position neurons, related to the position of the target;
- motor error neurons signalling the difference vector between final and initial position.

The activity of some neurons may reflect the current position of the limb, derived from peripheral feedback or efferent copy of motor commands. However, the activity of many other neurons relates to the final point, although this has not yet been reached, i.e., they discharge during reaction time or movement time, reflecting a preplanned desired position (Hocherman and Wise, 1991) or ‘command function’ (Mountcastle et al., 1975) rather than current kinematics.

A key to understanding distributed representations of movement in the brain is the statistical distribution of responses in an ensemble of neurons in a given cortical area (see Georgopoulos et al., 1988;
Figure 12. Mean activity of six neurons during an arm movement supports the hypothesis that wrist position is coded in spherical coordinates. Each neuron is best tuned to changes in one spatial coordinate of the wrist: a and b, to azimuth (a, increasing from right to left; b, from left to right); c and d, to the distance of the wrist from the body (as the wrist gets closer, the neural activity increases in c, and decreases in d); and e and f, to elevation (e, increasing with downward movement; and f, upward). The wire frames correspond to the three workspaces depicted in the insets (top), with the corners indicating the position of the wrist relative to the monkey at the end of the movement to the corresponding target. Grey bars, the activity averaged during movement time; black bars, the activity predicted by a linear model of final wrist position in spherical coordinates. Calibration bars (hollow), 20 spikes s⁻¹. Modified from Lacquaniti et al., 1995.
Figure 13. Histogram of the distribution of activity in all neurons recorded in SPL shows that most are tuned to a single coordinate. The plot is based on homogeneous coordinates and values have been normalized to express the relative gain of each spatial coordinate in any given neuron. Distance ($\phi$) is plotted on the left side of the triangle, azimuth ($\chi$) on the right side and elevation ($\psi$) on the upper side. Values increase in the directions of the arrows, so the closer a neuron is to one vertex of the triangle, the closer its activity relates to that spatial coordinate. In contrast, the activity of neurons nearer the centre of the triangle relates more evenly to all three coordinates. The height of the prisms above the base is proportional to the number of neurons whose coordinates fall in a given interval. Modified from Lacquaniti et al., 1995.
Georgopoulos, this volume). This shows, for instance, if the optimal responses of the individual neurons in an ensemble distribute uniformly in all directions or whether they cluster around preferred axes. In SPL, the positional code in ego-centred coordinates does not seem to be uniform in all three dimensions (Lacquaniti et al., 1995). About 70% of the neurons have tuning functions that cluster around either azimuth, elevation or distance (Fig. 13), indicating that a different subpopulation of neurons may code for each spatial coordinate. The separation is, however, incomplete as there is significant crosstalk between the three channels.

What is the functional significance of representing the information about distance, elevation and azimuth of hand movements with distinct groups of neurons? This representation correlates with the psychophysical observation that the spatial parameters are processed in parallel and largely independently (see above). Keeping the spatial information for the three axes separate could be important for sensorimotor coordination, as it would allow easier matching between sensory feedback and information related to motor commands.

Matching would be best achieved with a hybrid combination of sensory and motor spatial axes (Carrozzo and Lacquaniti, 1994). Although each neuron may represent only a single aspect of space, complete information about limb position can be reconstructed by simple summation of individual contributions in a population of neurons (Lacquaniti et al., 1995). This can be demonstrated in a layered neural network model whose intermediate layer contains positionally tuned neurons that can be trained to generate the position of the hand in body-centred coordinates. Whether global reconstruction of limb position takes place in SPL or in other cortical or subcortical levels remains to be determined.
The skilful handling of objects requires the use of visual information about their spatial characteristics to produce appropriate patterns of hand and finger movements. Several neurophysiological and clinical studies support the idea that action-oriented visual information of this type is synthesized in the posterior parietal cortex (see Goodale and Milner, 1992; Sakata and Taira, 1994). Single-unit recordings in the parietal cortex of primates have revealed neurons whose activity is related to the natural actions of reaching and grasping (Mountcastle et al., 1975; Sakata et al., 1995). In particular, ‘manipulation’ neurons, selective for the pattern of hand movement or the 3-D characteristics of the manipulated object, have been described (Taira et al., 1990; Sakata et al., 1992, 1995). Based on the observation that lesions to inferior temporal cortex do not affect reaching and grasping abilities but do disrupt object recognition (Ungerleider and Mishkin, 1982), we propose that the visual input required for manipulation arises from visually sensitive neurons in the parietal cortex.

**Manipulation-related neurons in parietal cortex**

The activity of neurons in AIP in the anterior part of the posterolateral bank of the intraparietal sulcus (Fig. 19a) was recorded while monkeys performed object-manipulation and object-fixation tasks. The monkeys either handled four types of object that required different patterns of movement (pull lever, push button, open pull knob, pull knob in a groove) or simply fixated them. The tasks were executed both in the light and dark.

Neurons with activity related to these tasks were classified as ‘motor dominant’, ‘visual and motor’ or ‘visual dominant’ (Fig. 14). Motor-dominant neurons were active during object
Figure 14. Types of neurons that are involved in object manipulation in the anterior intraparietal (AIP) area. The raster plots and histograms show the selective activity of a single neuron of each type for particular objects and conditions. **a**, motor-dominant neuron that preferred a pull knob. It was active during manipulation (movement in light and dark) but did not respond to a visual input (object fixation). **b**, object-type visual-and-motor neuron that preferred a push button. Its requirement for both movement and visual input is shown by its reduced activity in the dark and weak response during object fixation. **c**, object-type visual-dominant neuron that preferred an upright pull lever and required visual input (active during object fixation and movement in the light but not in the dark). Key, the monkey pressed an anchor key before movement began; Object, period when the object was held. Modified from Taira et al., 1990; Sakata et al., 1992.
manipulation and 80% of them were highly or moderately selective for one object (Sakata et al., 1995). Their activity correlated with active hand movements (Fig. 14a). Visual-and-motor neurons, on the other hand, required visual information on the object or surrounding space. They were more active during object manipulation in the light than in the dark or during object fixation (Fig. 14b). Some of these neurons had object fixation-related activity and so were classified as ‘object’ type (Fig. 14b); the activity of the remainder, classified as ‘non-object’ type, was probably related to the combined view of the hand and the object. Visual-and-motor neurons had the same object preference in both the manipulation and fixation tasks.

**Visual-dominant neurons**

The task-related neurons classified as visual dominant had purely visual responses (Fig. 14c). Their activity profile was the same for object manipulation in the light as for object fixation but they were silent during movement in the dark. That is, hand movement alone did not activate them. As with visual-and-motor neurons, both object and non-object types were found. The visual-dominant neurons were highly selective for the shape of both the fixated and manipulated objects and they generally preferred the same object in both manipulation and fixation tasks (Fig. 16).

Visual-dominant neurons may be involved in the temporary storage of visual information about objects (Fig. 15; Murata et al., 1996). In a delayed-manipulation task, the light was turned off after object presentation and the monkey had to wait for a Go signal before making its reaching and grasping responses (Fig. 15e); for the delayed-fixation task, the light was turned off while the monkey fixated the object. For example, a neuron that was active during movement and fixation in the light (Fig. 15a,c) but silent during both in the dark (Fig. 15b,d), discharged tonically during the delay period in both tasks (Fig. 15e,f). We interpret this as evidence that the neuron maintained a signal of the object’s
Figure 15. A visual-dominant neuron with sustained activity during delays. Neuronal activity in six tasks is shown: manipulation of the plate in the light (a) and the dark (b); during object fixation in the light (c) and the dark (d), and during the delayed manipulation (e) and delayed fixation with the light off (f). The rasters and histograms are aligned at the onset of movement (a, b) or at key down (c-f). Small triangles beneath the rasters indicate the start of specific hand movements. Upward deflection in the light trace denotes illumination of object. Fix, monkey fixates object; Hold, monkey holds object; Delay, monkey waits for Go signal in interval between the second and third vertical dotted lines. Modified from Murata et al., 1996.

image for a short period after the object itself disappeared. This signal is presumably the representation of the shape and orientation of the object. For example, the neuron shown in Figure 16 responded to the sight only of a horizontal square plate out of the six shapes presented and it displayed sustained activity during a delay period only after the presentation of the plate.
**Figure 16.** Selective response and activity of the visual-dominant neuron shown in Figure 14c while fixating (Fix) six objects with simple geometrical shapes and in a delayed-manipulation task (Delay, Hold; see Fig. 15). This neuron showed a strong preference for the horizontal plate in both tasks. The histograms are aligned at the onset of illumination. Reproduced with permission from Murata et al., 1996.

**Selectivity for the 3-D orientation and shape of objects**

Manipulation neurons are also selective for the orientation of the longitudinal axis of objects in 3-D space (Fig. 17; Sakata and Taira, 1994). The visual input to these neurons may come from the caudal part of the lateral bank of the intraparietal sulcus (cIPS; see Fig. 19a). Neuronal activity in this region was recorded during presentation of luminous bars or plates of different sizes and orientations as visual stimuli while the monkey fixated a spot in
the centre. Using a stereoscopic computer-graphics display, we presented 3-D stimuli with binocular disparity. Most of the axis-orientation selective neurons preferred thinner and longer objects (Kusunoki et al., 1993), except for a few that preferred an intermediate thickness. One such neuron responded maximally to a display of a cylinder that appeared to be 10 cm in diameter and 20 cm long at a viewing distance of 1 metre (Fig. 18a). Changing the cylinder to a square column or plate resulted in a drastic decrease in the neuron’s response (Fig. 18b). In the same area we also recorded neurons selective for surface-orientation. Unlike the axis-orientation selective neurons, these preferred flat and wide objects to long and thin objects (Shikata et al., 1996). Almost all of these neurons were sensitive to binocular disparity.
**Figure 18.** A neuron selective for 3-D shape. It responded strongly to a tilted cylinder of intermediate thickness and length (10x20 cm) (**a**) but was much less active when shown a square column or plate (**b**). Modified from Sakata et al., 1996.

**Visual and motor information for object manipulation**

Our results suggest that the properties of 3-D objects used to guide manipulation movements are extracted in a subdivision of the dorsal processing stream that runs through V3a, cIPS and AIP (**Fig. 19**). This dedicated pathway is connected on the motor side to the postarcuate region of ventral premotor cortex, where neurons with highly specific activity related to distal movements of grasping have been described (reviewed in Jeannerod *et al.*, 1995).
Figure 19. 

**a**, axis-orientation selective neurons and surface-orientation selective neurons were recorded in the lateral bank of the caudal intraparietal sulcus (cIPS) in the region shown stippled. The intraparietal, lunate and parieto-occipital sulci are shown opened up. Modified from Colby et al., 1988.

**b**, hierarchy of visual areas, including a subdivision of the dorsal stream that seems to be specialized for coding of 3-D features used for object manipulation. For abbreviations, see Glossary. Modified from Felleman and Van Essen, 1991; Zeki and Shipp, 1988.
The functions of this parieto-frontal network may be the matching of visual information about 3-D features of objects recorded by visual-dominant parietal neurons with the motor commands for the appropriate patterns of hand movements for object manipulation generated by premotor neurons. As the latter have a direct output to motor cortex, they could trigger the instructions for the movement. The parietal motor-dominant and visual-and-motor neurons may also be a part of the feedback loop for comparing desired manipulation movements with those that are effective.

Involvement of motor areas in the medial frontal cortex of primates in temporal sequencing of multiple movements

Jun Tanji

The medial frontal cortex of primates contains multiple motor areas (Dum and Strick, 1992; Tanji, 1994). Although the main direct projections to the spinal cord arise from M1, the other areas probably contribute to motor performance both through direct corticospinal projections and projections to M1. How these areas participate in the organization of motor acts remains unclear. Neurophysiological studies have related the discharge of medial frontal cortical neurons to preparation for and execution of a variety of movements (Shima et al., 1991; Matsuzaka et al., 1992) and studies of simple motor tasks have revealed only slight differences between the supplementary motor area (SMA) and M1 (Okano and Tanji, 1987). The more recent results discussed here indicate that SMA could be critically involved in more complicated and demanding motor tasks, such as the performance of memory-guided sequential movements (Mushiake et al., 1991; Tanji and Shima, 1994).
**Motor areas in the medial frontal cortex**

Early workers divided the primate frontal cortex into several distinct regions based on cytoarchitectonic and connectivity criteria. Two main divisions were recognized: M1 (BA 4) and non-primary motor cortex (BA 6). The latter was subdivided into the premotor cortex (PM) on the ventrolateral face of the hemisphere and SMA dorsomesially (Fig. 20). In addition to these somatomotor areas, there are two oculomotor fields (frontal eye field, FEF, and supplementary eye field, SEF).

![Diagram of motor areas in the monkey cortex](image)

**Figure 20.** Multiple motor areas in the monkey cortex seen in a diagrammatic top view of one cerebral hemisphere (below). Two coronal sections (above) at levels indicated with arrows show the extensions of the motor areas down the wall of the longitudinal fissure. The approximate locations of seven motor areas are depicted: M1, SMA, pre-SMA, PMd, PMv, CMA, FEF and SEF. For abbreviations, see Glossary.
Recent studies indicate that the SMA is not a single functional area but can be subdivided into caudal and rostral parts, named SMA-proper and pre-SMA (Matsuzaka et al., 1992). These differ on several criteria that support the idea that pre-SMA participates in higher-order sensorimotor processes and is less directly related to motor performance than SMA-proper (reviewed by Tanji, 1994). First, the two subdivisions have different cortico-cortical connections (Fig. 21). The pre-SMA receives projections from prefrontal, anterior cingulate and ventral premotor cortices, whereas inputs to SMA-proper come from primary sensory and motor

Figure 21. Scheme of the connectivity of the cortical motor areas showing that information flows differently through the PM, pre-SMA, SMA-proper and CMA to M1. Each of these areas receives inputs from different parts of prefrontal or parietal cortex, alone or in combination. Their outputs converge directly or indirectly on M1. Reciprocal pathways, e.g., from M1 to PMd, are not shown. Pre F, prefrontal cortex. For other abbreviations, see Glossary.
cortices and the superior parietal lobule, as well as pre-SMA. Second, only the SMA-proper projects to M1 and the spinal cord. Third, the activity recorded from single neurons related to motor tasks are not the same in the two areas. In monkeys trained in a spatial delayed-response task, neurons with phasic responses to visual cues and tonic preparatory activity were more frequent in pre-SMA, whereas movement-related activity was more abundant in SMA (Matsuzaka et al., 1992).

The mesial frontal cortex also contains areas in the banks of the cingulate sulcus that traditionally have been assigned to the limbic system. Several lines of evidence indicate that they are also motor areas. These cingulate motor areas (CMA) connect to both cortical and subcortical motor structures, with direct projections to motor cortex and to the spinal cord (Dum and Strick, 1991). They contain multiple representation of the body and mapping them with intracortical stimulation evoked movements that resembled those evoked in M1, although higher current intensities were necessary and complex movements were more frequent (Luppino et al., 1991). Neurons in the banks of cingulate sulcus discharged during self-paced and signal-triggered key pressing movements; in most neurons the activity was related to the movement but preceded muscle activation (Shima et al., 1991). Neuronal activity in the rostral and caudal parts of the region differed quantitatively, indicating that CMA has two subdivisions.

**Planning multiple movements: the role of SMA**

A fundamental aspect of motor behaviour is motor planning, i.e., organizing the execution of a series of movements in a specified order. Patients with a lesion in SMA are impaired in the performance of sequential movements and in motor tasks requiring memory (Halsband et al., 1993), indicating that mesial frontal cortex participates in motor planning. This hypothesis is supported by tests with monkeys trained to execute sequential motor tasks based on memorized information.
In the first series of experiments, three monkeys were trained to execute a sequential motor task using either visual or memory guidance (Mushiake et al., 1991). The experimental apparatus contained four touch pads that could be illuminated from behind. In the visually guided task, three of the pads were illuminated sequentially and the monkeys had to reach out to them. In the memory-guided task, the monkeys rehearsed a previously learned sequence without visual guidance. Neuronal activity was recorded in M1, PM and SMA while the monkeys performed both tasks. (As this study predated the subdivision of SMA, both parts are included under the traditional definition of SMA.) Neuronal activity was analysed for three periods: the delay period, lasting from the instruction signal to the first triggering signal (pad illumination); the premovement period, which corresponded to the reaction time of the first movement; and the movement period, encompassing the three movements.

Most M1 neurons had similar activity during both tasks in all three time periods. Neurons in SMA were preferentially active during memory guided trials, especially during the delay period, whereas PM neurons were more active during the premovement and movement periods in visually guided trials. Two selective types of neuron were found: sequence-specific and transition-specific. The first type was active only in the memory-guided task before and during the execution of a particular sequence (see below; Tanji and Shima, 1994); they were found mainly in SMA. The transition-specific type, active only during periods when the monkeys learned a new sequence before memory guided trials, was more common in PM. Neurons of both types may provide signals required for organizing the performance of sequential motor tasks.

In a second series of experiments, the properties of these neurons were examined in more detail. Two monkeys were trained to perform sequences of three movements using a handle that could be turned, pulled or pushed (Tanji and Shima, 1994). Each
sequence was first learned during five trials guided by three coloured lights to indicate correct movements. The monkeys subsequently executed the memorized sequence six times without visual guidance. Electromyographic recordings showed that the forelimb muscles contracted similarly during visually guided and memory-guided sequences and were relaxed during waiting periods, a pattern very different from that found in neurons in SMA-proper.

Recording from 206 neurons in SMA-proper while the monkeys performed memorized sequences revealed three patterns of neuronal discharge. The activity of 26% of the neurons reflected the specific order of intended movements but not the preparation for the first movement. For example, the neuron shown in Figure 22 was

![Figure 22](image)

*Figure 22. Activity of a neuron in SMA-proper that was excited preferentially before three memory-guided movements performed in the specific order turn-push-pull (below). In comparison, it showed little activity with a different sequence (above). In the raster displays, each row represents one trial and the marks represent individual discharges; total activity at each time interval is shown in the histograms. Small squares, crosses and triangles denote the time of the trigger signal, movement onset and contact with target. Triangles on the x axis indicate the start of the first movement. Reproduced with permission from Tanji and Shima, 1994.*
tonically active before the execution of a turn-pull-push sequence but not before turn-push-pull or other sequences. Another 36% had a ‘time-linking’ property; as illustrated by the neuron in Figure 23, they discharged during the waiting period between two specific movements wherever these came in the sequence but did not respond to other combinations of movements. The third type (12%) were similar to most neurons recorded in M1 (n = 106), where neither of the first two types were found. They discharged in close relation to the execution of a movement, i.e., activity started shortly before a movement and continued throughout it.

**Figure 23.** Selective activity of a neuron in SMA-proper during a waiting period between the performance of a push and a pull movement (top, Seq1 and Seq3). It did not respond when turn followed push (Seq3) or the first movement was turn (bottom, Seq4). This pattern indicates a role in linking two motor events in a specific order. Reproduced with permission from Tanji and Shima, 1994.
A *model for memory-guided movement sequences*

A simple model of neuronal operations performed during the retrieval of sequential movements from memory is proposed in Figure 24. It consists of three levels of organization based on the types of neurons described above: sequence memory, sequencing and output specification. At the sequence-memory level, sequence elements (*Fig. 22*) indicate the specific sequence to be recalled from memory (123, 132, ...) and initiate the recall. At the sequencing level, time-linking elements (*Fig. 23*) code for the transition between specific items in a sequence (12, 13, 23, ...) and participate in the production of behavioural responses. At the output specification level, output elements (1, 2, 3) provide direct implementation of the responses in the required temporal order. These three levels of organization probably reflect the way SMA-proper participates in the performance of sequential movements. The recall of longer sequences and the existence of a hierarchy of internal representations remain open questions.

![Figure 24. A simple model for retrieving sequences of movements from memory. To perform three movements in various temporal orders or sequences, information about a correct sequence has first to be retrieved, then decoded to obtain an appropriate sequence of output codes before the individual outputs required for each movement can be specified. For further explanation, see text.](image-url)
As the main motor output of the cortex, M1 is densely connected both to other parts of the cortex and to subcortical structures and therefore has a prominent role in the specification, initiation and execution of motor acts. A long-standing question concerns the nature of the representation in motor cortex (reviewed in Georgopoulos, 1991). The discharge of neurons in M1 relates to muscular activity, output force and torque (Georgopoulos et al., 1992; Wise, 1993) and there is now strong evidence that it also relates to the kinematics of movements, i.e., parameters such as direction and velocity, and to higher-order processing of sensorimotor information (Georgopoulos et al., 1986, 1989, 1993; Pellizzer et al., 1995).

It has also been established that a large number of neurons are simultaneously engaged in even a simple motor task and that information relevant to ongoing behaviour is represented by the whole population of neurons in M1. Calculating the population vector from the activities of many neurons with similar responses has proved to be a powerful tool for monitoring covert processes in M1, such as mental transformations of the direction of movement.

**Directional tuning of neurons in motor cortex**

During arm reaching movements towards visual targets, the hand follows relatively straight trajectories. Neurophysiological studies have shown that the activity of motor cortical neurons is modulated effectively and in orderly fashion by the direction of movement (Georgopoulos et al., 1982, 1986). Single neurons in motor cortex were recorded while monkeys performed arm movements in eight directions. The discharge of motor cortical neurons was maximal for a particular direction of movement and became progressively less for directions further from the preferred direction (Fig. 25).
Figure 25. Tuning of a neuron in M1 with preferred direction approximately down-right. Neuronal activity was recorded while a monkey reached to visual targets at various points in space. The activity during eight replications of the movement toward each target is shown as sweeps in the raster plots. The longer bars in each trial indicate, from left to right, target on, beginning of movement (MOV) and end of movement. Reproduced with permission from Georgopoulos et al., 1986.

A mathematical analysis revealed that the neuronal discharge is proportional to the cosine of the angle between the preferred direction and the direction of movement (Georgopoulos et al., 1982, 1986). 224 out of 282 neurons in M1 were found to be directionally tuned, although the tuning of most neurons was broad, and preferred directions were distributed throughout 3-D space (Georgopoulos et al., 1986). The direction of movement is not, however, indicated by the activity of a single broadly tuned neuron but rather by the weighted vector sum of the activities of a population of directionally tuned neurons; this is termed the neuronal population vector (NPV). (For the mathematical derivation of the NPV, see Georgopoulos et al., 1986.) It is an index of directional information processing underlying ongoing movements; for instance, the NPV calculated over 224 cells accurately indicated the direction of movement (Georgopoulos et al., 1986). We have been using it to monitor covert operations during cognitive tasks.
**Mental rotation**

The mental rotation paradigm, a classic task in cognitive psychology, requires subjects to identify the orientation of objects viewed from different angles (Shepard and Metzler, 1971). As the time taken to produce a correct response increases with the angle between a reference view of the object and the test view, it is thought that subjects may mentally rotate the image of the test view to match the reference view. A motor task adapted from this paradigm requires the subject to make arm movements at various angles from a stimulus direction (Georgopoulos and Massey, 1987). In humans, psychophysical measurements indicate that the reaction time, i.e., the time between stimulus presentation and movement onset, increases linearly with the angle of the rotation (Georgopoulos and Massey, 1987). This is consistent with a progressive shift in the covert direction of motor intention during the reaction time between the instructed and desired directions of movement.

This hypothesis was confirmed in monkeys using the NPV to visualize the directional motor output in M1 during a similar task (Georgopoulos et al., 1989; Lurito et al., 1991). Single cells (n = 294) were recorded in the motor cortex of two monkeys while they performed planar arm movements in the direction of a stimulus (direct trials) or at 90° counterclockwise from the stimulus direction (rotation trials) (Fig. 26a). The preferred direction was calculated for each neuron from its activity in direct trials; the NPV was calculated every 10 ms after the appearance of the stimulus from the preferred directions of all the directionally tuned neurons recorded in M1 during direct and rotation trials.

In direct trials, the direction of the population vector coincided with the direction of movement but in rotation trials, the NPV turned counterclockwise from the stimulus to the movement direction during the reaction time (Fig. 26c). For both conditions, the angle of the NPV was a linear function of time (Fig. 26d) and its length started to increase soon after stimulus onset, stabilizing before the movement started (Fig. 26b). The cognitive process
underlying this mental rotation task thus involves the actual rotation of an imagined vector through the shortest angular distance.

**Figure 26.** Mental rotation of the neuronal population vector. 

- **a,** in a direct trial (left), the direction of the stimulus (S) and the movement (M) are identical. In a rotation trial (right), the angle between S and M is 90°. 
- **b,** the neuronal population vector points towards M in a direct trial (left) but changes direction from S to M in a rotation trial (right). 
- **c,** plotting a set of population vectors illustrates the rotation process. 
- **d,** changes in the direction of the population vector during a direct and a rotation trial. Reproduced with permission from Georgopoulos et al., 1989.
**Context-recall memory scanning**

A task known as context-recall memory scanning requires subjects to identify the item that followed a designated item in a previously presented list (Sternberg, 1966). Using a visuomotor version of this task in humans showed that different coding mechanisms may be involved in mental rotation and context-recall tasks (Pellizzer and Georgopoulos, 1993). This has been confirmed in monkeys by recording neuronal activity in M1 while the animal performed a visuomotor context-recall task (Pellizzer et al., 1995). The monkey responded to visual instructions displayed on a video monitor by applying a directional force pulse to a semi-isometric handle. Two tasks were used (Fig. 27). In the control task, a yellow stimulus appeared at one of eight positions arranged in a circle. When it turned blue, the monkey had to reach in the stimulus direction. In the context-recall task, three yellow stimuli (S1, S2, S3) were presented successively. When either S1 or S2 turned blue, the monkey directed its response towards S2 or S3, respectively.

*Figure 27. Context-recall task. See text for details. Reproduced with permission from Pellizzer et al., 1995.*
Most cells (n=544) were directionally tuned in the control task. The activity of a neuron tuned for the downward direction during the context-recall task is shown in Figure 28. Although downward-directed movements were made from both S1 to S2 and S2 to S3, they were instructed by stimuli in different positions in a sequence. In the first condition (Fig. 28, left), the neuron became active at the Go signal but in the second condition activity started only 100-150 ms after Go (Fig. 28, right). The NPV calculated every 10 ms from the activity of directionally tuned neurons behaved differently in the two conditions: in the first, it pointed in the direction of movement but in the second, it switched abruptly from stimulus direction to movement direction. The difference may be because S2 is present in every trial, either as instruction or target.

The abrupt shift in the direction of the NPV during the context-recall task contrasts with the slow rotation observed during mental rotation (Pellizzer et al., 1995). The time of the shift during context recall was largely independent of the angular distance between the instruction and the target, which further argues against a

**Figure 28.** The activity of one neuron during the context-recall task. Its preferred direction, determined in the control task, was downward and the monkey was required to make the same movement from the stimulus (S1 or S2) to the target (S3). The tests differ in the times at which the Go stimulus is shown in a sequence. With S2 as Go stimulus, this neuron shows a sudden shift from stimulus-related to movement-related activity. Reproduced with permission from Pellizzer et al., 1995.
Figure 29. Comparison of mental rotation and context-recall tasks. The activity of neurons with preferred directions intermediate between the directions of the stimulus and the movement remains constant in the context-recall task but changes dramatically in the mental rotation task, indicating that the activity shift seen during context recall does not pass through intermediate positions. Histograms start at the Go signal (time = 0). Asterisks indicate a statistically significant difference of activity in the two conditions. The arrows indicate the average time at which the population vector begins to change direction (Begin) and when it attains the direction of the motor response (End). Reproduced with permission from Pellizzer et al., 1995.

rotation process being used in this task. If rotation were being used, neurons with preferred directions intermediate between the instruction and the target should increase their activity during the interval between stimulus and response in the context-recall task. As Figure 29 shows, this was not the case. The mean activity of such neurons increased only during mental rotation and not in context recall, which does not engage neurons coding intermediate directions. The mental rotation task involves an internal transformation, whereas the context-recall task reflects a switching process.

Although these mechanisms have been demonstrated in M1, other brain regions are likely to participate in the setting up of such mental representations. Where these are and what they contribute remains to be determined.
The cortical and subcortical control of eye movements

To line up an object in the visual field on the fovea, where resolution is greatest, it is often necessary to move the eyes, sometimes followed by the head. In primates, this is accomplished by two pathways that converge in the superior colliculus (the rostral division of the tectum in the mammalian midbrain), one through V1 and the parietal and frontal cortices, the other a direct projection from the retina to the superior colliculus. The saccade, a rapid eye movement that redirects the line of sight, has been particularly well studied. The lateral intraparietal area and the frontal eye fields are involved in the analysis of sensory signals that guide saccadic eye movements. Neurons in the lateral intraparietal area are active during a delay imposed in a visual saccade task; here Richard Andersen interprets the function of this activity as encoding of intention and spatial location, whereas Michael Goldberg presents evidence for its role in eye-centred representations and attention to spatial location.

Both the lateral intraparietal area and the frontal eye fields project to the intermediate and deep layers of the superior colliculus, which also receives inputs from cortical regions essential for the control of head, trunk and limb movements, such as M1 and PM. Klaus-Peter Hoffmann demonstrates that the superior colliculus may have a role in the control of arm movements that is similar to its role in eye movements. He also examines the specificity of information in cortico-subcortical circuits, taking as an example a specific subset of the information available in middle temporal and medial superior temporal cortex that reaches the nucleus of the optic tract and the dorsal terminal nucleus, structures dedicated to the generation of slow eye movements.

Many of the neurons in the deeper layers of the superior colliculus discharge at high frequency just before saccades begin but each neuron is active only in association with saccades with a particular
The representation of intention and spatial location in monkey posterior parietal cortex

Richard A. Andersen

The primate posterior parietal cortex (PPC), located between primary sensory and motor cortical areas, is known to be important for the processing of spatial information. Early studies established that it contributes to visuospatial behaviour, although the exact nature of this involvement was not clear (Mountcastle et al., 1975; Robinson et al, 1978). Both human patients and non-human primates with unilateral or bilateral lesions in the PPC show deficits related to sensorimotor integration, one of the most prominent being optic ataxia. As well as a general impairment of visually guided motor control (Balint, 1909; see Jeannerod, 1994), oculomotor functions, such as smooth-pursuit eye movements and saccades, are also impaired.
A specific region of PPC in monkeys, the lateral bank of the intraparietal sulcus or lateral intraparietal area (LIP) has been found to participate in the control of voluntary saccades. Many neurons in LIP exhibit activity during a delay in a saccade task. I argue here that a large component of this activity represents the intention of the monkey to make a saccade rather than attention to the sensory information (see Goldberg, this volume, for another view).

**Background**

Recent studies of parietal lesions in both humans and non-human primates (in humans, only with lesions in the right hemisphere) revealed that impairments in saccades were restricted to voluntary movements; spontaneous saccades were unaffected. In monkeys, electrical stimulation of specific regions of the PPC elicited saccadic eye movements and retrograde tracers injected into the FEF, an area in frontal cortex known to be involved in the control of saccades, predominantly labelled LIP, now considered as the posterior eye field (Andersen et al., 1990a; Barash et al., 1991a, b).

The involvement of LIP in the generation of saccades was confirmed by single-unit recordings in the behaving monkey. Neurons in LIP produce a burst of activity during regular visually guided saccades. Using a memory-guided single saccade task demonstrated that this activity can be separated temporally into sensory and motor phases (Andersen, 1989). In this task, a visual stimulus is flashed briefly in a neuron’s visual receptive field while the monkey fixates a central target; the saccade can be made only once the fixation light is switched off. Many LIP neurons revealed a tonic discharge during the delay period in addition to a visual response and a burst of activity tightly related to the onset of the saccade.

**Nature of the delay-period activity**

Does the activity in the delay period represent holding the sensory information in memory, i.e., the location of the target with respect
Figure 30. Delayed double saccade task designed to determine whether activity in LIP neurons is related to sensory memories or plans to make movements. 

(a) timing of stimuli and eye movements in the task. The monkey fixates a point (continuous bar) while the first (T1) and second (T2) visual targets are flashed. Following T2, the fixation point remains illuminated for a delay period (m1), after which the monkey makes saccades (S1, S2) to the two targets (lower trace). The intersaccadic interval is the second memory period, m2.

(b) spatial arrangement of stimuli in the five classes of the delayed double saccade task and predictions of the responses during m1 that should be made if the neuronal activity represents either sensory memory or motor plan. Each panel shows the location of the fixation point (FP = cross), a neuron’s receptive field (RF = dashed semicircle), the locations of the two visual targets (T1, T2 = spots). The size and direction of the arrows indicate the amplitude and direction of the saccades (S1, S2). The table below the diagram summarizes the target positions with respect to the RF and whether saccades are in the neuron’s preferred direction, i.e., into its motor field (MF). Modified from Mazzoni et al., 1996.
to the receptive field, or does it reflect the plan to make a saccade towards the target? A delayed double saccade task, modified from the original double saccade task devised by Mays and Sparks (1980), was used to dissociate these possibilities. In the original task two saccade targets T1 and T2 are briefly flashed in sequential order at different spatial locations. The second target disappears within the shortest saccade reaction time. The movement required for the first saccade corresponds to the site of retinal stimulation but to make the second saccade the system has to take into account both the retinal position of the second target and the previous eye movement. Thus spatially tuned activity occurring after the first saccade but preceding the second should represent preparation for the impending saccade.

We have extended this task by introducing a delay period, m1, before the execution of the first saccade; the interval between the performance of the two saccades is here termed m2 (Fig. 30a). Five classes of delayed double saccade tasks using similar spatial locations but different temporal sequences (Fig. 30b) were employed to test activity in the delay period more systematically. The logic of this experiment is that the sensory-memory and motor-plan hypotheses should give the same activity in classes 1, 2 and 3 during the m1 period, because the movement the animal plans to make and the stimulation of the receptive field are spatially congruent. In contrast, in classes 4 and 5 the second stimulus appears in the receptive field but the first movement is planned outside the receptive field. The motor-plan hypothesis predicts no activity during m1, whereas the sensory-memory hypothesis predicts activity.

A neuron tested with class 1-4 tasks (Fig. 31a) revealed a response to a visual stimulus flashed in its receptive field and a build-up of activity during m1 in classes 1 and 3. In contrast, when tested with tasks of classes 2 and 4, where the first saccade is directed away from its receptive field, the neuron showed no visual response and no activity during m1; however it discharged during
Figure 31. Examples of two LIP neurons showing that activity during delay periods in the task are more related to the planned movement than to the memory of the target location. 

a, activity of a neuron while the monkey performed classes 1-4 of the delayed double saccade task. 

b, comparison of single (left) and double (right) saccade tasks shows that the second neuron was tuned to movement into its motor field (see text for details). Each panel includes: discharge rasters for each trial (top); time histogram of the firing rate (middle) and a trace of the horizontal and vertical eye positions (bottom). The vertical dotted lines and the thick lines below each panel show the presentation of the visual stimuli. On the left of each panel, the spatial arrangement of the task is shown (see Fig. 30). Modified from Mazzoni et al., 1996.
m2, when the saccade was towards the receptive field, even in class 2 where no stimulus ever appeared there. The lack of response in m1 in class 4 is consistent with the motor-plan hypothesis and not the sensory-memory hypothesis; the activity in m2 for classes 2 and 4 is also consistent with the motor-plan hypothesis. That is, the memory-delay activity was stronger before saccades whose amplitudes were more appropriate to the motor field of this neuron (m1 in the class 1 task and m2 in the class 4 task).

Tuning of the activity in the memory period to the direction of the saccade is also shown by comparing the discharges observed in a single memory-guided saccade task with those in a delayed double saccade task in class 5 (compare left and right panels in Fig. 31b). In the single memory-guided task, the saccade is made into the receptive field, whereas in the delayed double saccade task, the second stimulus falls in the same location as the stimulus in the single saccade task but the first eye movement is planned out of the receptive field. Activity was suppressed during the m1 period (as it was in this neuron in the single memory-guided saccade task for saccades away from the receptive field). This result is again consistent with the planning of a movement and not the coding of a sensory memory.

Out of 46 neurons recorded in two monkeys, in 38 (82%) the activity during the memory period fitted statistically with the motor plan hypothesis (Fig. 32a, motor plan group). The activity of the remaining 18% is compatible with the sensory-memory hypothesis (Fig. 32a, sensory memory group). The neuronal discharge during the first memory period, m1, was quantified using an activity index:

$$I_a = \frac{(m1 \text{ activity} - \text{background activity})}{\text{background activity}}$$

When $I_a$ is zero, m1 activity is similar to background, whereas when it is close to 1.0, m1 activity is about twice the background level. When the mean values of $I_a$ for the five classes of delayed double saccade task are plotted for the motor-plan group (Fig. 32a), $I_a$ values are above 1.0 in the tasks where the first
saccade was made into the motor field of the neurons (class 1 and 3), whereas tasks requiring a first saccade in the opposite direction resulted in $I_a$ values around zero (class 2, 4, 5). In contrast, for the sensory memory neurons $I_a$ was between 0.5 and 1.0 for all tasks (Fig. 32a). The dependence on direction of movement is obvious, even when the values for both groups are combined (Fig. 32b).

**Figure 32.** Summary of data from 49 LIP neurons demonstrates that activity during the delay period in most of them reflected what the animal intended to do. In a few neurons activity related to the memorized location of the target. 

- **a**, upper panel: the 38 neurons with $m1$ responses that fitted statistically with the motor-plan hypothesis. Lower panel: the eight neurons whose $m1$ response fitted the sensory-memory hypothesis.
- **b**, all neurons in this study. Mean values plus standard error of the $m1$ period activity index, $I_a$ (see text), are given for the five delayed double saccade (DDS) classes. Modified from Mazzoni et al., 1996.
Change in plan

Because most LIP neurons seem to code for the intended eye movement, their activity may represent the plan for making an eye movement independent of whether the movement is made. We therefore designed a task in which the animal’s plan for making a specific eye movement was altered without any overt change in performance. This change-in-plan experiment comprised eight classes of saccade tasks presented in random order. In all of them, the monkey was required to perform a saccade to the most recent target.

Classes 1 and 2 are single memory-guided saccade tasks with the target either in the motor field of the neuron (Fig. 33a) or outside it (Fig. 33b). Classes 3 and 4 are single change-in-plan tasks with the first target in the motor field and the second target away from it (Fig. 33c) and vice versa (Fig. 33d). Here there was less activity after m1 in the class 3 task and an increase in m2 in the class 4 task. This outcome was even more obvious in the double change-in-plan tasks (class 7 and 8), where the first and third targets are in the motor field and the second away from it (Fig. 33g) and vice versa (Fig. 33h). Here the animal had to change the plan for the intended movement twice within one trial; the activity pattern of the neuron changed according to the direction of the intended movement.

The observation that LIP neurons are active for plans for movements which do not have an obligatory link to their execution may provide a unifying thread for a recent observation. When two lights are flashed and the animal makes a saccade to only one of them, activity appears after the first eye movement for the location that codes the oculomotor coordinates of the second stimulus, even if the stimulus is no longer present (Duhamel et al., 1992). This result is similar to the memory double saccade experiment above (class 2) and earlier double saccade experiments (Gnadt and Andersen 1988), except that the second saccade is not made. Based on these results, Duhamel et al. (1992) proposed that LIP codes sensory signals in retinal coordinates
Figure 33. Activity of an excitatory LIP neuron coding the movement plan in the change-in-plan task. Changes in a planned movement resulted in changes in the neuron’s activity, which also related to the intention to make movements even when they were not performed. a - h, for description of the eight classes of trial, see text. Conventions as in Figures 30, 31. A, target in the receptive field; B, target outside receptive field; m3, third memory (delay) period. Reproduced with permission from Bracewell et al., 1996.
and that the retinal location of the remembered sensory signal is remapped in retinal coordinates to anticipate reafference of retinal signals coding the second target after the eye movement. Our results provide an alternative explanation: that the animal does consider making an eye movement to the second target but this plan is not executed. In other words a majority of the neurons active in the memory period are coding intended movements in motor coordinates, rather than sensory signals in retinal coordinates.

**Parietal cells code the type of movement being planned**

A definitive test of intention is to show that the delay-period activity is contingent on the type of movement the animal plans to make. Bushnell *et al.* (1981) claimed that the activity of PPC neurons did not differentiate between the animal programming an eye movement or a reaching movement to a stimulus that was retinotopically identical. Moreover, if neurons showed a larger response when a stimulus was a target for a movement compared to when it was not, the enhancement was the same for both reaching and eye movements. This result was interpreted as proof that PPC is concerned with sensory location and attention and not with planning movements (Bushnell *et al.* 1981; Colby *et al.* 1995).

We have recently repeated these experiments, with different results (Snyder *et al*., 1996). The monkey fixated a light in a button and pressed the button with its hand. Next a light appeared briefly in the visual field; depending on the colour, the animal had to plan either an arm or an eye movement to the remembered location. After a delay, it made the eye movement without moving the limb or vice versa. During the memory period, two-thirds of the neurons sampled (n = 276) in PPC were selective for the requirement to make an arm or an eye movement. Interestingly, nearly half of the sensory responses to the flashed targets also distinguished between the type of movement called for. Much of the activity in PPC is thus concerned with what the animal plans to do, that is with intentions.
These data lead us to conclude that a large component of delay activity in LIP neurons encodes the next movement rather than the memory of the spatial location of the target for a saccade. Some neurons do code the sensory memory but there are fewer of them. The tuning of the neurons implies that the coding is in motor coordinates. Their activity is not linked in an obligatory manner to overt behaviour but rather reflects the animal’s intention or plan to make the next movement. Lastly, the activity of most neurons in PPC during the delay period is specific for the type of movement (reach or saccade) that the animal plans to make.

Attentional and spatial mechanisms in the parietal cortex

Michael E. Goldberg

Studies on patients with lesions in parietal cortex have also emphasized the role of the PPC in attentional processes dedicated to a specific region in space. These patients show several impairments in attention, such as a neglect contralateral to the lesion side or a shift of attention into one visual hemifield (for review, see Ungerleider and Mishkin, 1982). We have investigated the neural basis of these attentional processes in more detail using single-neuron recordings in awake behaving monkeys. Neurons in LIP discharge in response to behaviourally relevant stimuli, regardless of whether these are targets for an eye movement or not (see also Andersen, this volume). They differ in this from neurons in the FEF, a subset of which discharge only before purposive saccadic eye movements and do not respond to visual targets even if these are the target for a delayed saccade (Bruce and Goldberg 1985). Using several behavioural tasks, we have examined the activity of LIP neurons to characterize better their role in the processes underlying visuospatial attention.
**Attentional modulation in LIP**

The discharges of neurons in LIP are significantly modulated by ongoing attentional processes. As the histograms in Figure 34 show, even the background activity of the neurons changes according to whether the monkey does not or does have to pay attention to a peripheral location or make a saccade to it. In a memory-guided delayed saccade task, the neurons discharge at a rate significantly higher than background immediately before the saccade but this activity is significantly less than the response to the appearance of a visual stimulus in a fixation task, even though the stimulus is behaviourally irrelevant. This activity is significantly enhanced when the monkey has to attend to the stimulus in a peripheral attention task and even more so when the stimulus is the target for a subsequent eye movement in a delayed saccade task (Colby et al., 1995). These experiments demonstrate that there are three parallel and perhaps independent inputs to neurons in LIP: a visual input, a presaccadic signal and an attentional control.

![Figure 34](image_url)

*Figure 34. Attention enhances the average discharge rates of a population of 30 LIP neurons. The greatest discharge is evoked by a visual target to which the monkey must attend. Note that the response to a flashed stimulus to which the animal does not make a saccade is significantly greater than the presaccadic discharge of the neuron. Reproduced from Kusunoki et al., in press.*
Stable target and attention

To understand the effects of attention in more detail we have developed a new experimental paradigm, based on the observation that the behavioural tasks used to investigate PPC are far removed from everyday experience. The visual activity of parietal neurons is usually determined by studying their responses to the appearance of a flashed target in their receptive fields; attentional enhancement is studied mostly by analysing the difference in response when the monkey can ignore the flashed target compared with using it in some way (Robinson et al. 1978; Bushnell et al. 1981). In the real world, however, lights rarely flash and it is difficult not to attend to an object that appears suddenly. The visual response studied in the fixation task could thus have an attentional component grafted on to it, even though the animal is not required to attend to the object.

We have developed a more realistic and stable paradigm, the stable-target task, in which an array of eight targets for saccadic eye movements is always visible and stays stationary on a screen in front of the monkey (Fig. 35c,d; Kusunoki et al., in press). Each trial begins when the monkey fixates a point at the centre of the array. The saccade to fixate that point brings one or more of the members of the array into the receptive field of the neuron under study. An extra cue then appears that matches one member of the array and the monkey must make a saccade to this target. The movement is directed by the pattern of the cue, not its location; in other words, at this point the ventral visual stream is telling the dorsal stream where to go.

The responses recorded from a single neuron in LIP during the standard delayed response task and the stable-target task are compared in Figure 35. This neuron responded briskly to the onset of a light flash but did not discharge immediately before or during a saccadic eye movement towards a target in its receptive field that had been flashed previously (Fig. 35a). A saccade made to the centre of the array that brought the stimulus into the receptive field produced no significant discharge (Fig. 35b). When the cue
Figure 35. Comparison of the responses of an LIP neuron in the standard delayed saccade task and the stable-target task. 

a, in the delayed saccade task, there is a vigorous visual and a weak presaccadic response. 

b, no response when a saccade brings a stable target into the receptive field. 

c, the response develops as the cue indicates that the monkey should make a saccade to the target; note that in this experiment the activity occurs closer to the saccade. 

d, lack of regular response when the cue dictates a saccade elsewhere. The cartoons show the saccade (arrow) and the symbols that are present on the screen in each experiment. Reproduced from Kusunoki et al., in press.
matched the stimulus in the receptive field, however, the neuron began to discharge some time after the appearance of the cue but before the saccade (Fig. 35c). It did not respond reliably when the cue dictated a saccade elsewhere (Fig. 35d). The considerable scatter in latency between trials indicates that the focus of the monkey’s attention shifted at different times in different trials (Fig. 35c).

A response in the stable-target task did not generally require the neuron to show presaccadic activity in the delayed saccade task. When it responded to both tasks, the activity was usually stronger in the stable-target task than in the delayed saccade task. Presaccadic activity increased only when a cue outside the receptive field instructed the monkey to make a saccade into the receptive field (cf. Fig. 35c and d). When the cue appeared in the receptive field, the neuron responded identically regardless of the direction of saccade dictated by the cue. However, when the cue dictated a saccade in a direction outside the receptive field, the activity decreased before the beginning of the saccade.

These observations indicate that the activity evoked by visual stimuli in LIP neurons has an obligatory dependence on attention. Attention can be shifted to a stimulus that suddenly appears or by an exogenous cue that directs the monkey to a pre-existing stimulus. The responses in PPC parallel this allocation of attention. Although some LIP neurons discharge before saccades, this activity is weak unless the animal is attending to a stimulus at the endpoint of the saccade. Neurons may discharge strongly in response to a cue outside the receptive field dictating a saccade to a stimulus in the receptive field but not if the same cue dictates the same saccade made without a stimulus in a learned-saccade paradigm (J. Gottlieb and Goldberg, in preparation). These results suggest that LIP is involved in the generation of spatial attention rather than the planning of saccades.

Reference frames
Another issue is the reference frame used by LIP neurons. Early models of the saccadic eye movement system (see Sparks, this
assumed that the retinal location of a target provides the exclusive visual input for driving a saccade. However, the double-step task, in which two stimuli appear and disappear within the latency of a single saccade, demonstrated that a retinotopic analysis is inadequate for the generation of saccades. Subjects make successive accurate saccades even though the second saccade cannot be computed from retinal information alone as it requires information about the eye movement. This led to the conclusion that the oculomotor system has access to the position of the target in a supraretinal reference frame. Even so, detailed studies always showed that the receptive fields of neurons were strictly tied to the retina. The influence of the position of the eyes in the orbit on neuronal discharges was considered as evidence for non-retinocentric coding that could not be detected in the discharge of single neurons but could be deduced from the population of neurons (Zipser and Andersen, 1988; Andersen et al., 1990b).

An alternative hypothesis, that the proper retinotopic signal might be calculated dynamically using the retinal position of the target and a corollary discharge signal about the impending saccade, has been supported by studies on neurons in the superior colliculus, FEF (M.M. Umeno and Goldberg, in preparation) and LIP (Fig. 36; Duhamel et al., 1992; Goldberg et al., 1990; Walker et al., 1995). LIP neurons respond to a brief visual stimulus that, by definition, has to be flashed within the receptive field to elicit a response (Fig. 36a). But they also respond to stimuli flashed at a spatial location that an impending saccade will bring into their receptive fields (Fig. 36b), even though they do not respond to a stimulus in that location when no saccade will be made (Fig. 36c) or when a saccade is made to a new fixation point without a stimulus in either receptive field (Fig. 36d).

A predictive response was found in 28% of such neurons, i.e., their activity increased even before the saccade started. Such responses could merely be presaccadic activity that never generates a saccade. Arguments against this interpretation are that the
**Figure 36.** Predictive visual response in an LIP neuron.  

- **a**, the neuron responds to a stimulus in its current receptive field (RF), i.e. when it is looking at fixation point (FP) 1.  
- **b**, it is also active when a light is flashed in the future RF if the monkey intends to make a saccade towards a second FP.  
- **c**, it does not respond to a stimulus elsewhere on the retina if the monkey does not intend to make a saccade to that point or **(d)** when the monkey makes a saccade to a point where there is no stimulus.  

The diagram above each raster shows horizontal (H) and vertical (V) components of eye position, timing of stimulus and direction of saccade represented by an arrow. Reproduced from Kusunoki et al., in press.
predictive responses are also seen in purely visual neurons but not in neurons without visual responses that discharge before saccades, such as the movement neurons in the FEF and the burst cells in the intermediate layer of the superior colliculus. The effect occurs even when the monkey plans a second saccade outside the receptive field of the neuron.

The predictive response may be temporally specific; alternatively it could be a non-specific breakdown of the receptive field around the saccade. Two receptive fields can be defined during a saccade: the current one related to the present centre of gaze and the future one related to the forthcoming centre of gaze. Detailed examination of the temporal relationship between these two revealed a specific change in excitability for each of them around the saccade (Fig. 37). The predictive response thus has a specific effect, i.e., the excitability of the present receptive field decreases at the same time that the excitability associated with the future receptive field shows a highly nonlinear increase. This excitability change precedes the saccade (Kusunoki et al., in press).

**Functions of LIP neurons**

These experiments suggest that LIP neurons describe the vector from the current or impending centre of gaze to an attended stimulus. The mere presence of the stimulus in the receptive field is neither necessary nor sufficient to drive the neuron. The generation of a saccade to the location of the receptive field is associated with a rather weak discharge unless the stimulus is present. Activity is greatest when the monkey must attend to a stimulus in the receptive field whether or not a saccade to the stimulus will be made.

LIP neurons are organized in oculomotor coordinates: they respond to stimuli that will be brought into their receptive fields by a saccade or to a recent stimulus at a location that will subsequently be brought into the receptive field by a saccade. This requires visual responsiveness and a corollary discharge of the impending movement. It is independent of presaccadic activity and is specific:
Figure 37. Perisaccadic changes in the excitability of an LIP neuron. A stimulus was flashed for 100ms in either the future or the current receptive field of a neuron immediately before, during or after a saccade. Activity evoked by the stimulus is plotted against time between disappearance of the stimulus and beginning of the saccade. The excitability increases before the saccade in the future receptive field and decreases before the saccade in the current receptive field.

excitability decreases in the present receptive field as it increases in the future receptive field. We conclude that LIP neurons describe the vector of visuospatial attention in spatially accurate gaze-centred coordinates.

The specific role of cortico-pretectal and cortico-tectal connections in the control of eye and limb movements

Klaus-Peter Hoffmann

Lesions in single, clearly circumscribed areas of monkey cortex produce asymmetrical sensory and motor impairments. For example, a unilateral lesion in the motion-sensitive MT or MST areas causes a decrease in the gain of slow eye movements towards the lesioned
side, as well as a specific deficit for detection of moving stimuli. Such effects seem to run contrary to the numerous studies showing that populations of neurons in many visual cortical areas continuously represent stimulus parameters such as movement, direction or speed. The question of how a lesion in an area that uniformly represents a stimulus parameter can cause only a limited range of impairments led us to predict specific connections from these cortical areas to subcortical structures whose signal processing is selectively impaired by damage to their cortical inputs.

Our subcortical explorations have taken us to the pretectal nucleus of the optic tract (NOT) and the dorsal terminal nucleus (DTN) of the accessory optic system, which are both involved in slow eye-movement control, and to the superior colliculus, which contributes to the regulation of orientation of gaze and reaching. We are discovering profound similarities in the cortical–subcortical circuitry involved in the control of arm movements and of eye movements.

**Cortico-pretectal projections involved in slow-phase eye movements**

The NOT and the DTN are good examples of subcortical structures that may be affected by cortical lesions. They are dedicated to the generation of slow-phase eye movements during visual pursuit and to horizontal optokinetic nystagmus (the rolling of the eyeball that stabilizes the gaze during head movements and, in more general terms, prevents involuntary slip of the retinal image). NOT/DTN neurons discharge selectively to movements of the visual stimulus towards the recorded side (ipsiversive) and high frequency electrical stimulation of the NOT/DTN causes slow ipsiversive horizontal eye movements. Specific connections from MT and MST to the NOT/DTN complex, mediating information only about ipsiversive stimulus movements, could thus explain specific oculomotor impairments after lesions of these cortical areas. We tested this hypothesis by investigating the response
characteristics of neurons in both cortical areas and by using electrical stimulation in the NOT/DTN to identify specific cortico-pretectal projections.

The visual responses of neurons in the NOT/DTN complex are well characterized (Hoffmann and Distler, 1989). The receptive fields are usually extensive, always including the fovea and often spreading substantially into the ipsilateral hemifield (Fig. 38a; Hoffmann et al., 1992). The neurons respond exclu-

**Figure 38.** Evidence that a subset of neurons in cortical areas MT and MST project to the pretectal nucleus of the optic tract (NOT) and dorsal terminal nucleus (DTN). a, size and extent of visual receptive fields in NOT/DTN are compared with (b) those of neurons in cortical area MT that project to NOT/DTN. The length of each line depicts the field size of an individual neuron; the extent to left and right of 0° represents the spread of the fields in the ipsi- and contralateral halves of the visual field. c, a subset of antidromically identified neurons in MT have receptive fields similar to those in NOT/DTN (heavy outlines in upper panel), with large fields especially prominent in cortical layer 5 (lower panel). (c) modified from Raiguel et al., 1995.
sively to ipsiversive motion of the stimulus (Fig. 39a), i.e., those in the left NOT/DTN increase their discharge during movement of a visual stimulus to the left but movement to the right (contraversive) usually decreases activity below the level of the spontaneous discharge. NOT/DTN neurons also increase their discharge during ipsiversive slow phases of nystagmus and smooth pursuit if the eye moves slower than the visual stimulus (Ilg et al., 1993; Ilg and Hoffmann, 1996). However during optokinetic after-nystagmus (a continuation of the ongoing eye movements after the stimulus is switched off and the monkey sits in total darkness) their activity immediately decreases to spontaneous level. Thus, NOT/DTN neurons are purely sensory and do not carry a motor signal.

Receptive fields in MT and MST differ remarkably in size, ranging from a few degrees in parafoveal neurons to more than 40°, sometimes even extending into the ipsilateral hemifield (Fig. 38b, c). In MT, neurons with very large receptive fields are located mostly in cortical layer 5, the output layer with projections to subcortical targets (Fig. 38c; Raiguel et al., 1995). Individual neurons in MT and MST also respond selectively to the direction and speed of a moving visual stimulus. Unlike a sample of NOT/DTN neurons, which exclusively responds to ipsiversive motion, a population of MT/MST neurons uniformly covers all possible frontoparallel stimulus directions (Fig. 39b). Taken together, these findings indicate that MT and MST send a specific subcortical projection to the NOT/DTN complex.

This was verified when neurons at the border between MT and MST were found to be activated by antidromic stimulation in the NOT/DTN (Figs 38b, 39c; Ilg and Hoffmann, 1993). These neurons were all selective for ipsiversive movement and were the only ones with large receptive fields that cross the vertical zero-meridian (Fig. 38b); i.e., their properties are very similar to those of an ‘average’ NOT/DTN neuron (compare Figs 38a and 39a with 38b and 39c). This projection from MT/MST to NOT/DON can thus
Figure 39. Further evidence that some MT/MST neurons project to the NOT/DTN. Preferred directions of movement of a population of neurons from (a) the NOT/DTN and (b) MT/MST. In (b) the location of a dot with respect to the centre of the circle represents the optimal stimulus velocity (preferred direction and speed) for a given neuron; outer circle: 100° s⁻¹, inner circle: 10° s⁻¹. The neurons likely to project to NOT/DTN are represented by heavy dots. N, nasal visual field; T, temporal visual field. (c) preferred directions of antidromically identified MT/MST neurons projecting to the NOT/DTN, which show a clear bias for ipsiversive stimulus directions, compared with the overall population of MT/MST neurons, which have a uniform distribution of preferred stimulus directions. (b) modified from Movshon et al., 1995.

explain the specific impairments generated by cortical lesions in areas MT/MST. The neurons in this circuit are particularly interesting for studying how the sensory information processed and encoded by a population of neurons is transmitted to and specifically read out in other cortical or subcortical target areas.
The role of the superior colliculus in the control of arm movements

The projections from PM and M1 to superior colliculus led us to investigate whether there is a similar cortical–subcortical interplay in the control of arm movements. By using a delayed saccade/delayed reach paradigm (Werner, 1993) visual, saccadic, oculo-motor and skeleto-motor responses in superior colliculus neurons can be distinguished. A monkey was required to make a saccade to a peripheral target, which it fixated until a cue instructed it to point to the target after a given delay. Over 50% of a sample of more than 700 neurons in two monkeys displayed activity related to reaching movements. A few also showed either visual or saccade-related responses, or both. The reach-related neurons were found from the superficial to the very deep layers of the superior colliculus and even in the underlying reticular formation; there was no evidence for topographic organization at any depth.

In 80% of the reach-related neurons, activity was greater for movements of the contralateral arm than of the ipsilateral arm. In the population of neurons, reach-related activity covered all three phases of the reaching cycle (premovement, forward and return). Most neurons were active predominantly during the forward movement but some neurons discharged only during the return movement. Some neurons were active only during a single phase; others had peaks of activity related to two or all three phases of the cycle.

Monitoring the contractions of several neck and shoulder muscles with electromyographs (EMG) while recording from superior colliculus neurons showed that reach-related activity in the superior colliculus always leads the earliest signal in the EMG. More than 70% of the reach neurons were active during the forward movement before the arm started to move and over 50% discharged even before the onset of the earliest EMG. Some neurons showed a tight temporal coupling between their discharge and the EMG from shoulder and arm muscles. No such
coupling was seen with neck muscles, ruling out the possibility that the discharge of the superior colliculus neurons is related to intended head movements.

Most of the neurons were spatially tuned, i.e., their activity varied with respect to the position of the target. Reach movement fields were broad, often including both visual hemifields. When the tuning patterns for saccadic and arm movements are compared for neurons that responded during both movements, no coincidence can be seen between the two movements fields, indicating that saccade and reach activity were encoded in different frames of reference. The coding of arm trajectory by superior colliculus neurons could be represented by the neural population vector, as seen in spatially tuned neurons in M1 (see Georgopoulos, this volume). Statistical analysis revealed, however, that a gaussian function provided a more accurate mathematical description of the spatial behaviour of these superior colliculus neurons (Kutz et al., in press) than the cosine tuning used for modelling M1 activity (Georgopoulos et al., 1983; see Georgopoulos, this volume).

Reference coordinates for reaching: The tuning data led us to ask in which coordinate frame the reach activity was encoded. One possibility is a head- or body-centred frame of reference, in which arm movement is encoded regardless of the location of a target on the retina or the position of the eyes in the orbit. An experiment using a fixation-reach task has failed to answer this question because the head always rested in the same position on the trunk. In this task, a monkey had to maintain central fixation even when reaching for a peripheral target. For most of the neurons, tuning for the different target positions did not change regardless of whether the monkey kept central fixation or looked at the peripheral target (Fig. 40). Only a few neurons responded more strongly or exclusively in one task or the other.

To determine which movement parameters, such as muscle force, trajectory or endpoint, are encoded by reach-related neurons
Figure 40. Activity of a superior colliculus neuron in (a) the saccade-reach task and (b) the fixation-reach task. This neuron shows the same systematic variation of its activity during reaching to each of the four targets, although retinal target positions and gaze direction are different in the two tasks, as shown in the central boxes in (a) and (b). In (a) the target is always on the fovea during the reach, in (b) on the peripheral retina. Modified from Stuphorn et al., 1996.
in the superior colliculus, a task was employed in which the initial resting position of the arm was varied. In the previous two tasks the initial position was at the monkey’s hip level but here the hand started at either hip or eye level. Because this produced completely different trajectories, it allowed coding for the starting position, the trajectory of the arm and the final target position to be dissociated. Ten out of 15 neurons investigated revealed similar spatial tuning for both tasks, i.e., they code the target position rather than the direction of the limb to the target (Fig. 41; Stuphorn et al., 1996). This is completely different from neurons in the motor cortex, which are reported always to code for the movement trajectory (see Georgopoulos, this volume).

The cortical input to the reach-related neurons in the superior colliculus originates in PMd. Using antidromic stimulation in the superior colliculus or orthodromic stimulation in PMd while recording in the other structure confirmed previous anatomical reports that PMd sends a projection to the superior colliculus. The neurons in PMd that provide the inputs to the superior colliculus neurons always had reach-related activity similar to that of their target neurons.

Based on these considerable similarities in the circuits controlling limb and eye movements, we propose there are two parallel sensorimotor pathways subserving gaze and arm orientation that include motor cortical areas, the deep layers of the colliculus and brainstem centres. A cortico-subcortical circuit for the gaze orienting system involving the frontal eye field and the superior colliculus has been demonstrated (Schiller et al., 1980; Segraves and Goldberg, 1987). We think that there may be a similar circuit for arm orientation involving PM and the superior colliculus. Which model for gaze orienting in the superior colliculus (see Sparks, this volume) applies for orienting the arm has to be tested by further experiments. We favour the idea that the output of the superior colliculus for arm orienting should be considered as a request or template rather than a command.
Figure 41. Activity of a reach-related neuron in the superior colliculus reveals a spatial tuning with respect to target location. The discharge did not depend on whether the hand started from eye level (a) or hip level (b), implying that this neuron was not strongly influenced by the trajectory of the arm when reaching. Modified from Stuphorn et al., 1996.
The ascendancy of the cerebral cortex in mammals naturally raises questions about the role of the archetypal subcortical centres we share in common with other classes of vertebrates. For the optokinetic as well as the gaze and limb orienting systems, the ancient subcortical visuomotor control centres, the NOT/DTN and the superior colliculus, are not so much dominated by the cerebral cortex as served by it. We suggest that understanding the organization of cortical output to subcortical centres may be helpful in understanding the evolution and behavioural functions of different areas in the cerebral cortex.

Testing the predictions of different models of the saccadic system

David L. Sparks

A long standing problem in oculomotor research is the spatial-to-temporal transform: how the anatomical (spatial) code of saccade metrics (direction and amplitude) found in the superior colliculus is transformed into the temporal signals required by motor neurons for generating saccadic eye movements. The influential study by Robinson (1972) showed that electrical stimulation at a particular site in the superior colliculus always generates a saccade with a particular metric (spatial encoding). This led to construction of a topographic map depicting direction and amplitude of elicited saccades as a function of stimulation site in the superior colliculus. Neurophysiological studies in the following years have shown that the collicular neurons always encode a certain change in eye position rather than the final position of the eyes in the orbit. An impending saccade is signalled by the activity not of a single neuron but rather of an ensemble of neurons. It is predominantly the location of this population within
the topographical map that encodes the information about the saccade (Schiller and Koerner, 1971; Sparks, 1978, 1986; Sparks and Jay, 1986; Sparks and Mays, 1980).

This spatial coding seems to be inappropriate for generating the pulse–step signals required for saccadic rotations of the eyes. First, a pulse of activity in the eye-muscle motor neurons produces the phasic increase in muscle tension needed for overcoming the viscosity of the oculomotor apparatus (eyeball and eye muscles) and to move the eye at high velocity. Then a step of tonic activity causes the sustained change in muscle tension required to hold the eye in the new orbital position and to overcome the elastic properties of the orbital tissue. It is agreed that the signal for generating saccades coming from the superior colliculus is fed into two pulse–step generators in the pons and the rostral midbrain, one dedicated to generating horizontal, the other to vertical saccades.

Disagreement exists, however, as to how the pulse-step sequence is generated. Although numerous models have been developed to account for the spatial-to-temporal transform, there has been a paucity of critical experiments testing their differential predictions. Here I describe three experiments (the dissertation work of M.J. Nichols) designed to test the differential predictions of various classes of models of the saccadic system. The first tested position versus displacement models, i.e., whether the input into the pulse-step generator is desired position or desired displacement. The second compared the predictions of common-source models with those from cross-coupling models for the coordination of horizontal and vertical components of oblique saccades. The third set of experiments examined whether the probable feedback comparators are of independent or vectorial type.

**Position versus displacement models**

Position and displacement models and their outputs predicted to produce a change in vertical position of the eye are compared in
Figure 42. Comparison of position and displacement type models for the input to the pulse–step generator, the output of which drives the ocular motor neurons. Signals from the superior colliculus specify the change in both horizontal (ΔH) and vertical (ΔV) position of an ensuing saccade. The two signals are converted in separate circuits, each involving a comparator and an integrator, which generate the pulse and step signals required by the extraocular muscles responsible for the horizontal and vertical rotations of the eyes. Only the circuit for the vertical component is shown here. CVP, current vertical position of eye in orbit; DVP, desired vertical position. For further explanation, see text.

Figure 42. Position models (Robinson, 1975; van Gisbergen et al., 1981) assume that the collicular signal of the desired change in eye position (ΔH, ΔV) is combined with a signal of the current position of the eye in the orbit to generate a signal of the desired position of the eye. In contrast, displacement models (Jürgens et al.,
1981) assume that a desired displacement rather than a desired position signal is used as the reference signal for the comparator that controls the duration of the pulse. The desired displacement reference signal is compared, movement by movement, to a signal of the displacement that has already occurred during the saccade. The signal of actual displacement is produced by a neural integrator circuit that is reset at the end of each saccade. The integrator may be reset actively or, as illustrated in Figure 42, passively because it is leaky. As the time required for the integrator to reset is assumed to be less than the 200-300 ms interval between saccades, the presence of this integrator may go unnoticed.

If this resettable integrator really exists and decays gradually during intersaccadic intervals, then the two classes of models make dramatically different predictions about the consequences of stimulating the superior colliculus immediately after a visually guided saccade. The response of the pulse-step generator will differ depending on when the saccadic command arrives during the integrator’s decay period. Any residual value of the integrator will automatically be subtracted from the next displacement command at the comparator. In contrast, the position models predict no relationship between onset of stimulation and saccade amplitude.

Assume that stimulation of a site in the superior colliculus under control conditions produces a saccade with a 10° upward component. What happens if the site is stimulated immediately after a 4° upward visually guided movement? According to position models, the desired displacement signal of 10° upward would be combined with a signal of the current vertical eye position (4° upward) to produce a signal of 14° upward, the desired vertical orbital position. The displacement model predicts that, if stimulation occurs exactly when the visually guided movement ends, the current value of the resettable integrator (4°) will be subtracted from the stimulation-induced desired displacement of 10°, resulting in a stimulation-induced movement of 6°. Similarly, if stimulation
occurs after a 16° upward visually guided movement, position models predict that a 10° upward saccade will move the eyes 26° upward, whereas with displacement models a 6° degree downward saccade is expected. Thus, if the displacement model is correct, truncation, overshoot or even reversal, depending on the preceding saccade, should be seen. The position model, on the other hand, predicts that the amplitude will be independent of the size of the preceding saccade.

The predictions of the displacement model have all been reproduced experimentally (Fig. 43; Nichols and Sparks, 1995). Stimulation at exactly the same site in the superior colliculus using constant stimulus parameters led to saccades of different sizes and even direction, dependent on the size and direction of

![Figure 43](Image)

**Figure 43.** Experimental testing of models for the input to the vertical pulse-step generator. **a,** the amplitude of saccades elicited by stimulation at a single collicular site are plotted as a function of the amplitude of the preceding visually guided saccade. The strict linear relationship fits with the predictions of the displacement model. Open squares indicate the amplitude of the control saccade. **b,** four examples of stimulated saccades showing overshoot, truncation and reversal, as predicted by the displacement model. Reproduced with permission from Nichols and Sparks, 1995.
the preceding visually guided saccade. The activity of superior colliculus neurons thus should be considered to be a request signal for an impending saccade rather than a command signal that is inexorably obeyed. The movement that is actually executed depends upon the state of other neural elements in the saccade-generating circuit, not just the locus and level of collicular activity.

The slope of the plot in Figure 43a depends on the amount of integrator discharge that has occurred before the onset of the stimulation-induced movement. As the leaky integrator has an inherent time constant, the displacement model predicts a maximum effect of, for instance, truncation directly at the end of the saccade and an exponentially decreasing effect depending on the time constant of the integrator. This was verified experimentally by maintaining the size of the preceding saccade constant but varying the time of onset of the train of microstimulation pulses. The non-stationary effect, i.e. the resettable neural integrator, was found to decay gradually over about 150 ms (Fig. 44). An exponential function with a time constant of about 45 ms provides the best fit and accounts for 97% of the data variance (Fig. 44a). This time constant also explains why, with a normal temporal separation of 200-300 ms between saccades, a first saccade does not alter the performance of the following one.

**Common-source versus cross-coupling models**

Saccade-generator models also differ in how they account for the coordination of the horizontal and vertical components of oblique saccades. For purely horizontal or purely vertical saccades, the duration increases linearly with saccade amplitude. For oblique saccades, so-called component stretching occurs: the peak velocity of each component is reduced from the value it would have for a purely horizontal or vertical saccade of the same amplitude and the durations of the components are prolonged. Two competing classes of models account for this phenomenon: common-source models, in which the ratio of synaptic weights at each point in the collicular
Figure 44. Time constant of the leaky integrator in the displacement model. The amplitudes of the elicited saccades are plotted as a function of the interval between the visually evoked and electrically stimulated saccades for two data sets (a, b). The exponential function fitting the data points represents the decay of the leaky neural integrator, with a time constant of about 45 ms. In naturally occurring saccades the integrator should decay to zero within the average intersaccadic interval of 200-300 ms. Reproduced with permission from Nichols and Sparks, 1995.

map between the horizontal and vertical pulse–step generator circuits is held to dictate component velocity; and cross-coupling models, which assume that component stretching occurs because of inhibitory interactions between the horizontal and vertical pulse–step controllers.

We tested the predictions of these two types of models using the experimental approach outlined above. Sites in the superior colliculus were stimulated electrically immediately after either vertical or horizontal visually guided saccades. Under these conditions, the amplitude of the component that corresponds to the direction of the preceding visually-guided movement varies systematically, while the other ‘constant-amplitude’ component remains essentially constant. As with visually guided saccades, the peak velocity of the constant-amplitude component in stimulation-evoked saccades decreased as the amplitude of the
orthogonal component increased (Nichols and Sparks, 1996). The component stretching effect in stimulation-evoked saccades was qualitatively indistinguishable from component stretching in matched, visually guided movements even though the locus of stimulation-induced activity in the superior colliculus was fixed from one stimulation-evoked saccade to the next. Because the component stretching in stimulation-evoked oblique saccades does not depend on the locus of activity in the collicular motor map, these results are inconsistent with the predictions of common-source models. They are, however, consistent with the predictions of cross-coupling models.

**Vectorial-comparator versus independent-comparator models**

In a third set of experiments (Nichols & Sparks, in press), we tested the differential predictions of two classes of models with different types of comparator: vectorial and independent. Vectorial comparator models assume that a single comparator controls the amplitudes of both horizontal and vertical components of the movement for a desired oblique displacement. The comparator receives feedback from both horizontal and vertical displacement integrators but does not maintain separate representations of horizontal and vertical dynamic motor error, i.e., the discrepancy between the desired and the accomplished displacements. If, for example, feedback from the vertical channel were increased or decreased, the horizontal component of a movement should be modified accordingly, because the movement would terminate when the sum of feedbacks from the horizontal and vertical channels matched the desired displacement vector. Collicular stimulation following various perturbations of the vertical feedback should thus influence both components of the ensuing stimulation-evoked saccade and result in saccades all with the same vectorial amplitude (*Fig. 45a*).

In contrast, independent-comparator models assume that separate signals for the desired horizontal and vertical displace-
Figure 45. Comparison of models with vectorial or independent comparators in the generation of oblique saccades. a, b, predictions of the two models. The oblique saccade resulting from collicular stimulation (control) is shown as a solid line; the dotted lines represent the results of perturbations predicted by the two models. c, experimental data are consistent with separate and independent horizontal and vertical comparators. Upward-directed (filled circles) or downward-directed visually guided saccades (filled triangles) were followed by saccades evoked by collicular stimulation at a single site. The vertical amplitude is affected by the preceding saccade, whereas the horizontal amplitude is not. Open circles: control saccades.

ments are used as references for independent and separate horizontal and vertical feedback comparators. As the two components do not influence each other, this model predicts the independent manipulation of the horizontal and vertical amplitudes of oblique stimulation-evoked saccades (Fig. 45b).

For every stimulation site tested, the amplitude of the horizontal or the vertical component (depending on the direction of the
preceding saccade) of stimulation-evoked saccades varied systematically but the amplitude of the orthogonal component was roughly constant (*Fig. 45c*). Thus, the horizontal and vertical amplitudes of oblique stimulation-evoked saccades can be manipulated independently, an effect that can be readily accounted for by independent comparator models but not by vectorial-comparator models.

**Towards simplicity**

The numerous modifications and extensions of Robinson’s original feedback model of saccadic control (Robinson, 1975) make many different assumptions about what types of signals are required as inputs to a pulse–step generator circuit and the types of feedback comparators used, among other things. Because they have rarely faced certain empirical tests, they all remain viable and so it is no longer certain exactly which transformations of collicular signals are needed for generation of the motor signal. Progress in understanding how collicular signals are transformed into those required by the motor neurons involved in the control of saccadic eye movements will be greatly facilitated by more experiments that, like those reported here, reduce the number of competing models.
The node of the ventral stream is the inferotemporal cortex, which receives visual information from V1 through V2 and V4. In this stream the various attributes of objects required for their recognition are processed in separate channels before being integrated by neurons in the inferotemporal cortex that respond to complex stimuli. As in the dorsal stream, evidence is emerging that functions may be distributed through several areas. This is elegantly demonstrated by Nikos Logothetis, using binocular rivalry to examine how the visual cortex deals with ambiguous information. In the more anterior areas of the inferotemporal cortex, particularly area TE, Keiji Tanaka has revealed a map of moderately complex features of objects, including faces, in which several views may be represented in neighbouring cortical columns, perhaps assisting the recognition of unfamiliar views from information stored in memory. The use of view-based information as a short cut to recognition in situations where detail is unnecessary is demonstrated by Hanspeter Mallot using psychophysical experiments. The theme is taken further by David Perrett, who finds view-invariant face neurons in the superior temporal sulcus, as well as neurons that respond to particular aspects of faces, such as direction of gaze, that are probably important in social communication.

On the neural mechanisms of unstable percepts

Nikos Logothetis

How much does the neural activity at different processing stages in the cortex relate to the physical stimulation of the retina and how
much to the picture the brain creates from this input? Ambiguous figures, such as the perspective-inverting Necker cube, are excellent tools for exploring such questions because the retinal pattern produced by the picture stays the same, given steady accommodation, but the percept changes. Ambiguous figures are hard to study in animals but experiments using binocular rivalry, a closely related phenomenon, are yielding data that challenges our concepts of how visual information is processed in the cortex.

**Ambiguous figures and binocular rivalry**

The psychology and psychophysics of ambiguous pictures have been studied since before the time of Helmholtz and there is an extensive literature on them. This great interest reflects the excellent opportunity that such figures provide for probing the mechanisms that the brain uses to construct a visual percept. As the image of the figure on the retina remains constant, the percept must be created by selective central processes representing the attempts of the brain to derive a definitive and unambiguous picture of the visual environment. Either one or the other version of an image may exist, for instance, either a vase or two faces in the figure–ground reversal picture but not both together. In the absence of conclusive context information, the dominant interpretation of the ambiguous image switches randomly between the two possible interpretations.

It is practically impossible to train monkeys to respond to the perceptual changes in such sophisticated images or to report on which version they perceive. It is also difficult to find enough suitable ambiguous figures to test many single neurons. Using binocular rivalry bypasses these difficulties: when different images are presented to each eye, stable vision gives way to perceptual alternations in which the view of one eye dominates for several seconds before being replaced by the other. Psychophysical experiments (see below) demonstrate that ambiguous figures and binocular rivalry both belong to the same general category of multistable phenomena and point towards the same neural mechanisms.
Several assumptions about binocular rivalry are conventionally held (reviewed by Blake 1989). It is considered to have a central origin. Peripheral factors, such as eye movements, can alter the dynamics of rivalry but are not its cause as it occurs even with afterimages or images stabilized by compensating for small eye movements; neither does adopting artificial pupils nor paralysing the intrinsic eye muscles affect the degree of control over rivalry. The striking perceptual alternations during binocular rivalry have been attributed by some investigators to fluctuations in attention (Walker, 1978). Others regard it as arising from the structural organization of the visual system. Although they do not deny that attention can modulate the rivalry alternations (Lack, 1978), they posit that binocular rivalry reflects strong competitive interactions in the visual system at the level where the inputs from the two eyes combine to establish single vision. Suppression of one input seems to operate nonselectively over a broad range of stimuli and involves the suppression of the eye (and thus of the entire monocular channel), rather than the suppression of a particular stimulus. As rivalry exerts no influence on the growth of spatial frequency, orientation or aftereffects specific for the direction of motion, processing of information about the adapting stimulus is thought to be uninterrupted during suppression, at least as far as the primary visual cortex, favoured as the site of binocular rivalry.

Combined electrophysiological and psychophysical studies in primates have enabled us to determine the validity of these assumptions (Leopold and Logothetis 1996, see also Logothetis and Schall 1989).

**A psychophysical fingerprint**

Binocular rivalry can be best studied at the single neuron level by presenting the eyes with competing stimuli that are either optimally or non-optimally oriented for the recorded neuron. Experiments thus began by determining the location of the receptive fields, the occular dominance (the relative strength of responses to stimuli
presented to left and right eyes) and the orientation preferences of neurons in areas V1, V2, V3, V3a and V4 while the monkeys fixated a spot. The animals then learned to respond to two orthogonal gratings presented to both eyes simultaneously (Fig. 46a). After achieving 95-100% success, the monkeys learned to ignore mixed stimuli, i.e., images which had sub-components with checker-like patterns (Fig. 46b).

**Figure 46.** Discrimination training for appropriate behavioural responses to ambiguous and non-ambiguous stimuli. The monkeys had to keep their eyes on a fixation spot in all trials to allow determination of the receptive field properties of neurons and to secure similar experimental conditions. **a**, in the first training step the monkeys learned to indicate left-tilted and right-tilted gratings, presented in a non-rivalrous manner to both eyes, by pressing a left or right lever. **b**, in the next step they learned to signal ambiguous stimuli, i.e., checker-like patterns resulting from rivalrous stimulation, by letting go of or not pressing the lever. The lever-pressing response does not, therefore, always parallel the stimulus sequence. The animals were rewarded initially for each correct response, later at the end of every observation period.
Several controls were used to make sure the animals were correctly reporting their percepts under binocular stimulation: intermixing binocular with congruent stimulation; repetition of stimuli; exchanging the monocular input to the eyes; presenting the same images to both or just one eye; and presenting artificially fused stimuli. In addition, psychophysical effects that can be demonstrated in both monkeys and humans give binocular rivalry a specific signature, distinguishing it from other processes (Leopold and Logothetis 1996). These include:

- the randomness of dominance periods which, if normalized by the mean duration, can be approximated by a particular ($\gamma$) distribution with characteristic parameters (Fig. 47a; Levelt, 1965);
- the randomness of sequences of dominance (between left- and right-tilted gratings), which can be tested by auto-correlation and by Lathrop statistics;
- an inhibition effect: the duration of dominance for the image in one eye is reduced if the stimulus strength is increased for the other eye. Doubling the intensity of the stimulus in one eye, e.g., by increasing contrast, decreases the dominance duration of images relayed to the other eye, rather than extending the dominance periods of the first eye (Fig. 47b). This inhibition seems to be based on a different set of neurons to those responsible for the perception of the stimulus.

**Neuron responses during binocular rivalry**

The recording described here were obtained from neurons at the border between V1 and V2 (V1/V2) and in V4 in two monkeys experiencing binocular rivalry (Fig. 48). Rather surprisingly, about 80% of the neurons tested in V1/V2 and about 60% of those in V4 remained active all the time, irrespective of whether the percept was their preferred or non-preferred stimulus. These non-modulating neurons were sensitive to the stimulus in conditions where rivalry was not present, responding only to their preferred orientation. Most of the remainder responded during rivalry to an orientation
Figure 47. Temporal dynamics of binocular rivalry in monkeys. **a**, frequency histogram showing the distribution of the rivalry phases, i.e., periods of dominance and suppression of one eye’s view. The black line is a γ-function fitting the data. The parameters of this distribution for the monkey were not significantly different (two-tailed t-test) from those obtained for human observers. **b**, inhibitory effects on the duration of the dominance phase produced by varying the stimulus strength. The contrast of the grating shown to one eye was varied (circles) and to the other eye fixed at 1.0 (diamonds). Modified from Leopold and Logothetis, 1996.

different from the one they preferred when rivalry was not present: 18% of the neurons examined in V1/2 and 38% of those in V4 showed this modulation (Fig. 48, 49). Twelve of the V4 neurons responded best when their preferred orientation was perceived, six when their preferred orientation was suppressed and the remaining eight showed no preferred orientation during congruent stimulation. All but one of the neurons showing response modulation during rivalry were binocular.
Some response-modulating neurons had no orientation tuning when tested in the preliminary fixation task but showed an orientation preference under rivalry conditions. Such modulation could reflect the effect of top-down processing on the neuron’s responsiveness during ambiguous visual stimulation. Other neurons showed significantly more activity when confronted with a stimulus during a discrimination task than in simple fixation. Whether such neurons mediate the conscious perception of a stimulus can be answered only when the types and connections of these neurons are established and any special properties discovered.
**Figure 49.** Peristimulus-time histograms for two V4 neurons during binocular rivalry, one suppressing its non-preferred input (a), the other suppressing its preferred input (b), as judged by matching the activity of the neuron to the monkey’s behavioural response (dotted line). Note that the neuron responses begin well before the monkey signals its experience and last several hundred ms after. Lefthand panels, monkey reports perceptual dominance of the neuron’s preferred orientation; righthand panels, dominance of non-preferred orientation.
Contrary to the common assumptions about rivalry, outlined above, these results show that there is no single site in the cortex where the percept is decided once and for all. Rather, the information coming from both eyes is preserved over several processing stages. This is astonishing — as binocular rivalry is a very strong effect, many more neurons might be expected to follow the percept at earlier stages. Instead, many neurons even in the intermediate stages of visual processing carry monocular information that may not contribute to the percept. As almost all of the neurons involved in the modulation are binocular, the effect cannot be based simply on the competition of monocular channels.

**Rivalry of eye-independent stimuli**

Further support for this view comes from a second series of psychophysical experiments (Logothetis *et al.* 1996). The same left- and right-tilted gratings were used but the images presented to the eyes were swapped after every 333 ms, i.e., at 3 Hz. To mask the moment of swapping, the images were continuously flickered on and off at 18 Hz, independent of the slower changes. As the two eyes received an ever-changing input, swapping the images excluded the possibility of competition between them. Even so, the percept changed randomly, with a mean dominance period of 2.35 s in all subjects and individual episodes persisting several seconds; the data fitted the *γ*-distribution described above. Other conditions for binocular rivalry were also met. Sequential dominance and suppression phases were completely uncorrelated, a clear indication of binocular rivalry as the fluctuations showing such random distributions are virtually impossible to create intentionally. The inhibition mechanism described above was also demonstrated: increasing the stimulus strength of one stimulus led to decreased dominance periods for the other one.

As the effects of swapping stimuli between the eyes were virtually indistinguishable from normal binocular rivalry, we presume that the same mechanisms are at work, involving competition between
the stimuli rather than between the eyes, as the information presented to the eyes changed frequently. The typical features of randomness can also be observed for perceiving ambiguous pictures such as the Necker cube and even in monocular rivalry, seen when conflicting stimuli are presented alternately to one eye, so we assume that these phenomena all belong to the same class.

These experiments support the traditional assumption that binocular rivalry is a central selective process that may be modified by attention, although attention is not the cause of the rivalry. Contrary to common assumptions, there is no single site in the visual cortex at which rivalry occurs and there is no competition between monocular channels that completely suppresses the input coming from one eye. These conclusions do not exclude local inhibitory interactions between the monocular images that could contribute to visual processing. Such mechanisms may be essential for stereopsis and for establishing the ‘singleness’ of binocular vision.

**Inferotemporal cortex and object recognition**

*Keiji Tanaka*

In primates, recognition of objects by their visual images is a flexible process that tolerates many changes, e.g., in viewing angle, distance and illumination. Primates can also deal with novel objects based on previous experience. Anatomical and lesion studies have shown that the anterior part of the inferotemporal cortex (IT), the area known as TE, contains the neuronal circuitry essential for the flexibility of visual object recognition (Dean, 1976; Gross, 1973). Our electrophysiological and optical recordings in this area are revealing a columnar representation of object features, in which related features may be grouped into larger units (Tanaka, 1996a).
Figure 50. An example of the reduction process used to determine the critical feature for activating individual neurons in TE. The histograms show responses averaged over ten repetitions of the stimuli (is⁻¹, impulses s⁻¹). The bars under the histograms indicate the period of stimulus presentation and the numbers above give the magnitude of the responses normalized to 1 for the image of a water bottle (top). Reproduced from Tanaka, 1996b.
Feature mapping in TE

The IT is divided into areas TEO posteriorly and TE more anteriorly. Area TE in turn projects to anterior parts of the superior temporal sulcus (STS) as well as to regions outside the visual cortex, including perirhinal cortex, prefrontal cortex, striatum and amygdala (Iwai and Yukie, 1987; Barbas, 1992; Saleem and Tanaka, 1996). The studies discussed here are limited to the dorsolateral part of TE in the anaesthetized monkey.

We have developed an electrophysiological method for determining the features critical for activating single neurons in TE (Fig. 50; Tanaka et al., 1991; Fujita et al., 1992; Kobatake and Tanaka, 1994). The first step is to discover which of a large number of 3-D objects effectively stimulates a neuron. A computer image of this object is made and then simplified step by step to identify the features critical for activation of the neuron. In the example shown in Figure 50, the original stimulus was a water bottle; the computer analysis revealed that the critical feature for the recorded neuron was a vertically elongated ellipse with a downward protrusion. Based on such reduction processes we consider that features critical for activation of TE neurons are moderately complex.

Long electrode tracks either parallel or perpendicular to the cortical layers revealed that neurons preferring similar features are organized in columnar modules about 500 µm in diameter that extend through the depth of the cortex (Fig. 51; Fujita et al., 1992). Neurons in one column respond to similar but not necessarily identical features, whereas those in neighbouring columns are activated by completely different features.

Spatial organization of columns

More recently we have confirmed that this area is organized into feature columns by using optical imaging of intrinsic signals (Fig. 52; Wang et al., 1996). This method is based on the consumption of energy derived from glucose metabolism by active neurons (Frostig et al., 1990). The uptake of oxygen required for
Figure 51. Responses of neurons recorded along a penetration perpendicular to the surface of TE. The responsiveness of the neurons was tested with the set of stimuli shown at the bottom, which were selected with reference to the critical feature of the neuron indicated by an arrow. Effective stimuli are listed separately for individual recording sites in the order of effectiveness. *, p<0.01, otherwise p<0.05; IN, initial unit of penetration; NR, non-responsive unit; WM, white matter; m, multiunit recordings; s, single-unit recordings. Reproduced from Tanaka, 1996b.
glycolysis results in an increase of deoxygenized haemoglobin in nearby capillaries. Because haemoglobin absorbs more red light when deoxygenized than when oxygenized, cortical regions with high neuronal activity appear dark when illuminated with red light. An advantage of optical imaging is that neuronal activity can be monitored simultaneously over an area of cortex about 4 x 6 mm². Because the signals are very small, the signal-to-noise ratio was improved by averaging images during 40 trials of stimulus presentation, lasting 4 s. The raw signal was divided by the average signal obtained while the monkey watched a blank screen, to remove the basal level of activity resulting from reflected light. Stimulus selectivity was determined for 20-30 single neurons at different locations in the same region by making repeated electrophysiological recordings over 2-3 months.

TE generally appeared darker than auditory cortex or superior temporal gyrus when complex visual stimuli were presented but localized darker spots developed in response to particular stimuli (Fig. 52); their positions were constant in measurements separated by several hours. Local activation was stimulus specific and the

**Figure 52.** Optical imaging of a column responding to a green and white rectangle. 
(a) activation during stimulation with the optimal feature is higher than (b) during stimulation with a white square; 
(c) the image resulting from dividing the first response by the second. Crosses mark the site of the electrode penetration during which the stimulus was identified as the critical feature of one neuron, whose response is shown in the histograms (left).
activation spots for different stimuli were found in different locations. Spots were on average 490 μm in diameter, similar to the column diameter obtained electrophysiologically. Each critical feature determined by electrophysiological recording activated up to seven spots in the imaged areas, one of which overlapped the electrode penetration site. As the metabolic changes caused by activity of a single neuron are very small, these spots must represent a cluster of neurons all responding to the same, moderately complex feature. Some of the multiple activation spots were also seen in response to simpler components of the critical feature but the spot covering the electrode penetration site was evoked only by the critical feature.

**Responses to faces**

Optical imaging has also provided unique results regarding the representation of faces. All five of the neurons recorded in one penetration specifically responded to faces. Most of the face-sensitive neurons we encountered required most of the face for maximal activation, i.e., we could not reduce the effective stimulus to selected facial features (cf. Perrett, this volume). Some of these neurons responded maximally to front views, others to profiles, so five views of a doll’s face were presented, all of which activated spots around the electrode penetration site (Fig. 53). However, the centre of the activation differed slightly for each view: as the face was rotated from the left profile to the front to the right profile, the centre shifted by 400 μm. Identical results were gained in three monkeys. One of them was presented with two faces that both activated the same cortical area but the shift in the centre of activation resulted only from rotation of the face, not from changing the horizontal location of its features or the position of special features, such as the nose. Thus, instead of discreet columns with little overlap, faces seem to be mapped as a continuum of changing features. This may not be limited to faces but could be a more general feature of spatial organization in TE because we found that
**Figure 53.** Overlap of activation spots evoked by five views of a doll’s face. The outlines of the spots circumscribe the pixels where activation was significant at p<0.05.

Different but related non-face features also activated partially overlapping spots (Fig. 54).

**Uses of a continuous map**

A continuous map could simply represent the direction of gaze or it might be used for transformation, e.g., of the front face observed to match a remembered profile of the same person. A task like this would be difficult to perform using a visual alphabet, i.e., by combining numerous feature modules. Alternatively, a continuous map could produce a broad tuning of cortical cells for certain directions of feature space, which might be advantageous for associating different but related images, such as different views or illumination.
It seems unlikely that the map is continuous throughout TE; because the feature space is multidimensional, a patchy representation in columns is more probable. Several columns representing different yet related features may overlap to compose a larger unit capable of extracting invariance while retaining their specificity (Fig. 54). We do not yet have enough data to decide if the columns are arranged in a pinwheel-like fashion similar to that of the orientation domains in V1.

The view-based approach to visual coding

Hanspeter Mallot

To find our way around the world we need a functional representation of the environment but this does not necessarily have to be a complete and sophisticated 3-D model; simpler representations could be used in many situations. Visual psychophysicists and computer scientists have suggested several models based on essential spatial features of the environment, including depth maps; the $2^{1/2}$-D sketches of Marr (1982); parametric surfaces, such as
generalized cylinders or superquadrics, as well as volumetric descriptions of objects (for review see Haralick and Shapiro, 1992). Larger-scale spatial relations in the environment could be represented as topographic maps, similar to street and terrain maps. Such representations are powerful tools in machine vision, where the goal is to derive complete descriptions of imaged scenes. In contrast, biological systems are special-purpose devices designed to extract exclusively the information they really need, so it is questionable whether the brain uses such complex and rather abstract schemes and, if it does, to what extent.

We have been investigating whether more context-related solutions are used and have identified several visual problems that can be solved without the construction of information-rich models. These view-based solutions seem to be employed for problems that require an efficient behavioural response, although they may not apply to more generalized cognitive processes.

**Global stereopsis**

Stereoscopic vision is assumed to provide a point-by-point depth map, derived by evaluating the disparity of all local features in the two monocular images (or ‘half-images’) reaching the eyes, leading to a spatial 3-D model of the image. Standard theories require the identification of the pairs of corresponding features, i.e., image elements depicting the same object in the scene, in the two half-images. In principle, however, several other differences in the half-images could be used to produce stereopsis and depth perception without establishing details of the correspondence between local features.

We have investigated the minimum cues required to produce stereopsis by presenting human subjects with the half-images of stereograms presented correctly (orthoscopic) or exchanged (pseudoscopic) (Fig. 55; Arndt et al., 1995). Stereopsis is present if exchanging the half-images affects the perceived depth of the image. If it does not, then perceived depth is being determined
Figure 55. Intensity-based stereopsis. When cross-fusing the two images on the left of each row, an orthoscopic view of a sphere or cylinder can be seen. Fusing the two images on the right produces a pseudoscopic view of the same objects. According to conventional theories of stereopsis, it should be impossible to obtain a stereo impression from rows 3 and 4, which lack discrete features that could provide disparity information. The most likely mechanism is image difference or global correlation.

by other, monocular cues, such as shape-from-shading. A stereoscopic impression is easily obtained by fusion of images containing a structured texture, such as those in rows 1 and 2 of Figure 55, even though row 2 contains no shading. The two stereograms can still be distinguished when no localized features are present (row 3) and even with images that have been designed to exclude or control for
all disparity-related information (row 4). These have no localized features; all intensities are smoothly distributed so that there are no edges and no disparate peaks or centroids. Centroids, also termed centres of gravity of the intensity profile, are often assumed to define the perceived location of blurred dots or lines (Arndt et al., 1995, Mallot et al., in press).

Although the stereoscopic image produced by rows 3 and 4 is coarser than for textured images, the differences in the intensity profiles carry enough information to produce stereopsis. This could be extracted using a square-difference map: the overall intensities in the two half-images would be correlated by shifting the whole monocular images until they matched maximally; the remaining differences could then be used to estimate depth (Arndt et al., 1995). This hypothesis predicts that image regions with high contrast should contribute more to the overall perception of depth than those with lower contrast. Using the stimuli in row 3 as well as similar images of less and more elongated ellipsoids and measuring the perceived overall depth offset between the ortho- and pseudoscopic presentations, we have confirmed that this is so (Mallot et al., in press).

This type of global stereoscopic mechanism could be implemented biologically by an array of disparity-tuned neurons. The peaks of activation for the two monocular inputs would be in different parts of the array but the centre of activity in the whole array would represent the average depth of the binocular image, even if false matches between image points were not eliminated. Further interactions between neurons in the array might extract even more stereo information from the disparity input than an average depth value. The mechanism could be important for guiding the vergence eye movements required for depth perception.

**Recognition of rotated objects**

The recognition of known objects in rotated views is another problem that requires some form of mental representation (see
also Tanaka, Perrett, this volume). It has previously been suggested that the brain constructs a complete, orientation-invariant 3-D model, perhaps based on cuboids, that can be mentally rotated. This was tested by presenting subjects with computer-generated images of wire-frame, cuboid-based or amoeba-like objects containing all the 3-D information necessary to create a complete model (Fig. 56; Bülthoff and Edelman 1992; Bülthoff et al. 1995). The subjects could not recognize objects in a view that differed by more than a certain angle from a familiar view. Recognition times increased significantly when the angle was greater than approximately ±30° from a familiar view of the object. If the brain builds a model representation of these objects, performance should clearly be better than this.

**Figure 56.** Recognition of rotated objects. Three sets of objects are seen in standard orientation (middle view in each set) and in four rotated views. The top set is an amoeba-like figure with substantial occlusions; the middle and bottom sets are wire-frame and cube-like objects whose structure is visible from most positions. Human subjects can identify views rotated only up to ±30° from the standard view, making it unlikely that the brain constructs a 3-D model of the object that can be rotated mentally. Reproduced with permission from Bülthoff et al., 1995.
This is corroborated by combined psychophysical and neurophysiological experiments in the monkey using the same set of artificial objects, in which view-specific neurons were found in IT (Logothetis et al., 1995). This supports the idea that IT holds canonical representations of objects that facilitate easy recognition in familiar orientations and could provide the basis for slower recognition of the objects from less familiar angles (see also Tanaka, this volume). A plausible biological mechanism could be based on the response pattern of a population of such neurons, broadly tuned for familiar objects (see also Perrett, this volume). The summation threshold of the population would be reached faster for more familiar views of objects, which elicit greater neuronal activity. The less familiar the stimulus, the longer it would take to elicit the appropriate population response, with less accuracy in the recognition of the object. This mechanism is what Georgopoulos (this volume) terms mental rotation, although it should be noted that this differs from the original notion of mental rotation (Shepard and Metzler, 1971), which involves an explicit 3-D mental model of the object.

**View-based maze orientation**

To find our way in unfamiliar towns without a map, we need to orient by recognizing landmarks in the environment, e.g., the particular scenery that we face when turning from one street into another. Unlike the recognition of objects discussed above, landmark recognition does not need to be orientation invariant because the decision about where to turn may depend on the view of a landmark from a particular angle. If the landmark appears the same from all sides, important spatial information is unavailable. For organisms with simpler nervous systems, such as bees, view-based orientation is essential as they seem unable to perform mental rotation. A bee’s body vector has to be aligned in a particular direction when it approaches food sources or home.
**Figure 57.** View-based navigation in a virtual maze to find a particular landmark. In the early stages of learning this task, subjects seemed to store simple associations between views and movement decisions. 

- **a,** map of the maze explored by clicking the buttons of a mouse. Each black dot represents a landmark visible when approaching a junction.

- **b,** the movement decisions that can be made when facing the central view.

- **c,** results for subject LBC. The diagonal entries in the lefthand matrix give the number of wrong decisions made by repeating the previous movement decision on returning to the same view. The middle and righthand matrices give residuals, i.e., the differences between the actual data and the best fitting models that assume either independence (middle) or persistence (right). These show that decisions made on subsequent encounters with a view are not independent; the righthand matrix demonstrates persistence with previous decisions at a rate of 64%. 

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LBC  p < 0.01  n.s.  l = 0.638
Human subjects were asked to navigate through an unfamiliar, maze-like virtual town (Fig. 57a) until they found a particular view (Mallot and Dartsch, 1995; Gillner and Mallot, 1996). Approaching each of the Y-junctions in the town, the subjects faced a certain view, usually a building, and used a mouse to select one of several movements that would bring them to another view (Fig. 57b). The goal was to find the shortest possible way to the required view.

After an initial trial-and-error phase, the number of errors decreased in consecutive trials as the subjects developed a representation of the town. The record of motion decisions for one subject (Fig. 57c) indicates a strong tendency to repeat the previous turning decision when encountering the same view; the decisions are not statistically independent. This is a valid strategy as long as it leads to the correct goal but is persisted with even when it is not successful. It shows that the first step is learning to associate certain views with certain turning decisions. This seems to be an intuitive, practical approach for simple route-learning navigation tasks, such as finding the way back to a hotel in an unfamiliar city.

This strategy treats the maze as a graph of places or junctions and the connections between them (Fig. 58a). It could be extended into a more versatile cognitive representation by organizing the collection of view-based movement decisions as a ‘view graph’ (Fig. 58b; Schölkopf and Mallot, 1995), in which two views are connected in one direction if one can be reached from the other in an immediate temporal sequence. The connections thus acquire egocentric movement labels rather than world-centred or extra-personal coordinates that can indicate only general directions like “go north”. The view-graph structure represents the adjacency of views rather than the adjacency of places. It is simpler to learn and to use than a full 3-D model as it provides a direct and efficient movement decision associated with particular views. A simple neural network (Fig. 58c) that is able to learn the view graph from a sequence of views and movement decisions has been implemented on an autonomous robot (Mallot et al., 1995).
Figure 58. The labelled view graph for representing spatial relations. **a**, a maze depicted as a graph of places and the connections between them. The connections can be described by instructions in allocentric (world-centred) coordinates, e.g., “go north” for connection $c_7$. **b**, a maze shown as a graph of views, mathematically equivalent to the place graph. Each node corresponds to a view, equivalent to a directed connection in the place graph. Two views are connected if they can be seen in a direct temporal sequence and connections can be labelled in egocentric coordinates, such as “turn left” from $v_7$ to $v_2$. **c**, a simple neural network that can learn the view graph from a sequence of views $((s_1,...,s_n)^t)$ and movement decisions $((m_1,...,m_k)^t)$. 
Different approaches for different cognitive requirements

These examples show that view-based solutions are adequate for several visual tasks. They seem to be special-purpose solutions that are employed where efficient operations are required. They do not attempt to provide a complete and invariant representation of the environment and do not necessarily obey the principle of least commitment (Marr, 1982) dear to practitioners of computer vision, because information retrieved in one context is not easily transferred to other problems. This principle is in any case violated by the phenomenon, revealed by double-dissociation experiments, that two behaviours requiring the same information can be selectively affected by lesions if they use independent information-processing channels.

The existence of view-based solutions does not exclude our ability to construct more detailed and sophisticated models that allow us to make mental pictures of objects and large-scale environments from different viewpoints. View-based mechanisms might indeed serve as the first step in building more complete representations and memory consolidation might involve a transformation of view-based to model-based representations. It remains to be determined which tasks inevitably require explicit models of the environment.

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View-dependent coding in the ventral stream and its consequences for recognition

David I. Perrett

We are building up a picture of how the face and body are represented by the complex but selective responses of neurons in the anterior part of STS and IT in monkeys. Studies of such neurons show that they may participate in understanding where other individuals are attending and hence support social interaction.
The time course of the neurons’ responses indicates that recognition of unusual views may not require mental rotation (see also Mallot, this volume). This area of the temporal lobe is also involved in interactions between information coded in the dorsal and ventral processing streams.

**Neurons selective for face and body views**

Some neurons in IT and STS respond to only one part of the face, e.g., the eyes, and if that part is covered the neuron stops discharging. As discussed by Tanaka (this volume), IT is organized in columns of neurons selective for moderately complex visual stimuli, which can be classified as feature detectors. Neurons in IT and STS sensitive to faces may integrate inputs from a special set of feature detectors. For example, sensitivity to concentric circles, which may specify eye-like features, is abolished by presenting an image composed of two half-circles (Perrett et al., 1982). Other geometric features could specify face-like parts. There are also face-selective neurons that respond to the entire face and are not activated by components of a face. The selectivity of some neurons for a particular face or person indicates that the tuning of at least some neurons is based on experience (Perrett et al., 1989).

Because most neurons in STS are selective for specific facial features, they also require a particular view and cease to respond when the crucial feature disappears as the face rotates in 3-D. Such gradual tuning functions depending on the view are found commonly in face-selective cells as well as in simple feature detectors. The outputs of a whole spectrum of neurons responding to front or back views, right or left profiles can be combined by neurons whose responses are viewpoint independent. Such neurons have been documented in IT and STS, although they are not common (Logothetis et al., 1995; Perrett et al., 1989, 1992; Perrett and Oram, 1993). Analysis of response latencies supports the idea of view-independent responses being generated by combining view-specific responses (Perrett et al., 1992). As a
working hypothesis, we suggest that face selectivity is not simple feature detection but is based on integration of multiple component inputs.

Recently, we have tested these neurons with views of a whole body or isolated parts of a body (Fig. 59). About 60% of the cells responding to faces or the head also responded to views of the body (Wachsmuth et al., 1994). Each neuron showed the same viewpoint specificity for heads or faces and body, i.e., neurons responding to the left profile of the head were also specific for the left profile of the body. This indicates that there are viewpoint specific descriptions for individual components and for the combination of the components.

**Figure 59.** Responses of an STS neuron that generalized across body parts but was selective for a particular action: it preferred the front view of the head, legs or upper part of the body moving toward the subject (black arrowhead). Mean and standard error of neuron discharge to front views (grey bars) and back views (light bars).
**View-dependence or mental rotation?**

A human subject takes longer to recognize a familiar object when presented with unusual views (see Mallot, this volume). Three-dimensional rotation of geometric figures and 2-D rotation in the picture plane produce similar results: the reaction time increases approximately linearly as the viewing angle becomes more unusual. This effect could be due to mental rotation (see Georgopoulos, Mallot, this volume) as unusual views could be transformed until they match a stored, view-specific template. Such transformations have been proposed for perspective view, for orientation and even for size.

But longer psychophysical reaction times with unusual views do not necessarily imply mental rotation. Rather, they could be explained simply by the behaviour of the neuronal population (Perrett *et al.*, in press). A population optimally tuned for the front of the face gives a progressively weaker response as the head is rotated (*Fig. 60a*). The cumulative response for 20 neurons rises fastest for the front view and slowest for the back view. A neuron receiving inputs from this population will reach threshold soonest for the strongest signal and reaction time will be longer when the signal is weak. The time taken for the population response to reach any theoretical threshold value for a follower neuron should thus get longer as the deviation from the front view of the face increases (*Fig. 60b*).

Similar results were obtained for a rotation in the picture plane, i.e., for different orientations. Controlling for visual fixation, 77% of the neurons found were tuned to the orientation of a face or body; other neurons reliably responded above control level to any orientation. Again, this orientation-independent tuning could be obtained by combining the outputs of neurons responding to upright or horizontal or inverted faces. More neurons responded to upright than to inverted faces and so the population response was maximal and developed faster with upright faces and was small and slower for inverted faces. The time for the population output to reach a chosen threshold value therefore increased from upright to inverted stimuli.
Figure 60. Rotating the head away from face view reduces both the responses of a population of neurons in IT and the time it takes for the responses to reach certain threshold values. **a**, average response of 20 neurons each selective for the face view of the head, plotted as the cumulative discharge above background. **b**, the time required for the cumulative response to exceed various threshold levels. Procedures for computing the cumulative response with and without normalizing maximum and minimum response (a procedure that forces all cells to contribute equally) produced equivalent results. Modified from Perrett et al., in press.
Changing the size of the stimulus produced the same pattern of responses. We project life-sized images at a distance of 4m and our monkeys never see people at more than 4m, so a half-size image is novel for them. As expected, the population response declined from life-size through half-size to quarter-size. Again, the response reached a chosen threshold value faster for life-size than for half- or quarter-size images. Images larger than life have not been tested.

The variation of the reaction time with orientation, view and size under the simple conditions we have investigated thus does not need to be explained by transformational processes such as mental rotation or mental size zooming. Object recognition in these conditions depends on how closely the visual stimuli match the selectivity of the neurons. Neurons in IT are sensitive to view, orientation and size, and experience shapes their selectivity for complex forms (Logothetis et al., 1995; Perrett et al., 1989 and in press). It is, therefore, to be expected that the larger proportion of the neurons will be selective for the most familiar views. As recognition seems to depend on the neuronal populations activated and the population response accumulates faster for objects seen in familiar views, the behavioural output will be faster for familiar viewing conditions without the need for mental rotation. This does not exclude the possibility that mental rotation is used in other tasks, especially learning new objects.

**Gaze direction: hierarchical inputs and population coding**

In addition to its selectivity for view, orientation and size, a face-sensitive neuron may code for the direction in which another individual is attending. Measuring eye movements of a monkey watching a video of other monkeys demonstrates that one animal follows the gaze or head direction of others (N. Emery and E. Lorincz, in preparation). In other words, monkeys recognize where other individuals centre their attention. There are multiple cues for the direction of attention: if the head is covered, it can be
**Figure 61.** A neuron in STS that shows hierarchically ordered responses to a set of stimuli. Elevated gaze overrides a specific view of the head but the neuron responds to a view of the body if the head is not visible. This coding cannot be part of a face-recognition process but is more likely to be related to analyzing the direction of attention. Modified from Perrett et al., 1990.

guessed from the body posture. This illustrates a reason why neurons found in IT and STS are both view- and orientation-selective. If profile-sensitive neurons were to generalize across orientations, a monkey would not be able to distinguish when its partner’s profile was level or looking up.

To code for upwardly directed attention, information about the face or profile looking up must be combined with information on head and body posture. We have found neurons that are selective for direction of gaze but not view dependent, e.g., responsive to a raised but not to a level head, both in front view and in profile, to upward gaze independent of head position and to body posture (Fig. 61). Thus this neuron will respond to radically different views provided the eyes are elevated. But there seems to be a hierarchy in the efficacy of its inputs: body posture alone can activate it but if the head is visible and not raised the response ceases, i.e., the head view modifies the response to the body view.
Superimposed on this, gaze in the wrong direction inhibits the response to an otherwise adequate head view.

Such complex neuron responses probably arise through combination of specific inputs from neurons with simpler responses. In this respect, viewpoint- and orientation- selective neurons, e.g., responsive only to the head view in left profile when rotated upward, can be considered as lower in the hierarchy. Through a high degree of interaction between inputs from neurons coding for different views of the body and for different orientations, a neuronal network may be built up that can provide a meaningful description of socially relevant body signals (Fig. 62).

**Figure 62.** A schematic representation of the connections and types of visual stimuli that may affect the responses of a neuron in STS signalling that another individual’s attention is directed downwards. The diagram shows how different types of visual input could interact through excitatory and inhibitory connections to establish selectivity for a conceptually coherent set of stimuli. The neuron (large circle) receives view-specific excitatory inputs from other neurons selective for the visual appearance of eyes down, head down and body posture. The connections establish a hierarchy in the sensitivity to different cues, here eyes>head>body. Gaze directed level or up prevents response to the head-down cues by presynaptic inhibition. Similarly, sight of the head directed level or up prevents response to the body posture. Modified from Perrett et al., 1992.
The population vector, commonly used to describe population responses (see Georgopoulos, this volume), may not be the best way to describe the behaviour of the face-sensitive neurons because it is sensitive to unevenly distributed response characteristics. In IT and STS there are many neurons that code for front view and profiles but relatively few code for half-profiles and back view. We are therefore testing Bayesian statistics for assigning the identity of a stimulus from the responses of neurons. Having characterized the responses of a small number of neurons to different views of a head, how accurately can the angle of view of an unknown stimulus be determined by assessing only the outputs of these neurons? We find that the stimulus can usually be predicted correctly from a randomly chosen population of about ten neurons, provided the responses last 0.5s. The exercise reveals the constraints on how the brain can utilize information encoded by populations of neurons and indicates how many neurons would be needed for the whole animal to make a decision of given accuracy in a given time period. The main questions for the future will be concerned with how well both brain and artificial networks can extract information about a stimulus from the activity of a population of neurons.

**Convergence between ventral and dorsal streams**

The motion-processing areas MT and MST and the posterior superior temporal polysensory area (STPp) send projections to part of the anterior STS, known as the anterior superior temporal polysensory area (STPa), where form and motion information can interact (Oram and Perrett, 1996). This area receives information about the attention of gaze and many neurons are motion sensitive, although we have no clear idea what kind of information is coming from the dorsal stream. There are indications that the predictability of how a stimulus may move strongly influences neuron responses in STPa. We have found that motion-processing neurons in STPa are inhibited when movement within the visual world is predictable.
from the monkey’s own movements. For example, neurons responded strongly to an object moving in the world but very little when the object was static and the monkey moved towards it (Hietanen and Perrett, 1996a). Similarly, the neurons were unresponsive when the monkey moved an object and could thus predict its movements but they responded when the experimenters moved the same object (Hietanen and Perrett 1996b).

In this instance, the dorsal cortical systems controlling motor acts seem to have a major role in setting up expectations for the complex visual changes that are consequences of the actions. The expectations are used to gate visual responses when visual changes are predictable. Such top-down influences of expectations on sensory processing are undoubtedly widespread. As expectations are difficult to control experimentally, they remain an exciting topic for future studies of visual processing.
One of the chief problems with the separate processing of different aspects of visual information is how coherent percepts are formed. As Young and Perrett have discussed above there are some areas where information from dorsal and ventral streams converge. Wolf Singer takes a look at three ways in which information could be identified as belonging together and describes experiments that test the hypothesis of synchronization between neurons responding to the same object. Working memory, which holds information while tasks are being completed, is examined in more detail by Patricia Goldman-Rakic. Following on from Ungerleider's human imaging studies (see Part I), she describes several domains in prefrontal cortex that each handle working memory for a different aspect of visual processing and postulates that they form parts of networks involving parietal or inferotemporal areas. A similar network may underlie the processing of language, in which recognition and delays also play a large part.

Synchronization as a mechanism for response selection in visual processing

Wolf Singer

The visual world consists of many objects abounding with different textures, colours, orientations and shadings. How our brains create consistent, meaningful representations from the confusing variety of stimuli, a process requiring segmentation and dynamic binding of distributed neuronal signals, remains a difficult and controversial problem. Two models for combining signals that originate from one object and not from another or the background, are consi-
Binding through convergence

Convergence is conceptually a simpler model. It assumes that neurons detecting simple features of the input, such as contrast, colour or orientation of edges, converge on to neurons that are tuned to detect a specific constellation of features. Several iterations of this convergence produce binding neurons in the later stages of processing that respond only when a specific set of input neurons is activated. The responses of these individual binding neurons could signal the presence of particular aspects of the perceived object, or ultimately, could represent the whole object itself.

A mechanism of this type probably works for stereotypic, familiar patterns, allowing them to be processed very rapidly, but it is difficult to see how it could deal with the large variety of changing, often unfamiliar, stimuli that animals encounter in their everyday lives. There are just too many features to cover with appropriately tuned neurons and the possible combinations and different views would require an enormous number of binding units. Combining all possible visual representations with all possible motor outputs constitutes another formidable problem. This model also requires a large reservoir of unspecified neurons, available for specification when new patterns have to be learnt and recognized, but there is no evidence for such a pool in the primate brain.

Population coding

The combinatorial explosion of representational units can be overcome by population coding, for which there is much support.
It allows stimuli to be efficiently represented by large populations of neurons that are broadly tuned for related features. For example, orientation-tuned neurons in V1 make the same response to a bar of optimal width that is slightly misplaced in the receptive field as to a non-optimal bar with optimal placement or to an optimal bar with perfect placement but low contrast. Although the response of a single neuron to all these stimuli might be the same, the exact position and orientation of the bar can still be derived from the population response of all activated orientation-selective neurons.

At first sight, population coding seems to make the numerical problem worse because large groups of neurons are required to represent a particular feature. But because neurons are broadly tuned, populations representing different features overlap and an individual neuron can participate in the representation of many different features. This greatly reduces the number of representational units required (Fig. 63a). The problem then becomes how an ensemble of neurons is defined. How does the system determine which of the many, rapidly changing clouds of simultaneously active neurons codes for this or that feature? This is a binding problem on the neural level, which could be resolved if the pattern of activity for one stimulus were made more salient than alternatives (Fig. 63b), e.g., by increasing the discharge rate of neurons that cooperate within the same ensemble. Such a mechanism is reliable but relatively slow because it takes several tens of milliseconds of temporal integration to distinguish between cells with high and low discharge rates. Thus, different ensembles can be segregated within a particular processing stage only if they succeed one another at intervals longer than the required integration time. More rapid succession would lead to overlap and neurons belonging to different ensembles would become confounded.

An alternative is to synchronize the discharges of neurons belonging to a particular ensemble so that their signals arrive simultaneously at the postsynaptic neuron. This greatly enhances the saliency of inputs due to spatial integration and, as it does so
**Figure 63.** Schematic representation of feedforward connections generating receptive fields (dashed lines) and reciprocal or feedback connections thought to be involved in creating neuronal ensembles (solid lines). **a,** a simplified diagram of connections within V1. The preference of neurons in cortical layer IV for particular features is assumed to result from specific combinations of feedforward connections, shown here for two horizontally tuned and one vertically tuned neuron. The outputs from the layer IV neurons go to other cortical layers, which make forward and reciprocal connections with extrastriate visual cortical areas, as shown in **c.** **b,** an example of perceptual grouping based on vicinity and collinearity. The line segments outlining a diamond pop out from the randomly oriented line segments forming the background because of their enhanced saliency. LGN, lateral geniculate nucleus. Modified from Singer, 1995.
jointly for all synchronized inputs, is an effective strategy for raising the saliency of selected inputs. If temporal integration windows are kept short, different ensembles can be generated in rapid succession. Moreover, the temporal signature of the output of an ensemble can in principle be preserved across several processing stages, provided that neurons function as coincidence detectors, which contributes further to reducing the ambiguity in simultaneously active ensembles.

**Binding by coincident signalling**

Binding by coincidence predicts certain experimental phenomena. The minimum requirements for synchronous inputs should be discharges in at least two neurons or populations within a few milliseconds. Given the distributed nature of cortical processing (Fig. 63c), synchronous activity should be observable both within and across cortical areas. Connections for which no explicit function has been found, such as those projecting back from higher cortical areas to earlier processing stages, the lateral connections that tie together areas at the same level of processing and the callosal projections, might all be important for co-ordinating synchronized activity. The binding criteria for forming ensembles would have to reside in the functional architecture of these synchronizing connections. As the criteria are acquired partly by experience and learning, the synchronizing connections that form ensembles would have to be plastic in both the developing and the mature cortex, and use-dependent modifications in these connections should be correlated with experience (Singer 1995).

Certain dynamic properties are also necessary. Individual neurons need to be able to change their partners rapidly, so that the representation can adapt to changing visual input. Only coherent activity, coding for meaningful interpretations of the environment, should be relayed. As coincident processing preserves the temporal pattern of activity, similar patterns should be observable in many processing stages. If synchronized activity accounts for the
recognition of objects, the probabilities of synchronization should reflect rules for perceptual grouping, e.g., Gestalt criteria.

**Experimental support for response selection by synchrony**

Experimental data from multi-electrode recordings in cat and monkey brain support many of these predictions. In lightly anaesthetized cats, neurons in the primary visual cortex with a preference for vertical bars discharge synchronously in response to a line moving in their receptive fields (*Fig. 64a*). If the line is split into two shorter ones that are moved into opposite directions, the individual neuron responses are as strong as before but the responses no longer occur in synchrony (*Fig. 64b*).

This is not an artefact of the anaesthesia, which creates a synchronization of the electroencephalogram (EEG) at frequencies below 10 Hz similar to that in sleep. On the contrary, the synchronization between neurons is enhanced during brain states characterized by desynchronization of the gross EEG (Munk et al., 1996). Stimulation of the mesencephalic reticular formation (MRF) shifts the power of the EEG from about 10 Hz to a peak at about 40 Hz, when it generally becomes desynchronized and resembles that of an awake animal. In this state the synchronization of local neuronal responses is enhanced but the selectivity for coherent stimuli is preserved. Often synchronous responses for coherent stimuli become apparent only after MRF activation (*Fig. 64c*) but bars that move in opposite directions in the receptive fields still do not create synchronization (*Fig. 64d*).

Similar effects were observed in motion-selective neurons in MT in awake monkeys trained to fixate a spot (Kreiter and Singer 1996). Such neurons are selective for the direction of movement of the stimulus and can respond equally well to a single bar or to two separate bars if the motion trajectories of the stimuli are selected appropriately (*Fig. 65*). This illustrates well that responses of single neurons are ambiguous. To distinguish between a single contour and two separate stimuli, the temporal relations between
Synchronized activity in cortical neurons in a cat results from stimulation with a single coherent moving bar (a, c) but not from two bars moving in opposite directions (b, d). This is not the effect of anaesthesia because desynchronization of the EEG by stimulation of the midbrain reticular formation increases the synchronized response to the coherent stimulus (compare c with a) but does not alter the response to the non-coherent stimuli (compare d with b). These differences are shown graphically in e. Reproduced with permission from Munk et al., 1996.
the firing patterns of at least two neurons have to be considered. It is not the response amplitudes but the synchrony that seems to contain the information about the relatedness of the contours evoking the responses. Synchronized responses occur only when the stimulus is coherent (Fig. 65a), whereas non-coherent stimuli do not elicit synchronous firing, even though each bar moves in the optimal direction for the receptive field of its respective neuron (Fig. 65b). These results reflect the behaviour of two populations of neurons that are active together only when stimuli are coherent but respond separately when the stimuli are not coherent.

Further evidence in support of synchronization was obtained by recording in various cortical areas of cats trained to press a lever in response to a change in a visual stimulus. After seeing a horizontal
grating, the cats had to hold the lever until a vertical grating appeared, then release it. The cross-correlations between neurons in multiple areas (visual areas 17, 18 and 21 in both hemispheres, association area 7 and pre-motor and motor areas 4 and 5) showed highly synchronized neuronal activity in certain frequency ranges while the animal was carrying out the task. This highly organized pattern, characterized by zero phase lag, appeared as soon as the animals concentrated on the task and broke down when the task was completed. During the reward period, zero-phase synchronization gave way to unsystematic, low frequency (10 Hz) oscillations with variable phase lags in different areas. The strength of synchrony among the various areas while the cat was performing reflected the presumed functional interactions required for the execution of this visuomotor task (Roelfsema et al., 1997).

Recent recordings of synchronized activity from neurons in the retina and the lateral geniculate nucleus of cats indicate that this form of coordination may be a more general phenomenon than previously assumed (Neuenschwander and Singer, 1996). The receptive fields of the neurons were widely separated, by more than 20°, yet the neurons responded in synchronization to stimulation by a continuous bar but not to two separate bars. This result is particularly surprising because the retina receives no feedback connections from higher levels of the visual system that could mediate the synchronization. Hence, it must result from intraretinal interactions.

Together with previous evidence (reviewed in Singer, 1993; Singer and Gray, 1995), these results support the possibility that the nervous system exploits the option to select responses and to associate them for further processing by coordinating the temporal patterning of distributed discharges. This strategy is ideally suited for solving the binding problems that result from parallel processing and population coding but it does require that neurons operate as coincidence detectors with a temporal resolution in the millisecond range (see Konnerth et al., 1996). Currently, this is a
controversial issue (see Abeles et al., 1994; Shadlen and Newsome, 1994; Softky, 1995; König and Engel, 1995) as the known biophysical properties of neurons can be interpreted in more than one way. As synchrony occurs with a precision in the millisecond range, it seems likely that neurons, when embedded in the appropriate network, can indeed operate with the required temporal precision. Studies in awake animals are now needed to examine direct relations between neuronal synchronization and perception.

Prefrontal cortex revisited: a multiple memory domain model of human cognition

Patricia Goldman-Rakic

There are several views of how the prefrontal cortex is organized. In the macaque monkey this region is subdivided into cytoarchitectonic areas 8 - 13, 45 and 46, following Walker’s map (Walker, 1940). It is traditionally assumed that each of these subdivisions has a unique and independent function. According to another, hierarchical view different prefrontal areas have different functions but some are considered to be subservient to others. The hypothesis espoused here regards the prefrontal cortex as a composite of information domains, with several cytoarchitectonic areas operating in a particular domain. For example, visual and auditory spatial information are located in area 46 in the principal sulcus and object-identity information in areas 12 and 45.

All these prefrontal areas, however, serve a common function, which we term working memory. This is a concept derived from cognitive psychology that represents the transient storage of information in the service of comprehension, computation and planning. Working memory can provide a stepping stone to long-term memory but, perhaps more important, it also represents a
work space for computational tasks, a mental sketchpad or blackboard of the mind. It holds information very briefly in order to connect one moment in time with the next, thus giving temporal continuity to experience. This process is essential for processing all sensory information and for linking sensory experience to motor action. It is also crucial in language for both constructing and understanding sentences.

We have discovered some cellular mechanisms in prefrontal cortex that may underlie working memory in the visual domain. In monkey we have been able to differentiate between prefrontal regions dealing with memory for location and memory for object identity (see Ungerleider, this volume, for comparable work on humans) and we propose that a network linking these regions with more posterior areas of the cortex may serve as a prototype of the distributed organization involved in other domains of working memory.

Cellular basis of working memory for location

In the classic working memory task, a monkey fixates a screen on which a target is presented in one of several locations. The target disappears and, after a delay period, the monkey has to make a saccade to the location of the target, a response that requires memory of the target location. Lesions of prefrontal cortex, particularly of area 46, which is important for spatial information, profoundly impair the animal’s ability to do such a task; with bilateral lesions the ability does not recover.

Neurons in area 46 display several types of location-specific activity: phasic responses when the target comes on; phasic activation just before, or after, the initiation of the response; and sustained activity specifically in the delay period. Many exhibit combinations of these time- and event-locked responses. The evidence is consistent with the idea that target-, delay-, and response-related neurons with common receptive fields are interconnected within a cortical column, in analogy with orientation columns in V1.
In area 46, nearly half of all task-related neurons increase their activity in the delay period. We consider this is likely to be the cellular correlate of working memory and it provides evidence that neurons can keep information on-line during a task. Such delay neurons have ‘memory fields’: some are active only when the monkey has to remember a particular location; others discharge for other locations. Some neurons have opponent memory fields, being activated for one location but significantly inhibited by the opposite location.

The nature of the code represented by delay-period activity in neurons with memory fields has been demonstrated using an antisaccade task that dissociates the location of the cue to be recalled and the location of the impending response. This revealed that not all delay neurons hold retrospective information about the stimulus; some are linked to the forthcoming response. On half the trials, the animal was required to make eye movements toward the target, on the other half away from it. Neurons were classified as encoding response direction if their activity during the delay period segregated with the location of the response, i.e., was enhanced before every directed response. Those in which the delay-period activity segregated with the direction of the target, independent of the direction of the response, were considered as coding for an iconic representation of the stimulus. By these criteria, approximately 60% of neurons with delay-period activity in area 46 coded for stimulus location, the rest for response direction (Funahashi et al., 1993).

Opponent memory fields could be produced by feedforward inhibition connecting pyramidal cells with opposite memory fields, so there are likely to be inhibitory interneurons in the microcircuitry of working memory. Simultaneous recording of interneurons and pyramidal neurons in prefrontal slices revealed that when a fast-spiking interneuron was active, the related pyramidal cell was inhibited and vice versa (Wilson et al., 1994). Often the activity of the interneuron was complementary to that of the pyramidal
cell, e.g., if the pyramidal cell was active for a 90° location, the interneuron would be active for the 270° location. This is the first demonstration in prefrontal cortex that interneurons can have preferential activity patterns.

**Pharmacology:** Several lines of evidence point to the dopamine input from the brainstem as a tonic modulator of the excitability of prefrontal pyramidal neurons, thus modifying their responses to extrinsic inputs (Goldman-Rakic, 1995). Immunohistochemical studies have shown that dopamine-positive axons form symmetrical synapses on the spines of pyramidal neurons, close to the excitatory inputs from the thalamus and other cortical areas. This is the first evidence in prefrontal cortex that dopamine-containing neurons make direct synapses, instead of releasing the neuromodulator in a diffuse and non-directed fashion. They may thus directly influence the excitability of the pyramidal neurons. Dopamine type 1 receptors are present in large numbers in prefrontal cortex and intracerebral injection of an antagonist enhanced the activation of some prefrontal neurons during the delay period without altering their general excitability (Williams and Goldman-Rakic, 1995).

**Working memory as a distributed system**

The connectivity of prefrontal cortex indicates that working memory is a truly distributed system. Tracer injected simultaneously into posterior parietal cortex and prefrontal area 46 revealed that both project to many of the same areas. In the upper bank of STS, for example, the inputs from parietal and prefrontal cortex coincided in patches measuring about 750 μm-1mm, the approximate dimension of a cortical column. In all, area 46 and the posterior parietal cortex connect with the temporal cortex, PM and pre-SMA, the anterior and posterior cingulate cortex and parts of the parahippocampal gyrus (i.e., the limbic system).

Area 46 is also heavily interconnected with subcortical motor areas, including a robust projection to areas of the superior colliculus involved in the control of eye movements (see Hoffmann,
Sparks, this volume) and one to the striatum (Fig. 66). It is partly through these subcortical connections that neurons in area 46 influence the direction, timing and perhaps accuracy of an eye or hand movement. Through these connections the idea of a target is translated into a memory-guided, as opposed to a sensory-guided, response.

Confirmation that parietal and prefrontal regions are part of the same distributed system comes both from the 2-deoxyglucose (2-DG) autoradiographic technique for assessing neuronal activity by monitoring glucose use and from electrophysiology. The 2-DG method was used to compare metabolic activity in cortex during tasks that did and did not require working memory. Parietal areas 7a, 7b, 7m and LIP were all activated by as much as 20% above control values, as were the non-overlapping subregions of area 46, with which the different parietal regions are connected.

In recent recording experiments we have demonstrated that posterior parietal neurons are indeed active during a delayed-response task. A comparison of neurons in the intraparietal sulcus and in the caudal prefrontal region, including area 8 in the anterior bank of the arcuate sulcus, showed that the same types of response occur in comparable numbers during an oculomotor delayed-response task in both prefrontal and parietal cortex (Fig. 67). The sensory response occurred earlier in the population response in parietal than in prefrontal cortex and there was a non-significant trend for saccadic responses to occur earlier in prefrontal cortex.

The circuit that links the dorsolateral prefrontal cortex (areas 46 and 8), the posterior parietal cortex and specific subcortical structures, we have called the spatial cognition network of the brain. Within it, sensory, association, motor and limbic functions are integrated for a common purpose, in this case operations within the spatial domain. Other circuits are similarly organized for non-spatial functions, each defined by the information it deals with. Each network has properties of re-entrance because most connections are reciprocal.
Figure 66. Anatomical connections of area 46 in the principal sulcus (hatched) with motor areas in the macaque monkey. Area implicated in forelimb movements (light stipple) include the arcuate premotor area (APA), pre-SMA and anterior portions of the cingulate motor areas (CMAr, CMAc) in the cortex (above), as well as the discrete zones in the caudate nucleus of the striatum (lower left). The FEF and the supplementary eye fields (SEF) in the cortex (dark stipple) and zones in the caudate nucleus and the superior colliculus (lower right; dark areas) are components of the oculomotor system. The cortex of the left hemisphere is shown from medial (top) and lateral (middle) aspects; striatum and superior colliculus shown in coronal section. Modified from Goldman-Rakic et al., 1992.
Figure 67. Single neuron recordings made in one monkey from prefrontal cortex (left panel) and parietal cortex (right panel) during an oculomotor delayed-response task, which tests for spatial working memory. There is a remarkable similarity in the task-related activity in neurons in the two areas. In each frame, rasters (top) are aligned at the start of the delay period for comparison; the histograms below summarize the responses. a, visual responses; b, delay responses; c, presaccadic responses; d, post-saccadic responses. Shaded regions on the lateral view of the brain indicate approximate areas of cortex sampled. Reproduced with permission from Goldman-Rakic et al., 1993.
**Generation of the delay-period activity**

Cooling the prefrontal region while recording from a parietal neuron reduced the delay-period activity, which recovered on rewarming. In some parietal neurons, cue-related or response-related activity was also diminished, although in others activity was enhanced. Similar results were obtained when recording in prefrontal while cooling parietal cortex. In the behaviour, however, distinct differences resulted from cooling the two areas: parietal cortex did not produce any impairments, whereas errors in all directions in eye and arm trajectories occurred contralateral to the cooled side of prefrontal cortex. There was a clear dissociation between sensory-guided and memory-guided responses: when the target was left on during the delay period, which means that the response was sensory guided, no deficit was evident.

We conclude from these experiments that prefrontal cortex is specialized for memory-guided performance, a function that cannot be compensated for by the functions of other structures; on the other hand, the more sensory functions of the posterior parietal cortex are more easily compensated by the flow of visual information to prefrontal neurons through other non-parietal pathways or the uninjured hemisphere. Although it is possible we did not cool a sufficiently large area of parietal cortex to produce a behavioural effect, previous studies of parietal lesions showing no impairment in the delayed-response task support our results. A PET imaging study with humans has recently confirmed that the dorsolateral prefrontal area is active only during memory-guided tasks by subtracting the activity occurring during a sensory-guided and a memory-guided task (Sweeney et al., 1996).

**Multiple working-memory domains**

Cortico-cortical connections indicate that different areas of the prefrontal cortex handle different types of information. In contrast to the principal sulcus, which receives its inputs from the dorsal stream through the parietal cortex (see above), areas 12 and 45 receive their
inputs mainly from the ventral stream: the ventral bank of STS, where neurons responding to faces have been found (see Perrett, this volume) and the lateral surface of TE, where moderately complex features of objects are mapped (see Tanaka, this volume). Recording experiments provide physiological confirmation of this separation. When a monkey is presented with pictures of animals, people or objects in a delayed-response task, neurons in areas 12 and 45 are active during the delay period in response to some features of the stimuli but do not differentiate between different stimulus

![Diagram of brain areas](image)

**Figure 68.** Recordings from areas 12/45 in the inferior prefrontal convexity during a working-memory task with faces or patterns show the specificity of delay-period activity for a particular stimulus and not for the intended direction of response. **a**, location of the area from which neurons were recorded. **b**, recording from a single neuron that selectively discharged during the delay period whenever a picture of a particular face presented at the centre of a screen instructed the monkey to move its eyes to the left at the end of the delay (top left panel); its activity did not increase when another face signalled a delayed eye movement to the right (top right). It was also not responsive to two patterns that signalled left (lower left) or right (lower right) saccades after the delay. Reproduced with permission from Wilson et al., 1993.
locations or between left- and rightward movement (Fig. 68; Wilson et al., 1993). Moreover, neurons sensitive to a face shown in the central visual field will not respond when the face is in the periphery, indicating an additional separation between central vision concerned with features and peripheral with position. We and others have now confirmed these results in humans, using fMRI with location and shape tasks testing for working memory. The ventral frontal region, where areas 12 and 45 are located, was activated selectively in the shape working memory task, particularly in the left hemisphere.

**A general model for working memory and its application to language**

The network elucidated here for the visual spatial system may be a prototype that could apply to other informational domains, such as the object recognition system. We propose that there are several

![Figure 69](image)

**Figure 69.** The two dissociable memory domains in the primate prefrontal cortex are illustrated schematically, with their connections to the two cortical visual streams. The posterior parietal cortex, concerned with spatial perception, connects with the dorsolateral region of the frontal lobe, involved in spatial working memory, whereas the inferotemporal cortex, involved in object recognition, projects to the inferior prefrontal region, where object identity is coded in working memory. Reproduced with permission from Wilson et al., 1993.
parallel working memory domains in prefrontal cortex, defined by their cortical connections with particular sensory association areas (Fig. 69). These prefrontal domains seem to be loops added on to the information processing areas that extend the dorsal and ventral streams into the working memory system. However, all prefrontal domains are reciprocally interconnected with each other and it is not clear whether these connections are excitatory or inhibitory or if they are subthreshold under most conditions. Simultaneous recordings in different domains are needed to clarify the neuronal activity in an area that is not involved in the current task. Many real-life tasks are likely, however, to involve more than one type of working memory.

The language system may also use a network of this sort. The circuits supporting language have an organization analogous to the spatial system, with interconnected posterior, medial and anterior areas in the cortex. Language processing has similarities with a visual memory task because it deals with a sequence of symbols that is produced and perceived over time; the temporary storage of information is an inherent part of comprehension. Working memory is necessary to store partial and final products of the computations required to process a stream of words, allowing us mentally to paste in other ideas that are mentioned separately (Just and Carpenter, 1992).

With the delayed-response tasks we are able to tap into the temporary storage of information. Assuming that this temporary storage is the same in different regions of prefrontal cortex, then understanding how it works in one system may provide insights into how it works in others, possibly even in the highest level of processing in the human brain — language.
CONCLUSION

Growth points

The preceding articles are good examples of the shift in viewpoint that has occurred in this field in the past few years. Experiments now embrace complexity, context is increasingly taken into account, functions are being seen as distributed across several areas and population selectivity is replacing single-neuron specificity as an explanation of neuron tuning. Many of the current results indicate an organization that is dynamic in both spatial and temporal domains. Brain imaging studies are beginning to make a substantial contribution to the analysis of distributed functions, although both the potentials and limitations of these technologies need to be carefully considered.

Design of experiments

Whereas in the past, experiments were designed with as few variables as possible, this approach is now being recognized as overly simplistic. As demonstrated by much of the work described in this volume, increasing the number of controlled variables is producing many interesting results (see, for example, Caminiti, Sakata, Tanji, Andersen, Goldberg, Logothetis, Goldman-Rakic). Particularly challenging is the demonstration that the strategy a monkey or human uses for a task can affect the frame of reference for sensory coordination (Lacquaniti), implying that the combination of variables producing a particular neuronal response change with context. The different interpretations of the activity of saccade-related neurons in LIP (Andersen, Goldberg) could also arise from the experimental context: there may be two types of neuron with different functions or one type responding differently under different conditions.

With the inevitable 3-5 year span of behavioural neurophysiology experiments, the balance of variables and context is of great concern in experimental design. Imaging is beginning to make a useful
contribution to this problem because of its capacity to provide a global picture. Used as an extension to psychophysics, imaging can help to formulate questions for physiological recording studies. Imaging studies do not, however, address mechanisms, for which both single-unit and, increasingly, multi-electrode recording continues to be essential. Imaging has not so far been extensively employed in monkeys, mainly because awake monkeys will not tolerate being placed horizontally in the bore of the scanner; there are also no good algorithms for use with non-compliant subjects to compensate for movement artefacts. This is, however, an area where human imaging studies can be used to inform the animal recording work. Another advantage of imaging, which is emerging from recent fMRI studies (Ungerleider), is the description of individual differences. It is essential to remember that life experience and environmental factors shape the individual nervous system within the framework laid down by evolution, which is particularly well illustrated here by the coding of social signals in IT (Perrett).

One limitation of imaging work is the loss of temporal resolution, although this may be overcome in the next decade by combining fMRI with magneto-encephalography and EEG. Another, more immediate, disadvantage lies in the subtraction method used in most task-oriented experiments, which gives the misleading impression that single areas are involved in single tasks. This reinforces the tendency to fixate on a specific area and attribute the whole of a function to it, which runs counter to the increasing awareness of the interaction between areas and the distributed, overlapping nature of processing in multiple areas. On the other hand, imaging can demonstrate how the same area may be activated in different tasks and how functions can shift as a task becomes automatic; for example, premotor cortex is active while a task is learned but is relatively silent once the pattern is established, leaving the main activity in M1.
Distributed networks

The problem of determining how different areas contribute to the same task could well be tackled by studying sequences of movements, for which activity in several areas has to be temporally coordinated. This requires a temporal working memory to link two elements together in time, for which the pre-SMA seems to play a role similar to that of prefrontal areas in spatial working memory (Tanji, Goldman-Rakic). The sequences themselves are probably produced in the basal ganglia but the cortex is required to hold the information over time about what to do next. The danger here is a tendency to think in terms of ‘meta-intelligence’ units, such as sequencers, rather than of the emergent properties in distributed networks now favoured by those working on sensory cortex and illustrated here for visuomotor coordination (Caminiti) and for spatial and object-focused working memory systems in prefrontal cortex (Goldman-Rakic).

Although thinking in terms of distributed networks is a significant advance, it is still important to remember that different cortical areas do play different roles in processing and that there is a hierarchy of functions in the cortical networks, from simple abstraction of parts of the signal in the most posterior areas to complex global integration in the most anterior areas (Young). Distribution of functions implies rather that no area operates alone or is solely responsible for a particular process and that each area depends for its operation on the overall activity of the network in which it is embedded. Representations of objects, for example, are not widely distributed but the neurons in IT depend on a network of inputs to produce their responses (Tanaka). Furthermore, the degree to which functions are distributed may vary from one pathway to another.

Ultimately, of course, the network is the whole nervous system and the effectiveness of the motor outputs from the cortex and superior colliculus depends on the state of the rest of the motor system. That is, the motor outputs should be seen in terms of requests rather than commands and the response of the whole system to these
requests is not predictable — an ‘uncertainty principle’ (Hoffmann, Sparks). The selection of motor plans and outputs has a specificity, seen for instance in the subsets of cortical output to the superior colliculus and the intimate relationship between the deep layers of the colliculus and the motor neurons. One possibility that needs to be tested is whether the colliculus is coordinating eye, head and hand movements as a form of spatial orientation, a ‘visual grasp reflex’.

**Coding**

A finding common to many of the articles in this volume is that both stimulus attributes and motor outputs are coded by populations of broadly tuned neurons. Specific information seems to be represented not by single neurons but by groups or populations with partially overlapping properties (Lacquaniti, Georgopoulos, Tanaka, Perrett). The information represented by segregated subpopulations of neurons may be represented by a single population if conditions are appropriate, as demonstrated for the spatial information about distance, elevation and azimuth of hand position and movement in the superior parietal lobule (area 5d). Here complete information about limb position is represented by a population of neurons, provided the spatial distribution of the parameters is symmetrical with respect to the origin of the coordinate system (Lacquaniti).

Tools such as the neuronal population vector (Georgopoulos) or multidimensional scaling (Sakata) are required to analyse and predict the coding in a population (although these are not necessarily mechanisms used by the nervous system). Although the population vector model does not depend on direction or physical space, it has the problem of too few parameters, as it depends on different levels of neuron discharge and thus on an even distribution around the periphery of the stimulus space. It is necessary to identify dimensions with continuity of attributes and to consider how discontinuous coding might be represented by neuronal activity.

Multidimensional scaling, on the other hand, is useful for faces
and chemical senses, where there is reduction of data and dimensions. If sensory inputs are each mapped on a continuum, then the continua intersect at unique multidimensional points. Such a description is largely taxonomic but nevertheless an important step in analysing the modulation of neuronal activity. Particularly in the ventral stream, there is a lack of information about the coding of various object attributions, such as curvature, graded shading, texture and the more complex aspects of colour processing, all required for the recognition of complex objects.

Sensory processing also has a hierarchical component. For instance, determination of 3-D shape starts with a simple discrimination of binocular disparity, goes through the computation of changes in disparity for the discrimination of surface orientation and curvature to end with the determination of 3-D form. Singularities, clustering, boundaries and context also need to be considered. A good example comes from the retina, where place coding is strong and unambiguous but colour coding is both continuous and dependent on context — a distinction that extends into the brain.

It would be a mistake, however, to consider that all neurons code in the same way, just as it is unlikely that all pathways have the same level of distributed processing. Different types of coding and processing may be required for different functions: rapid recognition leading to swift avoidance action requires a far less detailed and sophisticated analysis and is less dependent on context and feedback than navigating in a landscape; learning too may provide shortcuts to the recognition of familiar objects (Mallott). Thus in some areas, specificity lies in the activity of the population, whereas in others it is more a property of individual neurons, such as some of those sensitive to faces.

**Organizing principles for the ventral stream**

From the contributions to this volume it may seem that the organization of the ventral stream is less well understood than that
of the dorsal stream. Although this could merely reflect the balance of the participants at the meeting, it is more likely to indicate a fundamental problem with studying the ventral stream. Unlike the dorsal stream, where separate channels projecting to distinct motor output areas combine different sources of information for the visual and proprioceptive guidance of specific actions (Jeannerod, Caminiti), the ventral stream has the more global and abstract functions of object recognition and perception, which have no discrete outputs. Some of these difficulties and proposals for overcoming them are discussed here.

The representation in the ventral stream is at a lower functional level than action. It is also implicit, rather than explicit as in the dorsal stream. The first problem, therefore, is finding an experimental handle for examining recognition. One approach is to determine the operations in which recognitions are used, i.e., the actions that result from particular states in the IT neurons. Much of recognition is used for object discrimination and thus could be tested with experiments similar to those employed in the dorsal stream. There may also be parallels between flow sensitive neurons in MSTd (Bradley et al., 1996), the neurons in AIP involved in the shaping of the hand to grasp an object (Sakata) and the components of object recognition in IT (Tanaka). The stable-target task (Goldberg) may also be useful as a way of examining communication between dorsal and ventral streams. Because it requires recognition of a stimulus to trigger the neuronal response to a stable target, the decision of where to move the eye is based exclusively on instructions from the ventral stream.

Identifying the areas to which IT sends its outputs, many of which will either directly or indirectly be motor areas, will also help to give a clearer picture of ventral stream organization. There remains the problem that both animals and humans spend long periods when they overtly do nothing but may be engaged in recognition, evaluation and decision making.

Some pointers to separation of functions within the temporal
lobe already exist. Recognition categories have been established in monkeys and in humans with temporal lobe lesions, including tools, fruit and vegetables, animals and persons; in face recognition, identity, expression and orientation are processed separately. These categories imply different uses and the neurons responding to them are found in different locations: those involved in social interactions are found above TE (Perrett), whereas those in TE seem more concerned with the impersonal world (Tanaka).

There are still problems with defining the ‘vocabulary’ of IT, including determining the correct parameters for stimulating neurons. The representation need not be isomorphic with the external world, although it is object centred and probably invariant, in contrast to the scaleable metric used in most dorsal stream areas (optic-flow neurons are one exception). Even so, the basic coding mechanisms in the two streams are likely to be similar and synchronization of congruent inputs (Singer) may well be important for building up the complex receptive fields of IT neurons.

Experimental approaches worth considering include monitoring behaviours, such as feeding, that require ventral stream activity. Recording from the muscles of the vocal chords could provide information similar to that obtained from eye muscles in gaze control. In humans, thought is usually accompanied by subliminal activity in the muscles of the jaw, lips and tongue. PET experiments with humans to examine the separation of object from background are underway.

Once a correlation between a behavioural or perceptual event is established, conventional interventions such as lesioning and pharmacological manipulation can be used, as well as triggering or inhibiting cellular responses by stimulation. Microstimulation could also be used, although accuracy is a problem in the tight space of the temporal lobe and different stimulus combinations can produce apparently similar behaviours. Another approach is the use of large multielectrode recording arrays, which have been employed very successfully in the hippocampus. It is, though,
dangerous to seek close parallels with hippocampal mechanisms, which are thought to be very different to those in inferotemporal cortex.

In all such experiments, the tests are not straightforward and the results not easy to predict. Model making is thus an essential component of the experimental approach. Many of the parallels between the dorsal and ventral streams, as well as the exchange of information between them, could be explored with models, which may well help to highlight the differences in mode of operation in the two streams, as well as their similarities.


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The present publication reports the second meeting of this series, which took place in Strasbourg on April 24-26, 1996. HFSP is very thankful to the organizers, participants, editor and co-editors.

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