NEUROPSYCHOLOGY OPTION **03-Oct-2006**

Course Programme

The first three weeks will concentrate on the general question below. The two following weeks will look at more specific questions, in particular comparisons of the human brain with those of other primates. The last 5 weeks will be a section organised by Dr Simon Green emphasising evolutionary approaches..

General Topic for Weeks 1-5

The general question is —

"To what extent can cognitive (and other) functions be localized in the brain?"

It is possible to answer "not at all" from anti-reductionist standpoints, but my theme will be that questions about cognitive function can at least be related to evidence from neuroscience, and I will examine some of the various forms of evidence for localization of brain functions.

i) Brief review of basic brain anatomy: coarse localization in hierarchical organisation, lateralization, and functional topographic mappings in cerebral cortex. Also a brief account of the history of the debate over localization of function (e.g. see just the title of Goetz, 2000 for the nineteenth century origins.)

ii) More detailed localization of brain function especially in relation to vision: fractionation of functional circuits and the correlation with perceptual phenomena and perceptual deficits following focal brain damage. (Livingstone, 1988; Zeki, 1993; Ungerleider *et al*, 1998; Harris and Miniussi, 2003; Bartels and Zeki, 2004; Zeki, 2005).

iii) Recent trends in techniques: studies of brain localization in normal awake human subjects using **brain-imaging** techniques, for instance PET scans. fMRI and MEG. An early example was the paper by Lueck, Zeki et al. (1989) localizing the colour area (V4) in human subjects. Throughout the 1990s and still continuing is an ever increasing volume of studies identifying particular brain regions that are especially active during certain psychological states or tasks. Recent examples include: waking up (Balkin, Braum et al., 2002); embarrassment (Berthoz, Armony et al., 2002); "Out-of-body" experiences (Blanke, Ortigue et al., 2002; Blanke, Landis et al.,2004) and "Hearing voices (Hunter et al., 2003); joke appreciation (Goel and Dolan, 2001; Wild et al., 2003); "self-reflection" (Johnson, Baxter et al., 2002); experience of a supernumerary phantom limb (McGonigle, Hanninen et al., 2002); musical aptitude (e.g. Schneider, Scherg et al., 2002; van Zuijen et al., 2004) enjoyment of eating chocolate and unpleasant feelings due to eating too much chocolate (Small, Zatorre et al., 2001) hysterical conversion (Vuilleumier, Chicherio et al., 2001) and autobiographical memory (Piefke et al., 2003) and social conformity (Berns et al., 2005; King et al., 2006).

iv) Despite this enormous volume of publication using the new techniques supporting localization of function there has also been over the same time period towards evidence suggesting that there are several kinds of *plasticity* which may change the locations of particular brain functions. A variety of mechanisms underlying this are possible including short-term changes similar to learning, or long-term developmental or adult re-routing of brain connections. Examples include changes in the use of "visual cortex" in some congenitally blind individuals (Buchel, 1998; Zangaladze *et al*, 1999; Noppeney et al., 2003) and there are comparable findings in early deaf subjects, see Neville et al., 1998, Petitto et al., 2000; Finney et al., 2001; Corina et al., 2003). Cross-modal interactions between sensory processes often viewed as independent are emphasised in the recent reviews such as Shimojo & Shams (2001) and Majewska & Sur (2006). Another area in which fast-acting plasticity (or "re-mapping") is investigated is "phantom limb" phenomena after amputations. (e.g. Knecht *et al,* 1998, Melzack *et al*, 1997; Ramachandran and Hirstein, 1998; Farne et al., 2002, Mercier et al., 2006: see also the week 3 handout).

A separate development in the late 1990's was the finding that, contrary to previous textbook dogmas, new neurons are grown in adult mammalian (and avian) brains (Gould et al., 1999; Gross, 2000; Gould and Gross, 2002), which clearly increases the likelihood of brain plasticity after brain damage.

v) Implications for theories of cognition: the lesson of subsystems and subdivisions in perceptual processing; are there any general-purpose cognitive mechanisms? - will cognitive psychology be replaced by cortical physiology? (E.g. see the concluding paragraphs of Albright, Kandel and Posner, 2000: see p. 10).

- The question of whether cognitive function described at a psychological level should be identified with brain function at the physiological level at all is still a matter for debate.

- Even if it is assumed that cognitive activities depend on brain processes, there are doubts about whether individual functions, psychologically defined, ought to be identified with individual parts or regions of the brain, defined anatomically or in terms of their spatial location.

- This is an old argument, which used to be addressed in terms of evidence from animal studies and from human performance deficits after brain damage.

- In recent years however, associations between spatial locations in the brain and particular kinds of psychological function have been frequently made because of the availability of technologies which purport to allow for the spatial differentiation of degrees of brain activity during the performance of cognitive functions by normal human subjects. Such studies are often referred to as "**Functional brain imaging"** or "**Functional brain mapping."**

Marr's Three Levels

One often quoted account of the relationship between neurophysiological factors and others is due to David Marr (1982, pp24ff – see over page). He identifies three different levels at which questions need to be asked about any information-processing device, all of which need to be understood, but with the assumption that each level can understood to a large extent independently of the others.

Computational Theory	Representation and algorithm	Hardware implementation
What is the goal of the computation, why is it appropriate, and what is the logic of the strategy by which it can be carried out?	How can this computational theory be implemented? In particular, what is the representation for the input and the output, and what is the algorithm for the transformation	How can the representation and algorithm be realized physically?

Figure 1-4 The three levels at which any machine carrying out an information-processing task must be understood. (Marr, 1982, p.25)

This account is usually quoted by people who want to concentrate on goals and strategies or computational theories *independently* of the "hardware implementation" — in this case the neurophysiology. I will be starting in a "bottom-up" fashion, by reviewing the basics of the neurological evidence first.

The view **opposing Marr** is that, in the case of the brain, the details of the hardware are intimately related to functions at the psychological level. Examples are Barlow (1972, 1985), Crick, (1989), Albright et al. (2000), and at a popular level Zeki (1992) and many others. (See item iii. on page 1).

1. Basic Considerations of Neuroanatomy.

1.1 Gross levels of brain anatomy

There is a very obvious though crude differentiation between brain-stem, limbic system, basal ganglia, limbic system, cortex, etc. An important simple distinction is that between cortical and subcortical processing. It can be related to differences between: mandatory and optional processing; controlled and automatic process; voluntary and involuntary actions.

1.2 Left-right differences between hemispheres.

This will not be examined comprehensively, but is one of the commonest examples of psychological differences attributed to differences brain regions: global versus local; course or fine scale; spatial/verbal.

1.3 "Front-to-back" differences within cerebral cortex.

This is a rough and ready way of referring to contrasts between secondary and primary regions of sensory cortex, or more subtle differences between the function of anatomically separate "areas" or "maps" of sensory (or motor) cortex. The main example here is detailed analysis of how the visual system works . (E.g. see Zeki, 1978, 1993; Zeki and Shipp, 1988).

1.4. Neurophysiology of the visual system.

The general issue is inherently interdisciplinary, and therefore some account needs to be taken of the nature of the neurophysiological evidence. The organization of the visual system is the main case in point, and the summaries provided by Frisby (1979), and Hubel and Weisel (1977) are early sources for this. A review was provided by Zeki and Shipp (1988), and even more detail neuroanatomical findings are covered by Livingstone (1988) and Hockfield *et al* (1990) and Ungerleider et al. (1998). An extension of the general principles which apply in the case of the visual system to cortical organization more generally has often been made (e.g. Kaas and Collins, 2001).

READING FOR WEEKS 1 — 3 ONLY

A scan of the sections of the main reference (Zeki, 1993) around the extracts given on the previous page, and a selection of **two or three** of papers listed here or discovered in relevant journals would be basic recommended reading for these two weeks.

For example, you could read the sections of **Zeki (1993)** and the short review by **Büchel (1998)** on re-organization of cortical function in early blind subjects plus Büchel *et al* (1998) or Sadato *et al* (1998) for more detail on the brain-mapping studies of visual cortex function in during Braille reading. Scanning through the paper by Ramachandran and Hirstein (1998) is also recommended. A set of six individual papers published in each of the last two years is given below for more recent reference.

Main Textbook

Zeki, S.M. (1993) *A Vision of the Brain*. Cambridge: Blackwell Scientific. (Birkbeck at HGG [Zek], Short Loan; Bloomsbury/UCL at G 27, Psychology: Senate House at 67 ICL/Zek: Some extracts from this are included further on in the handout)

Other wide-ranging references

Albright, T. D., Kandel, E. R., & Posner, M. I. (2000). Cognitive neuroscience. *Current Opinion in Neurobiology, 10*(5), 612-624.

Cowey, A. The Ferrier Lecture 2004 – What can transcranial magnetic stimulation tell us about how the brain works? *Philosophical Transactions of the Royal Society B-Biological Sciences, 360(*1458), 1185-1205.

Posner, MI, Raichle, ME (1995) Précis of images of mind. *Behavioral and Brain Sciences,* Vol.18, No.2, Pp.327-339. (Also a more general reference)

Ramachandran, VS and Hirstein, W (1998) The perception of phantom limbs. The D.O. Hebb lecture. *Brain, 121*, no 9., pp. 1603-1630. (see also http://www.bbc.co.uk/radio4/reith2003/reith2003_lecture1.shtml)

Zeki, S.M, (1992) The visual image in mind and brain. *Scientific American, 267,* 68-76. (Special Issue on "Mind and Brain", September, 1992)

Tangentially Related Books

Damasio, H. (1995) *Human Brain Anatomy in Computerized Images.* Oxford University Press. (611.810222 DAM in stacks 1 week Loan at Birkbeck: source of overheads of individual variations in human brain anatomy.)

Elman, JL, Bates, EA, Johnson, MH, Karmiloff-Smith A, Parisi, D. & Plunkett K. (1996) *Rethinking Innateness: A connectionism perspective on development*. London: MIT Press. (Chapter 5, "Brain Development" especially pages 249-250: 155.7 ELM in Bk Libary).

Frisby, J.P. (1979) *Seeing*. Oxford University Press.

Gazzaniga, M.S., Ivry R.B., & Mangun, G.R. (2002) *Cognitive Neuroscience: The Biology of the Mind* (2nd edition). New York: Norton. pp 160-165, cortical visual areas; pp 171-180, visual deficits; pp. 647-652 "Plasticity in the normal adult brain". 2 copies at 153 GAZ in the short-loan collection (1 week loan).

References from 2004-2006

There are 9 abstracts from these years on pages 21-23.

Other references

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Arthurs, O. J., & Boniface, S. (2002). How well do we understand the neural origins of the fMRI BOLD signal? *Trends in Neurosciences, 25*(1), 27-31

Avenanti, A., Bueti, D., Galati, G., & Aglioti, S. M. (2005). Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nature Neuroscience, 8*(7), 955-960.

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Barlow, H.B. (1972) Single units and sensation: a neuron doctrine for perceptual psychology?. *Perception, 1*, 371-94.

Barlow, H.B. (1985). The Twelfth Bartlett Memorial Lecture: The role of single neurons in the psychology of perception. *Quarterly Journal of Experimental Psychology, 37A*, 121-45.

Barrett, D. J. K., & Hall, D. A. (2006). Response preferences for "what" and "where" in human non-primary auditory cortex. *Neuroimage, 32*(2), 968-977.

Bartels, A., & Zeki, S. (2004). Functional brain mapping during free viewing of natural scenes. *Human Brain Mapping, 21*(2), 75-85.

Bartels, A., & Zeki, S. (2004). The chronoarchitecture of the human brain - natural viewing conditions reveal a time-based anatomy of the brain. *Neuroimage, 22*(1), 419-433

Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *Neuroimage, 21*(3), 1155-1166.

Berns, G. S., Chappelow, J., Zink, C. F., Pagnoni, G., Martin-Skurski, M. E., & Richards, J. (2005). Neurobiological correlates of social conformity and independence during mental rotation. *Biological Psychiatry, 58*(3), 245-253.

Berthoz, S., Armony, J. L., Blair, R. J. R., & Dolan, R. J. (2002). An fMRI study of intentional and unintentional (embarrassing) violations of social norms. *Brain, 125*(8), 1696-1708.

Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain, 127*(2), 243-258.

Blanke, O., Ortigue, S., Landis, T., & Seeck, M. (2002). Neuropsychology: Stimulating illusory own-body perceptions. *Nature, 419*(September 19), 269 - 270.

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Büchel, C (1998) Functional neuroimaging studies of braille reading: cross-modal reorganization and its implications. *Brain,* Vol.121, No.Pt7, Pp.1193-1194.

Büchel, C, Price, C, Frackowiak, RSJ and Friston, K (1998) Different activation patterns in the visual cortex of late and congenitally blind subjects. *Brain,* Vol.121, No.Pt3, Pp.409-419.

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Crick, F.H.C. (1989) The recent excitement about neural networks. *Nature, 337*, 129-132.

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Gould, E., Reeves, A. J., Graziano, M. S. A., & Gross, C. G. (1999b). Neurogenesis in the neocortex of adult primates. *Science, 286*(5439), 548-552.

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Some extracts from Zeki (1993) "A Vision of the Brain"

(The substantive points made in this book do not differ from those in the Scientific American article: as the examples below show, the book is partly a history of controversies over cerebral localization of function).

Chapter 4: Colour in the cerebral cortex (Also "Cerebral achromatopsia" pp265-278)

Mackay and Dunlop (1899) wrote that "the facts in this remarkable case, the first, as far as we know, in which a *total* acquired colour blindness from a cerebral lesion has been supported by pathological examination, point strongly towards the conclusion that if there is a separate centre for colour, its seat is the grey matter of the fusiform gyrus."
Later on Zeki discusses other cases and says:

"The first important point to note about achromatopsia is that the retinal mechanisms mediating colour vision are intact in this condition... The fibres carrying the messages from the retina to the striate cortex are also intact. Hence the defect is entirely central, due to a specific lesion in the cerebral cortex. *In brief, with achromatopsia, we witness a condition in which the signals relayed to the brain are normal but the mechanism used to construct colours is defective.*" (pp 267-8)

Mackay, G. and Dunlop, J.C. (1899) The cerebral lesions in a case of acquired colour-blindness. *Scot. Med. Surg. J.* **5**, 503 -12.

Zeki, S. (1990) A century of cerebral achromatopsia. *Brain*, **113**, 1721-1777. (available in the UCL Clinical Sciences Library, entrance on University Street)

Chapter 10, p 82 A motion-blind patient.

Zihl *et al* (1983) described a patient who had suffered a vascular disorder, which produced bilateral lesions outside the striate area. She had several problems including difficulties in calculations and mild aphasia. But her inability to see objects in motion was very striking. She had difficulty in pouring tea or coffee because the fluid appeared to be frozen, like a glacier. She complained of difficulties in following speech because she could not see the movements of the mouth of the speaker, and, when crossing the road, was only aware of cars in isolated individual positions, either near or far away.

Zihl, J., Cramon, D. von & Mai, N. (1983) Selective disturbance of movement vision after bilateral brain damage. *Brain* **106**, 313-340

Riddoch, G. (1917) Dissociation of visual perception due to occipital injuries, with especial reference to the appreciation of movement. *Brain*, **40** 15-57.

Zeki S. (1991) Cerebral akinotopsia (cerebral visual motion blindness) *Brain*, **114**, 811-824.

Holmes, G. (1918) Disturbance of vision by cerebral lesions. *British Journal of Ophthalmology*, **2**, 353-384.

1. **PET Scans (Positron Emission Tomography)**
   Measures metabolism of oxygen or sugar. Takes half a minute or more. Only accurate to a centimetre or two. Requires ingestion of radioactive substances by subjects (e.g. carbon dioxide, water). There is a need to limit annual exposure to radiation.

2. **SPECT (Single Photon emission Computed Tomography)**
   Measures blood flow, takes seconds, involves ingestion of special chemicals as radioactive substances. Has similar disadvantages to PET but is cheaper. Clinical uses.

3. **(MRI) Magnetic Resonance Imaging**
   Producing anatomical, rather than functional information, is spatially accurate to millimetres rather than centimetres (the methods above: PET and SPECT). Requires exposure to high radio frequencies and to very strong magnetic fields. (About the strength of magnets used to pick up cars in junk yards.)

4. **f M RI (Functional Magnetic Resonance Imaging)**
   Measures blood flow. Can be used without ingestion of any chemicals, or with ingestion of contrast agents that are not radioactive. Needs strong magnetic fields like MRI.

5. **MEG/MSI (Magnetoencephalography/ Magnetic Source Imaging)**
   Measures the very small magnetic fields produced by the electrical activity of neurons. The spatial accuracy of the localization is about 2mm and it is claimed that the temporal resolution goes down to a single millisecond. Like the others, depends a lot on computational and statistical analyses of the raw data. Is non-invasive.

RELATED TECHNIQUES

6. **Direct (Electrical) Stimulation** of motor cortex of brain of **animals**, and direct recording from sensory cortex in response to peripheral stimulation (Grunbaum and Sherrington, 1908; Hubel and Weisel, 1977; Zeki, 1978).

7. **Direct stimulation of the brain of patients** prepared for brain surgery (e.g. Penfield and Roberts, 1959: still used, sometimes to check on the imaging methods — see Lee et al., 2000; Kreiman, Koch & Fried, 2000, Blanke et al. 2002)

8. **Transcranial magnetic stimulation (TMS)** of the cortex of human subjects. Large changes in magnetic fields are produced by currents passed through coils placed close to the scalp, which induces localized activites in neurons in the cortex or other structures.

9. **Near Infra-Red Spectroscopy (NIRS)** . Like MEG and ERP is very non-invasive compared to the others mentioned.

10. **Electroencephalography and Event-Related Potentials (EEG and ERP)**. These techniques have been used for many decades, and involve simply measuring brain activitiy via electrical potentials picked up by surface electrodes on the scalp. Originally did not include much information about the localization of brain activity, but greater computational sophistication means that claims can now be made for localized orgins of the electrical changes measured.

Localization of Brain Function

FOR	AGAINST
Broca (1861) etc	Flourens (1824)
Ferrier (1878)	Hughlings Jackson (1882/3)
Hughlings Jackson (1882/3)	Head (1926)
Penfield and Roberts (1959)	Lashley (e.g. 1950)
Brain (1965)	Rumelhart and McClelland (1986)
Zeki (e.g. 1992,1993)	Willmes and Poeck (1993)
typical brain imaging studies in the last 15 years emphazising localization	typical brain imaging studies in the last 10 yearss emphazising plasticity

ISSUES IN THE LOCALIZATION OF BRAIN FUNCTION

1. Genetic Predetermination vs Plasticity
2. Individual Differences both Genetic and Environmental
3. SCALE: single neurons to hemispheres
4. Local organization vs distributed systems
5. Dedicated or general purpose functions
   (e.g. STM? “Seeing”)
6. Degree of content or domain specificity for dedicated functions
7. What is “a function”?
   (what a neuron does, what a brain region does, what an animal does, or what a person does?)

FOR functional localization:

"Thus our present-day knowledge of the organization of the visual cortex goes some way to support theories of cortical localization of function which the early neurologists fought so hard to establish." (Zeki, 1978)

"manifestations differ according to the site of the lesion..... such topographical associations come about because particular parts of the brain were already required for some lower function, which played a part in the evolution of one of the many aspects of the use of language" (Head, 1926)

"Whenever two stimuli can be distinguished, in normal life or in a psychophysical experiment, then proper analysis of the impulses occurring in a single neuron would enable them to be distinguished with equal or greater reliability." (Barlow, l985)

in analogy to the motor cortex, the posterior parietal cortex is formed by a multiplicity of areas, each of which is involved in the analysis of particular aspects of sensory information. **There are no such things as multipurpose areas for space or body schema and** (d) the parietofrontal connections form a series of **segregated** anatomical circuits devoted to specific sensorimotor transformations. (Rizzolatti *et al*, 1998)

Work of the past decade attests that the single neuron approach to perception and cognition has been profoundly successful. (Albright, Kandel and Posner, 2000: p. 621)

Determining the local circuit organization of the cerebral cortex and how that organization relates to the processing of region-specific information is, however, dauntingly complex, and its elucidation — important though it may be — is among the most formidable challenges facing cognitive neuroscience in the next decade.
…..the field will continue to advance through a global circuit-based approach to cognitive representation by the brain. (Albright, Kandel and Posner, 2000: pp.620-621).

AGAINST functional localization

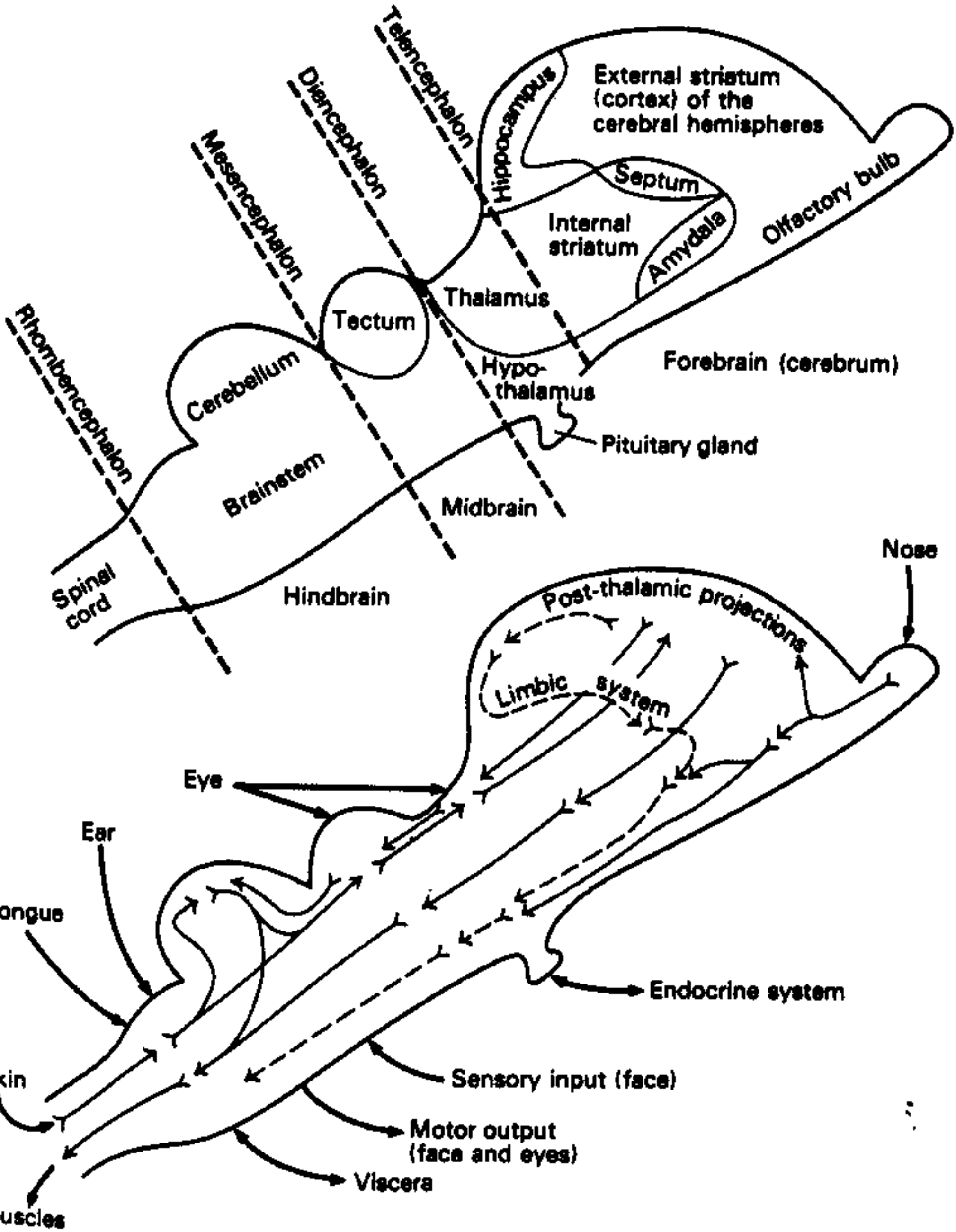
"..all of the cells of the brain, are participating, by a sort of algebraic summation, in every activity. There are no special cells for special memories." (Lashley, 1950).

"Dissociation of functions, as in isolated loss of colour vision.... are less clearly referable to injury in any specific region." (Lashley, 1948).

"It is not possible to demonstrate the isolated localization of a memory trace anywhere within the nervous system. Lmited regions may be essential for learning or retention of a particular activity, but withing such regions the parts are functionally equivalent. The engram is represented throughout the region" (Lashley, 1950, p478)

Results are used to argue against innate localization of linguistic representations, and in favor of an alternative view in which innate regional biases in style of information processing lead to familiar patterns of brain organization for language under normal conditions and permit alternative patterns to emerge in children with focal brain injury. (Bates *et al*, 1997)

A Compromise
"Another common source of confusion is the idea that distributed representation are somehow in conflict with the extensive evidence for localization of function in the brain (Luria, 1973). A system that uses distributed representation still requires many different modules for representing completely different kinds of thing at the same time. The distributed representation occur *within* the localized modules. For example, different modules would be devoted to things as different as mental images and sentence structures, but two different mental images would correspond to *alternative* patterns of activity in the same module. The representations advocated here are local at a global scale and global at a local scale." (Hinton *et al*; 1986 vol 2, p. 79).


Telencephalon
Diencephalon
Mesencephalon
Rhombencephalon
Spinal cord
Hippocampus
External striatum (cortex) of the cerebral hemispheres
Septum
Internal striatum
Amygdala
Olfactory bulb
Thalamus
Tectum
Cerebellum
Brainstem
Hypo-thalamus
Pituitary gland
Forebrain (cerebrum)
Midbrain
Hindbrain
Nose
Post-thalamic projections
Limbic system
Eye
Ear
Tongue
Skin
Muscles
Endocrine system
Sensory input (face)
Motor output (face and eyes)
Viscera

2. Anatomical Introduction

The principal anatomical features of the human brain are the two cerebral hemispheres that are approximately symmetrical and that are linked together by a great commissural structure, the corpus callosum. The hemispheres are intimately connected by enormous tracts of nerve fibres to the next lower levels of the brain, the immense neuronal complexes of the thalamus and basal ganglia (diencephalon).Great ascending and descending pathways, composed of millions of nerve fibres, link the cerebral hemispheres and the thalamus to still lower levels, the mesencephalon, pons, cerebellum, medulla and spinal cord. A detailed description of these pathways would be out of place here, but there will be refernce to some of them in the appropriate chapters on perception and control of movement, chapters E 2 and E 3 respectively.

From Popper + Eccles (1977) page 229.

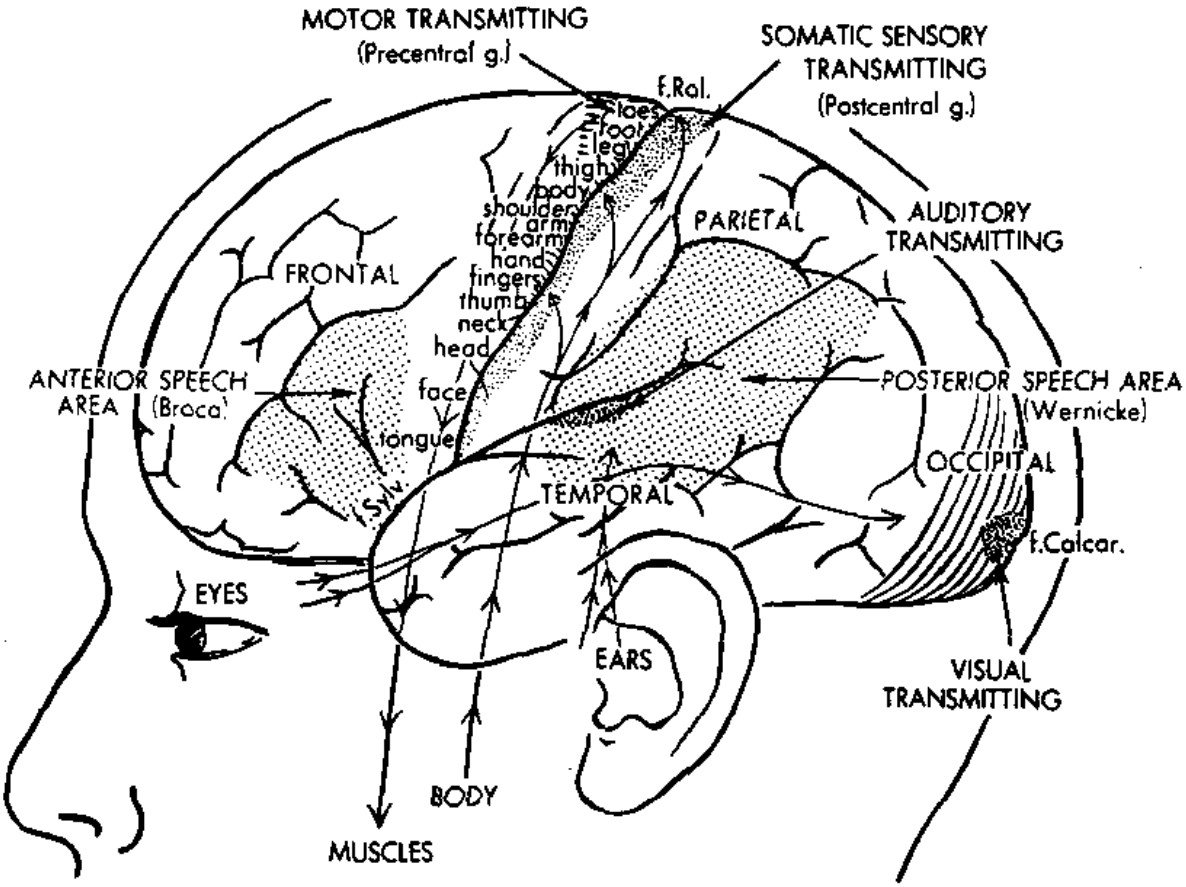
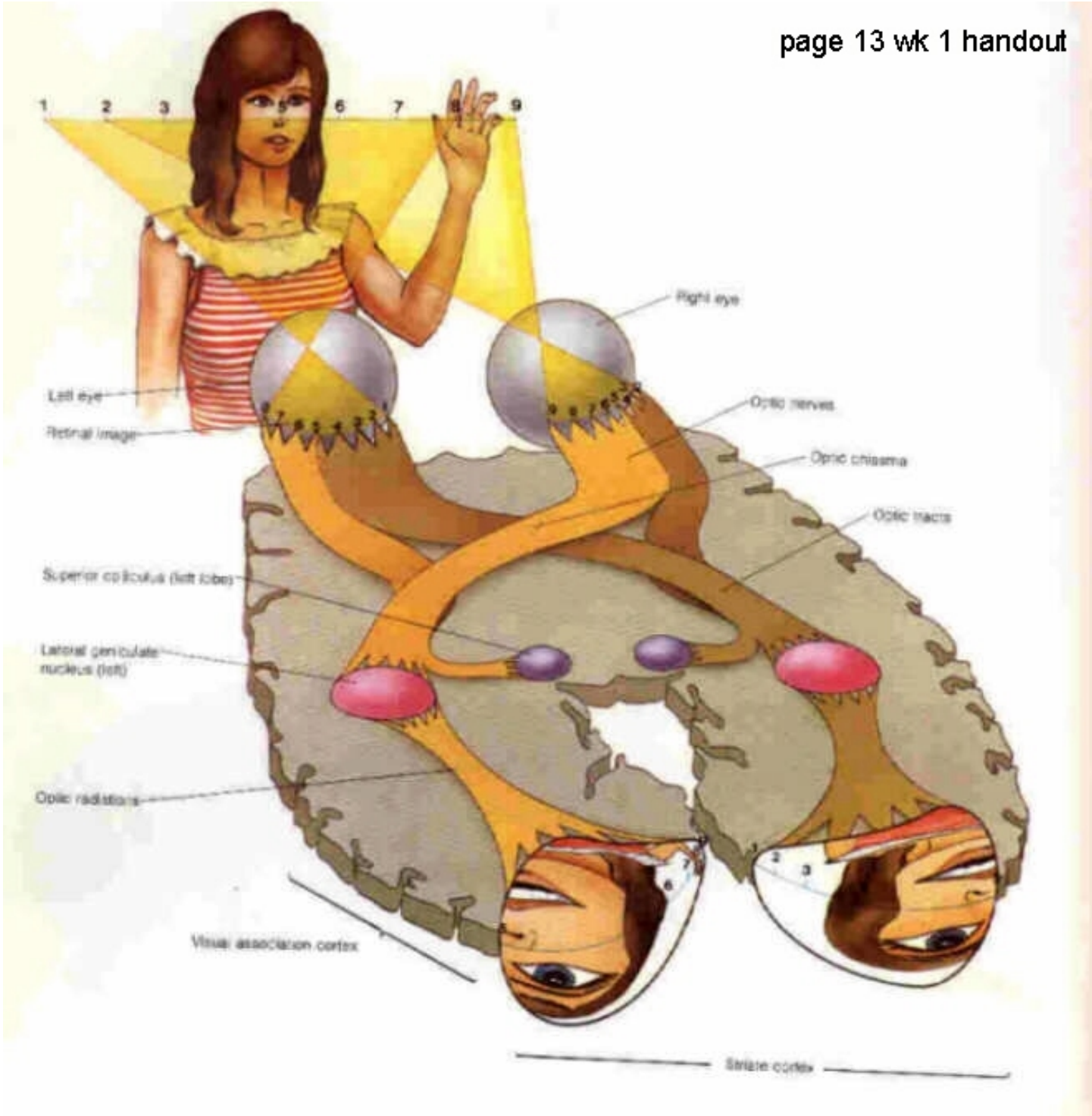


Fig. E1 – 1. The motor and sensory transmitting areas of the cerebral cortex. The approximate map of the motor transmitting areas is shown in the precentral gyrus, while the somatic sensory receiving areas (cf. Fig. E2 – 1) are in a similar map in the postcentral gyrus. Other primary sensory areas shown are the visual and auditory, but they are largely in areas screened from this lateral view. The frontal, parietal, occipital and temporal lobes are indicated. Also shown are the speech areas of Broca and Wernicke.


1
2
3
6
7
9
Right eye
Left eye
Retinal image
Optic nerves
Optic chiasma
Optic tracts
Superior colliculus (left lobe)
Lateral geniculate nucleus (left)
Optic radiations
Visual association cortex
Striate cortex

Zeki and Shipp 1988

> "....[.the subjective] effortless coherence within the visual image bears little trace of the internal subdivisions of function in the visual cortex that has become apparent from the past twenty years of research into the primate visual system. Anatomical, physiological and behavioral experiments in the monkey, and clinical studies of humans with cerebral lesions have established that different attributes of the visual scene, such as form, colour and motion, are processed in separate, anatomically distinct regions in the visual cortex, each executing its functions with considerable autonomy.
>
> ***This separation of function mirrors that found in the cerebral cortex as a whole..."***
>
> (p.311)

They want ultimately to answer Lashley's question of how the specialized areas interact to produce the integration evident in thought and behaviour -

Their answer is forward and backward connections along a serial pathway: Anatomical connections provide the basis for segregating features of the visual image into separate cortical areas: they suppose that there is communication between these areas at all levels to produce a coherent percept.

Zeki 1993, p. 5)

> "Central to this description is the theory of functional specialization. This theory supposes that different aspects of the visual scene are processed simultaneously, in parallel, but in anatomically separate parts of the visual cortex."

> "In short the study of colour gives us a vision of how the visual cortex works. The study of the visual cortex in turn gives us a vision of how the brain works."

Lashley's concepts of Mass Action and Equipotentiality (Lashley; 1929,1950)

These two inter-related terms were used in opposition to theories based on localization of function.

Lashley conducted experimental studies which suggested to him that the behavioural effects of removing a given amount of neocortex in rats did not depend on *where* the cortex was removed from. On the other hand he found a correlation between total lesion size and the extent of behavioural deficit. Thus he suggested that the cortex acted as an integrated whole (**Mass Action**) and that any particular small region of cortex was able to contributed equally towards the performance of a wide variety of tasks (**Equipotentiality**)

References

Lashley, K.S. (1929) *Brain Mechanisms and Intelligence*. University of Chicago Press

Lashley, K.S. (1950) In search of the engram. In *Symposia of the Society for Experimental Biology* (No IV): Cambridge University Press.

NEUROANATOMICAL SUMMARY (VISUAL SYSTEM)

Sensory input for vision, hearing and touch is initially mapped onto distinct areas of the cerebral cortex, called **primary sensory areas.** These are **topographically organized** – that is, the peripheral sensory areas (skin, retina) are mapped to cortical representations in a coherent way. Visual input goes to the occipital lobe, auditory input to the temporal lobe, and touch to the parietal lobe. There are also **secondary sensory areas** for each modality, and it is supposed that these have highly specialized functions.
Most is known about secondary sensory areas in the case of vision. (e.g. Zeki 1992)

> V1="Striate cortex"= primary visual cortex.
> Other visual areas may be referred to as "extrastriate cortex", "prestriate cortex" or secondary visual cortex.

"The first two visual areas, V1 and V2, are **segregators**, containing separate groupings of orientation, wavelength, and direction selective cells." (Zeki and Shipp, 1988 p316)

Outputs from V1 and V2 assemble separate signals in three **pivotal areas** —

> V3= dynamic form;
> V4= colour and static form;
> V5= movement (this area is sometimes called MT)

These pivotal areas marshal and redistribute the output of V1 and V2 to higher areas in the parietal and temporal lobes.

Broadly —
- the temporal lobe deals with "**what** is it" questions
- parietal lobe deals with "**where** is it" questions

SEGREGATION AND SPECIALIZATION

Specialized pathways begin in the retina, and continue through the subcortical relay in the Lateral Geniculate Nucleus (LGN), which has **Magnocellular (M)** and **Parvocellular (P)** layers.

Magnocellular System
- Is faster, with large receptive fields and greater sensitivity to contrasts: Sensitive to movement, not colour
- This system is relatively more concerned with the form of moving objects and with generating structure from motion.

Parvocellular System
- Thus (P)arvocellular system goes to one colour system and one for detailed form.. But both go through V2 to V4, which is specialized for colour. Not known what happens to form in V4 Speed of "Magno" make it best for movement, but both P and M have orientation.
- Cells in V4 has larger receptive fields and more complex properties than their counter parts in V1.
- The strategy of generating larger receptive fields - that is, gathering information from a wider part of the field of view - is probably essential to the computational process.

Lueck, Zeki et al., (1989)

Early this century suggestions for a colour centre in the human brain were dismissed. It has now been shown that there is an area specialized for colour (V4) in macaque monkeys. Also visual deficits in patients with lesions in similar places suggest that there is an equivalent specialization in humans.

In this study PET was used with normal human subjects: 3 male volunteers, 2 of whom were left-handed. They were presented with an abstract display of coloured squares and rectangles (a "Mondrian") on a monitor occupying the central 40^{o} of the visual field: on control trials the display was identical but compose of grays isoluminant with the colours (isoluminance was gauged by alternating gratings and adjusting the grays until the perception of motion ceased. *Ss* moved their eyes back and forward across a central line (5^{o}).

Complex PET methods: *Ss* inhaled radioactive CO_2 for 2 min: radioactive H_2O was produced in the lungs and monitored in arterial blood.

Each *S* had 6 trials: 1&6 = eyes shut; 2&5= colour;
3&4=gray

Each scan lasted 3.5 min with 15 min between trials (half-life is 2.1 minutes), with head in fixed position.

Results (special stats for small n)

No diff (colour-gray) in V1 (striate: V2 same). Just one area with large colour-grey diff. which was in the place expected, in region of lingual and fusiform gyri. "We presume this is the homologue of V4 in the monkey".

V1 had 14% increase for both stimuli, over eyes closed.
Colour area had 13% increase for colour cf gray.

Unexpected results

1. There was a small (3-5%) increase in the "motion area" (V5) on both colour and gray trials. A 4th *S* was tested with moving stimuli and showed a bigger increase in this area, and thus the increase in the original *Ss* may have been due to the eye movements.

2. In all *Ss* activity in the colour area was greater in the left hemisphere.

3. There was **no** major change in activity in the areas of the temporal lobe to which V4 projects. They suggest this may be because the task did not require any memory or experience.

Zeki (1992) in Sci Amer :book (1993) is "A Vision of the Brain"

"The study of the visual system is a profoundly philosophical enterprise"

"The modern concept of the visual brain has evolved only within past two decades" (all p.69).

Pathological conditions (p.73)

Lesions in specific cortical areas produce correspondingly specific visual syndromes.

- lesions to area **V4** lead to **achromatopsia**, in which patients see only in shades of gray. This is different from simple colour blindness: not only do the patients fail to see or know the world in colour, they cannot even recall colours from a time before the lesion. But if their retinas and V1 regions are healthy, their knowledge of form, depth and motion remains intact.

- lesions to area **V5** produces **akinetopsia**, in which patients neither see nor understand the world in motion. While at rest, objects may be perfectly visible to them, but motion causes the objects to vanish. But the other attributes of vision remain unscathed.

- No one has reported a complete and specific loss of form vision: area V3 forms a ring around V1 and V2; a lesion large enough to destroy V3 would probably destroy V1 as well and cause blindness. But –

- Some patients with lesions in prestriate cortex have a degree of form imperception. They have greater difficulty identifying stationary forms than when the same forms are in motion: they often prefer watching television to "real" vision because television is dominated by moving images. They often resort to the strategy of moving their heads when identifying stationary objects.

- a syndrome, "Chromatopsia", may follow diffuse cortical damage caused by carbon monoxide poisoning. These patients have vision that is severely comprised in all respects except one: their colour vision is affected only mildly if at all. The often try to identify all objects solely on the basis of colour: e.g. misidentifying all blue objects as "ocean".

MECHANISMS INVOLVED IN NORMAL AND ABNORMAL BRAIN DEVELOPMENT, INCLUDING SOME INVOLVED IN ADULT PLASTICITY (CF PP 249-250 OF ELMAN ET AL, 1996)

1. Growth of new connections
2. Elimination of normal connections
3 Retention of exuberant connections
4. Reprogramming of existing connections (aka learning especially "Hebbian Learning")
5. Compensation/redistribution of function
6. Neurogenesis. Since 1996 more evidence has been accumulated suggesting that new neurons are generated in some parts of the cortex of adult vertebrate brains including adult primates. (Gould et al., 1999; Gross, 2000)

Florence, SL, Jain, N and Kaas, JH (1997) Plasticity of somatosensory cortex in primates. *Seminars in the Neurosciences,* Vol.9, No.1-2, Pp.3-12.

"Over recent years, we have come to the suprising realization that sensory cortex is highly plastic in functional organization, even in adult brains."

1. LIMITED CORTICAL CHANGES OCCUR SOON AFTER INJURY
2. CORTICAL CHANGES MAY REFLECT SUBCORTICAL MODIFICATIONS.
3. NEW AXON GROWTH MAY FOLLOW MASSIVE INJURY (AMPUTATION)

Refers to figure 11.3 on page 92 of Zeki (1993) which shows how the size of the receptive field of individual neurons changes from area to area in the visual cortex of rhesus monkeys.

Cells in V1 have the smallest receptive field (i.e only light at a small spot at a particular place on the retina activates the neuron for some cells corresponding to only a fraction of a degree in the visual field), but the receptive field sizes in V2 are more than double the size of those in V1, and the cells in V3 typically have receptive fields more than double the size of those in V3.

Refers to figure 14.3 on page 127 of Zeki (1993).

If an electrode is moved gradually through a section of the motion area (V5) in a monkey's cortex, parallel to the surface of the cortex, stopping at small intervals to detect the exact directional preferences of directionally sensitive cells, then there is a very orderly shift in the preferred directions of successive cells.

By contrasts, doing the same thing going down perpendicularly to the cortical surface in V5 reveals that most cells in the "column" prefer the same direction of motion (similarly in V1 or V3A most cells in a vertical column prefer the same orientation)

Refers to the paper below.

McGonigle, D. J., Hanninen, R., Salenius, S., Hari, R., Frackowiak, R. S. J., & Frith, C. D. (2002). Whose arm is it anyway? An fMRI case study of supernumerary phantom limb. *Brain, 125*(6), 1265-1274.

Under normal circumstances, information from a number of sources is combined to compute a unitary percept of the body. However, after pathology these influences may be perceived simultaneously, resulting in multiple dissociated conscious representations. In a recent paper, we described subject E.P., a right-handed female stroke patient with a right frontomesial lesion who sporadically experiences a supernumerary 'ghost' left arm that occupies the previous position of the real left arm after a delay of 60-90 s. We used a delayed response paradigm with functional MRI to examine the haemodynamic correlates of E.P.'s illusion. Comparison of periods of time during scanning when the ghost arm was present against when it was not revealed a single cluster (9 voxels, $t = 5.11$, $P < 0.012$ corrected for multiple comparisons) located on the right medial wall in the supplementary motor area (SMA proper). Our results suggest that areas traditionally classified as part of the motor system can influence the conscious perception of the body. We propose that, as a consequence of her injury, E.P. is aware of the position of the phantom limb in this action space while also continuing to be aware of the true position of her real limb on the basis of afferent somatosensory information.

9 Abstracts from 2004-2006

Aron, A., Fisher, H., Mashek, D. J., Strong, G., Li, H. F., & Brown, L. L. (2005). Reward, motivation, and emotion systems associated with early- stage intense romantic love. *Journal of Neurophysiology, 94*(1), 327-337.

Early-stage romantic love can induce euphoria, is a cross- cultural phenomenon, and is possibly a developed form of a mammalian drive to pursue preferred mates. It has an important influence on social behaviors that have reproductive and genetic consequences. To determine which reward and motivation systems may be involved, we used functional magnetic resonance imaging and studied 10 women and 7 men who were intensely "in love" from 1 to 17 mo. Participants alternately viewed a photograph of their beloved and a photograph of a familiar individual, interspersed with a distraction-attention task. Group activation specific to the beloved under the two control conditions occurred in dopamine-rich areas associated with mammalian reward and motivation, namely the right ventral tegmental area and the right postero-dorsal body and medial caudate nucleus. Activation in the left ventral tegmental area was correlated with facial attractiveness scores. Activation in the right anteromedial caudate was correlated with questionnaire scores that quantified intensity of romantic passion. In the left insula-putamen-globus pallidus, activation correlated with trait affect intensity. The results suggest that romantic love uses subcortical reward and motivation systems to focus on a specific individual, that limbic cortical regions process individual emotion factors, and that there is localization heterogeneity for reward functions in the human brain.

Avenanti, A., Bueti, D., Galati, G., & Aglioti, S. M. (2005). Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nature Neuroscience, 8*(7), 955-960.

Pain is intimately linked with action systems that are involved in observational learning and imitation. Motor responses to one's own pain allow freezing or escape reactions and ultimately survival. Here we show that similar motor responses occur as a result of observation of painful events in others. We used transcranial magnetic stimulation to record changes in corticospinal motor representations of hand muscles of individuals observing needles penetrating hands or feet of a human model or noncorporeal objects. We found a reduction in amplitude of motor-evoked potentials that was specific to the muscle that subjects observed being pricked. This inhibition correlated with the observer's subjective rating of the sensory qualities of the pain attributed to the model and with sensory, but not emotional, state or trait empathy measures. The empathic inference about the sensory qualities of others' pain and their automatic embodiment in the observer's motor system may be crucial for the social learning of reactions to pain.

Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *Neuroimage, 21*(3), 1155-1166.

Romantic and maternal love are highly rewarding experiences. Both are linked to the perpetuation of the species and therefore have a closely linked biological function of crucial evolutionary importance. Yet almost nothing is known about their neural correlates in the human. We therefore used fMRI to measure brain activity in mothers while they viewed pictures of their own and of acquainted children, and of their best friend and of acquainted adults as additional controls. The activity specific to maternal attachment was compared to that associated to romantic love described in our earlier study and to the distribution of attachment-mediating neurohormones established by other studies. Both types of attachment activated regions specific to each, as well as overlapping regions in the brain's reward system that coincide with areas rich in oxytocin and vasopressin receptors. Both deactivated a common set of regions associated with negative emotions, social judgment and 'mentalizing', that is, the assessment of other people's intentions and emotions. We conclude that human attachment employs a push-pull mechanism that overcomes social distance by deactivating networks used for critical social assessment and negative emotions, while it bonds individuals through the involvement of the reward circuitry, explaining the power of love to motivate and exhilarate. (C) 2004 Elsevier Inc..

Berns, G. S., Chappelow, J., Zink, C. F., Pagnoni, G., Martin-Skurski, M. E., & Richards, J. (2005). Neurobiological correlates of social conformity and independence during mental rotation. *Biological Psychiatry, 58*(3), 245-253.

Background: When individual judgment conflicts with a group, the individual will often conform his judgment to that of the group. Conformity might arise at an executive level of decision making, or it might arise because the social setting alters the individual's perception of the world. Methods: We used functional magnetic resonance imaging and a task of mental rotation in the context of peer pressure to investigate the neural basis of individualistic and conforming behavior in the face of wrong information. Results: Conformity was associated with functional changes in an occipital-parietal network, especially when the wrong information originated from other people. Independence was associated with increased amygdala and caudate activity, findings consistent with the assumptions of social norm theory about the behavioral saliency of standing alone. Conclusions: These findings provide the first biological evidence for the involvement of perceptual and emotional processes during social conformity.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7*(5), 555-562.

The function of the fusiform face area (FFA), a face-selective region in human extrastriate cortex, is a matter of active debate. Here we measured the correlation between FFA activity measured by functional magnetic resonance imaging (fMRI) and behavioral outcomes in perceptual tasks to determine the role of the FFA in the detection and within-category identification of faces and objects. Our data show that FFA activation is correlated on a trial-by-trial basis with both detecting the presence of faces and identifying specific faces. However, for most non-face objects (including cars seen by car experts), within-category identification performance was correlated with activation in other regions of the ventral occipitotemporal cortex, not the FFA. These results indicate that the FFA is involved in both detection and identification of faces, but that it has little involvement in within-category identification of non-face objects (including objects of expertise).

Noppeney, U., Price, C. J., Penny, W. D., & Friston, K. J. (2006). Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex, 16*(3), 437-445.

The cognitive and neural mechanisms mediating category-selective responses in the human brain remain controversial. Using functional magnetic resonance imaging and effective connectivity analyses (Dynamic Causal Modelling), we investigated animal- and tool-selective responses by manipulating stimulus modality (pictures versus words) and task (implicit versus explicit semantic). We dissociated two distinct mechanisms that engender category selectivity: in the ventral occipito-temporal cortex, tool-selective responses were observed irrespective of task, greater for pictures and mediated by bottom-up effects. In a left temporo-parietal action system, tool-selective responses were observed irrespective of modality, greater for explicit semantic tasks and mediated by top-down modulation from the left prefrontal cortex. These distinct activation and connectivity patterns suggest that the two systems support different cognitive operations, with the ventral occipito-temporal regions engaged in structural processing and the dorsal visuo-motor system in strategic semantic processing. Consistent with current semantic theories, explicit semantic processing of tools might thus rely on reactivating their associated action representations via top-down modulation. In terms of neuronal mechanisms, the category selectivity may be mediated by distinct top-down (task-dependent) and bottom-up (stimulus-dependent) mechanisms.

Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The plastic human brain cortex. *Annual Review of Neuroscience, 28*, 377-401.

Plasticity is an intrinsic property of the human brain and represents evolution's invention to enable the nervous system to escape the restrictions of its own genome and thus adapt to environmental pressures, physiologic changes, and experiences. Dynamic shifts in the strength of preexisting connections across distributed neural networks, changes in task-related cortico-cortical and cortico-subcortical coherence and modifications of the mapping between behavior and neural activity take place in response to changes in afferent input or efferent demand. Such rapid, ongoing changes may be followed by the establishment of new connections through dendritic growth and arborization. However, they harbor the danger that the evolving pattern of neural activation may in itself lead to abnormal behavior. Plasticity is the mechanism for development and learning, as much as a cause of pathology. The challenge we face is to learn enough about the mechanisms of plasticity to modulate them to achieve the best behavioral outcome for a given subject.

Singer, T., Seymour, B., O'Doherty, J. P., Stephan, K. E., Dolan, R. J., & Frith, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature, 439*(7075), 466-469.

The neural processes underlying empathy are a subject of intense interest within the social neurosciences(1-3). However, very little is known about how brain empathic responses are modulated by the affective link between individuals. We show here that empathic responses are modulated by learned preferences, a result consistent with economic models of social preferences(4-7). We engaged male and female volunteers in an economic game, in which two confederates played fairly or unfairly, and then measured brain activity with functional magnetic resonance imaging while these same volunteers observed the confederates receiving pain. Both sexes exhibited empathy-related activation in pain-related brain areas (fronto-insular and anterior cingulate cortices) towards fair players. However, these empathy-related responses were significantly reduced in males when observing an unfair person receiving pain. This effect was accompanied by increased activation in reward-related areas, correlated with an expressed desire for revenge. We conclude that in men (at least) empathic responses are shaped by valuation of other people's social behaviour, such that they empathize with fair opponents while favouring the physical punishment of unfair opponents, a finding that echoes recent evidence for altruistic punishment.

Wieloch, T., & Nikolich, K. (2006). Mechanisms of neural plasticity following brain injury. *Current Opinion in Neurobiology, 16*(3), 258-264.

Brain insults cause rapid cell death, and a disruption of functional circuits, in the affected regions. As the injured tissue recovers from events associated with cell death, regenerative processes are activated that over months lead to a certain degree of functional recovery. Factors produced by new neurons and glia, axonal sprouting of surviving neurons, and new synapse formation help to re-establish some of the lost functions. The timing and location of such events is crucial in the success of the regenerative process. Comprehensive gene expression profiling and proteomic analyses have enabled a deeper molecular and cellular mechanistic understanding of post-injury brain regeneration. These new mechanistic insights are aiding the design of novel therapeutic modalities that enhance regeneration.

Journal availability

Acta Psychologica (vol 107 1-3)	UCL Psychology Pers	Birkbeck plus ScienceDirect
Aphasiology		BK since 1987
Brain	pre 1992 at UCL Clinical Sciences (on University St: not same bldg as Medical Sciences/DMS Watson)	BK since 1992, 1996 on shelves and now automatically online from Birkbeck
Cerebral Cortex	UCL Medical Sciences	
Cognitive Brain Research	UCL Medical Sciences	Online (ScienceDirect)
Current Biology	UCL Natural Sciences	Online (ScienceDirect)
Current Opinion in Neurobiology	UCL Medical Sciences	Online (ScienceDirect)
Journal of Cognitive Neuroscience		Birkbeck (Also online)
Journal of Neurophysiology	UCL Medical Sciences	
Journal of Neuroscience	UCL Medical Sciences	
Nature, Nature Neuroscience	UCL Medical Sciences	Birkbeck (NOT online)
NeuroImage	1994 ONLY (UCL)	OnLine (Academic Press) at Birkbeck.
NeuroReport	UCL Medical Sciences	
Proceedings of the National Academy of Sciences of the United States of America		Birkbeck + automatically online from Birkbeck. Vol 95 number 3 has a set of papers on brain imaging
Proceedings of the Royal Society, B,		Birkbeck (Also online)
*Seminars in the Neurosciences (*or *Seminars in Neuroscience)*		OnLine (Academic Press) at Birkbeck
Stroke	UCL Clinical Sciences (not same bldg as Medical Sciences)	
Trends in Neurosciences	UCL Medical Sciences	Online (ScienceDirect)

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UCL Clinical Sciences Library is in the Rockefeller Building with an entrance on University Street, between Gower St and Tottenham Court Road just South of the old University College Hospital Building.