The implications of recent developments in neuroscience

for research on teaching and learning

by

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1 Introduction

Neuroscience research is increasingly shedding light on our understanding of the structure and function of the brain. Recent advances in technology have enabled neuroscientists to discover more about how the human brain functions than ever before. Techniques such as functional neuroimaging, which measures activity in the brain as humans perform a certain task, and can be performed using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) (see appendix 1), have significantly pushed forward our knowledge of the brain and mind. This report is a selective account of developmental and cognitive neuroscience studies that are informative about learning and might be of relevance to research on teaching and learning.

In this report we use the word 'learning' to encompass all kinds of learning. When we refer to neuroscience, we include all kinds of study of the brain. That is, we include molecular and cellular neuroscience although we will discuss cognitive neuroscience and neuropsychology studies in more detail. By cognition we mean anything that refers to the 'mental domain' which includes emotions. When we refer to cognition or mind, we do not mean to separate them from the brain. We believe that the brain and mind have to be explained together. For posing questions and considering facts we will use a framework that combines environmental, biological, cognitive and behavioural levels of description (Morton and Frith, 1995; see below).

Examples of environmental factors	Examples of Intra-individual factors	Factor affected
Oxygen Nutrition Toxins	Synaptogenesis Synaptic pruning Neuronal connections	BRAIN
Teaching Cultural institutions Social factors	Learning Memory Emotion	MIND
Temporary restrictions e.g. teaching tools	Performance Errors Improvement	BEHAVIOUR

The notation in the diagram uses arrows to indicate causal connections. As can be seen, interactions of external factors with factors that are internal to the individual are all part of the causal explanation. Facts are situated at the behavioural and biological level, theories at the cognitive level. The notation can be used to think about links between biology and behaviour via the inferred cognitive level whose raison d'être is to bridge the gap between them.

1.1 Some preliminary caveats

1.1.1 Are neuroscientists in tune with educators – and vice versa?

Despite the remarkable progress, brain research has not yet found an application in theory or practice of education. And yet, one the major contributions neuroscience is capable of making is illuminating the nature of learning itself. Misconceptions about neuroscience, what neuroscientists are interested in, and how far neuroscience can extend in terms of its application to education, are only too easy to foster. Targeted research questions from educators need to be informed by current aims and methods to know what is feasible. At present, some of the most urgent questions in education may be best answered by methods from experimental psychology. However, with more active discussion between neuroscientists and educators, there is potential for totally new questions to emerge that so far could not be answered and hence were never asked.

There are many obstacles to interdisciplinary collaboration, not least the confusion caused by claims and counterclaims in brain research, which, however, is part and parcel of normal scientific progress. For example, what about the person who has a large brain lesion and no apparent behavioural abnormalities? Does such a case demonstrate that the brain plays an insignificant role in controlling behaviour – we can do without it? However, the contradictions in this example are less real than apparent. Firstly, the case demonstrates the resilience of the brain – just a tiny proportion of brain cells remaining in a certain area enables the person to behave normally. Indeed, neuroscience is crucial for discovering how the small part of the remaining brain enables normal behaviour, how compensation takes place and how adaptation happens. Secondly, the case may not have had extensive psychological assessments. So the person may seem normal, but might in fact perform below normal levels on appropriately sensitive tests.

1.1.2 What about genetics?

The expansion in genetics research over the past few decades has revealed how important genes are in creating the individual. It is likely that genes play a significant role in learning and learning disabilities, and this is the kind of question beginning to be investigated by genetics groups world-wide. Thinking about the educational implications of genetics research will be a hugely important task for the future. The jump from gene to behaviour is much greater than the jump from brain to behaviour. The work to be done in terms of bringing neuroscience into contact with education will facilitate the work that will eventually have to be done to bring insights from genetics to bear on teaching and learning.

1.2 A common vocabulary

If there is to be a new interdisciplinary approach, then what is needed most urgently is a common vocabulary between brain scientists and educationers. The starting point for building a common understanding could be through brain research into areas where educational research has already established a working hypothesis. Cross-disciplinary discussions have value in both process and outcome terms, but it is usually difficult to find common ground from which to launch the interaction, and shared criteria against which to judge its progress. The one-sided approach (can brain research be applied to classroom practice?) can lead to dangers. Therefore taking an interactionist approach (what do educationers need to know that can be informed from brain science?) is more appropriate. To this end, active and empirical collaboration between neuroscientists and educators would be necessary. Such collaboration will benefit from a concerted effort to find common ground. A forum in which neuroscientists and educationers discuss and distinguish their research questions and clarify terminology and methodological differences would be a crucial step. The goal of developing an interdisciplinary 'science of learning' cannot be usefully pursued by one or other of the disciplines taking the lead, but depends on each challenging the other with ideas and hypotheses to test and refine. For this task a mediator in needed.

1.3 The role of cognitive psychology

Interdisciplinary dialogue needs a mediator to prevent one or other discipline dominating. As our framework in section 1 suggests, cognitive psychology is tailor-made for this role. This is not to exclude developmental psychology, social science, education sociology, anthropology and evolutionary psychology, which all could be represented in an interdisciplinary forum. However, we believe that brain science can impact most readily on research on teaching and learning through cognitive psychology. If this is the case then the public's and teachers' conceptions of psychology may need attention. Amongst many teachers and teacher trainers there exists a profound mistrust of psychology, in part based on premature claims about applicability, and disinterest in academic psychology based on a belief that all that is worth knowing about teaching and learning is based on 'common sense' and professional experience.

1.3.1 Challenging common sense views

It might be hazardous to suggest that educational research itself does not or could not provide the best approach to many of the issues from its own resources and sound scientific thinking. Instead of asking how neuroscience can inform educational research, it might be more useful to think about how brain science *challenges* common sense views about teaching and learning. Instead of verifying (in terms of underlying neural activity) what educationers already know, it might be more useful to ask where research on the brain can offer information about learning and cognition that is counter-intuitive to the educationer. Two areas that come to mind, and which will be discussed in more detail later in the report are implicit learning and plasticity in the adult brain. Briefly, research on implicit learning has shown that the brain processes information that is neither attended to nor noticed. This tendency of the brain to do things 'behind one's back' is pervasive and might have repercussions on theories of teaching. Many different areas of neuroscience research have demonstrated that the adult brain is 'plastic' and capable of a remarkable amount of change and relocation of function, depending on how the brain is used. This research suggests that the brain is well set up for life-long learning and adaptation to the environment, and that rehabilitation is possible and worth investment. On the other hand, it suggests that there is no biological necessity to rush and put the start of teaching earlier and earlier. Rather, late starts might be reconsidered as perfectly in time with findings from brain research.

1.4 Tools used to study the brain

There are now many tools that can be used to study the brain. Electrophysiological studies involve recording from single neurons in the brains of animals while the animal is performing a certain task. This technique gives a direct measure of neuronal activity. Recording neuronal activity in humans is difficult, and studies recording from neurons of the human brain (for example during open skull surgery) are rare. But such studies are astounding in the wealth of detail they reveal about memories and actions that can be accessed by a mere 'touch' of a particular nerve cell. There are several other non-invasive ways of evaluating brain activity in humans and these relate to the behaviour of thousands and millions of neurons that are linked together in particular brain regions. Blood flow in the brain can be measured by brain imaging techniques. Blood flows to regions of the brain in which neuronal activity is highest and that require a replenishment of oxygen and glucose. PET and fMRI measure brain activity by detecting changes in blood flow during particular tasks in human subjects¹. EEG and MEG measure electrical and magnetic activity (respectively) arising from tracts of neurons on the surface of the brain. Transcranial Magnetic Stimulation (TMS) can be used to stimulate the neuronal tracts in a circumscribed region of the brain and to create temporary disruptions of function. Again, this can be used to investigate the localisation of function in the human brain. Lesion studies investigate the behavioural consequences of brain damage, and thus give an indication of what functions that area normally subserves. The effects of brain lesions can be evaluated in both animals and humans. Studies can investigate the effects of manipulating the chemical balance in the brain by using drugs that inhibit or excite certain chemical systems. In this report, we mention studies using all of these techniques, but focus mainly on functional imaging and lesion studies in humans.

¹ PET and fMRI are described and compared in appendix 1.

1.5 Layout of report

This report is split into three main sections. The first section covers advances in our understanding of brain factors in early childhood. We consider the relevance of these factors to learning that takes place between the ages of zero and seven years old. There is a serious lack of neuroscientific research on how the brain develops after the early years and before adulthood. Furthermore, longitudinal studies, with the same children being scanned at intervals, would be needed, and these are only just beginning to be done. In particular we know little about how processes such as learning and memory develop throughout adolescence. Recently, neuroscientific research has shed light on how the adult brain learns new material, how learning is affected by emotion, context and individual differences. The nature of learning throughout life will be the focus of the second section of this report. The third part addresses individual differences and learning problems. At the end of each section, we will list a selected number of research questions that could be addressed jointly by educationers and neuroscientists. These questions arose out of extensive discussion with a wide range of experts in the areas this report spans. Some of these questions might feed into research initiatives in a future multidisciplinary research programme on teaching and learning.

2 Early years learning

2.1 Uses and abuses of brain research to justify educational practice

As our framework (section 1) suggests, teaching can act as an independent factor, quite separate from biological and psychological functions. Yet, educators often cite scientific research on brain development when arguing for particular educational practices. For example, there are suggestions that children should begin the study of languages, advanced mathematics, logic, and music as early as possible (Beck, 1996; U.S. Department of Education, 1996). Such arguments claim support from established findings in developmental neurobiology. However, many neuroscientists and cognitive psychologists believe that current questions about educational practice, for instance, questions about the optimal start of formal teaching, cannot yet be answered by neurobiology (Bruer, 1999).

2.2 Brain development: Synaptogenesis and synaptic elimination

An adult human brain has about 100 billion neurons; at birth the brain has slightly fewer neurons. However, during development many changes take place in the brain. Neurons grow, which accounts for some of the change, but the 'wiring', the intricate network of connections between cells called *synapses*, sees the most significant change. Early in postnatal development, the brain begins to form new synapses, so that the synaptic density (the number of synapses per unit volume of brain tissue) greatly exceeds adult levels. This process of synaptic proliferation, called *synaptogenesis*, lasts up to several months, depending on the species of animal. It is followed by a period of synaptic elimination (or pruning) in which frequently used connections are strengthened and infrequently used connections are eliminated.

Most of what we know about how the brain develops comes from animal research. The first demonstration of synaptogenesis was in 1975, when it was found that in the cat visual system the number of synapses per neuron first increases rapidly and then gradually decreases to mature levels (Cragg, 1975). Further research carried out in rhesus monkeys demonstrated that synaptic densities reach maximal levels two to four months after birth, after which time pruning begins (Rakic, 1995). Synaptic densities gradually decline to adult levels at around three years of age, around the time monkeys reach sexual maturity. This experience-dependent process, which occurs over a period of years, reduces the overall synaptic density to adult levels, usually by the time of sexual maturity.

2.2.1 Different areas of the human brain develop at different rates

Brain development varies between species. Furthermore, the time course of synaptogenesis is different for different brain areas and different classes of neurons in the same brain region gain and lose synapses at different rates. Comparatively little research has been carried out on human infants because brain tissue can be studied only at autopsy. The only available data suggest that synaptogenesis in humans follows a different time course from that in animals. In the human visual cortex, there is a rapid increase in the number of synaptic connections at around two or three months of age, which reaches a peak at eight to 10 months. After that there is a steady decline in synaptic density until it stabilises at around age 10 years and remains at this level throughout adult life (Huttenlocher, 1990).

In the human frontal cortex - the brain area responsible for planning, integrating information and decision making - synaptogenesis occurs later and the pruning process takes longer than in the visual cortex². In this area, neuronal development continues throughout adolescence - synaptic densities start to decline around mid-adolescence but do not reach adult levels until about age 18.

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² See appendix 2 for diagram of the human brain.

In summary, while it is true that pre-school children have brains that undergo substantial and rapid changes and are more flexible than adult brains, this increased flexibility remains throughout adolescence at least in some brain areas.

2.2.2 How precisely can synaptogenesis be related to psychological function?

As our 3-level framework suggests, biological functions need to be related to psychological functions and these in turn have to be related to behaviour. When synaptogenesis begins in the visual cortex, at around 2 months of age, human infants start to lose their innate, infantile reflexes. At age 3 months, when synaptogenesis is well under way in the visual cortex, infants can reach for an object while visually fixating on it. At 4 to 5 months, infants' visual capacities increase. At 8 months, infants first show the ability to perform visual memory tasks, such as delayed-response tasks. In these an object is hidden from the infant's view and after a certain time delay the infant is allowed to reach for the object. Children's memory for hidden objects improves steadily between eight and 12 months. Although the emergence of these capacities coincides with synaptogenesis in visual cortex, they are not necessarily *causally* linked (Goldman-Rakic, 1987). Increases in synaptic density are correlated with the initial emergence of some skills and capacities, but these continue to improve after synaptic densities begin to regress to adult levels - humans are clearly able to learn new skills well into adulthood and old age. Thus, synaptogenesis may be necessary for the initial emergence of some abilities, but it cannot account for their continued refinement.

Most of what is known about brain development corresponds to the emergence of or changes in visual, movement and memory functions, which are acquired in almost any environment throughout the world at approximately the same age, well before children enter formal education. How synaptogenesis relates to later educational learning or to the acquisition of knowledge and skills such as reading, writing and numeracy is unknown.

2.3 Development and experience: the concept of critical periods

Researchers have known for the past 30 years that an animal requires certain kinds of environmental stimulation at specific times during its development if the brain's sensory and motor systems are to develop normally. To investigate developmental 'plasticity', Wiesel & Hubel (1965) temporarily covered one eye of new-born kittens. After about three months, the eye was uncovered and the researchers studied the connections between the two eyes and the brain. They found that this early visual deprivation led to a severe deterioration of neuronal connections in the visual areas of the brain and to virtual blindness. This is because the brain had received no stimulation from the deprived eye and it had wired itself to receive information only from the other, open eye. The kittens remained blind in the initially deprived eye. By comparison, the same or longer periods of complete visual deprivation had no such effects on the visual system of adult cats, nor on their ability to use the deprived eye to guide their behaviour when it was subsequently uncovered.

2.3.1 Recovery of function after deprivation

The irreversible consequences of early visual deprivation are often cited as evidence for the importance of early childhood education. However, subsequent research has suggested that some recovery of function is possible depending on the specific period of deprivation and the circumstances following deprivation. The shorter the period of deprivation the more recovery of function is possible. This is enhanced if the animal is trained to use the initially deprived eye after it is uncovered (Chow & Stewart, 1972; Mitchell, 1989).

2.3.2 Sensitive periods

Most neuroscientists now believe that critical periods are not rigid and inflexible. Rather, most interpret them as 'sensitive' periods comprising subtle changes in the brain's ability to be shaped and changed by experiences that occur over a lifetime. For some functions to develop normally, the animal must receive appropriate sensory input from the environment at some stage during development. However, this input tends to be very general in nature, including patterned visual stimuli, the ability to move and manipulate objects, noises, and speech sounds for humans. Such stimuli are available in almost all environments. Higher cognitive capacities, such as language, have several sensitive periods, many of which continue into adulthood, including second language learning.

Brain research findings and common sense in early childhood care go hand in hand: it is important that parents and teachers rapidly identify and, if possible, treat children's sensory problems, such as visual and hearing difficulties, so that they can regain normal function. They also suggest that recovery can occur and that learning can still occur later in life. This may be a different kind of learning and may be facilitated by different kinds of teaching. Whether sensitive periods exist for culturally transmitted knowledge systems, such as those responsible for reading and arithmetic, is currently unknown.

2.4 Sensitive periods in language

2.4.1 Development of language

Language and its components - sounds, vocabulary and grammar - are mastered in early childhood using powerful (possibly innate) learning mechanisms that help children to learn a vast amount by listening to and interacting with adults and siblings. Because children acquire language without any explicit instruction well before they enter formal education, it has been suggested that humans have a predisposition to learn and generalise the rules of language (Pinker, 1994). It is usually claimed that such a predisposition would have to rely on a dedicated neural system. If this was damaged or faulty, then language learning would be impaired.

2.4.2 Learning speech sounds

Learning one's own language initially requires categorising the sounds that make up language. New-born babies are able to distinguish between all speech sounds. Sound organisation is determined by the sounds in a baby's environment in the first 12 months of life - by the end of their first year babies lose the ability to distinguish between sounds to which they are not exposed (Kuhl, 1998). There is evidence that learning the sounds of one's own language begins *in utero* - even new-borns can distinguish between sentences spoken in their parents' native language and sentences in another language, presumably on the basis of prenatal experience with maternal speech (Mehler et al., 1988). Again, it is likely that some dedicated neural mechanisms for processing speech are present in the human brain.

It is well known that Japanese people cannot distinguish between R and L sounds. However, Japanese babies *can* detect the difference between R and L but only before 10-12 months. The Japanese language does not contain distinct R and L sounds so Japanese babies are not exposed to these sounds and lose the ability to distinguish between them. By one year they can no longer detect the difference between R and L. In contrast babies brought up in the USA at the same age become even better at hearing this distinction because they are exposed to these sounds in their language. Similarly, before about 12 months of age babies brought up in the USA can detect the difference between certain sounds common in the Hindi language, which after 12 months they cannot distinguish (Kuhl, 1998). This may be an example of learning within a distinct critical period.

2.4.3 Second language learning

Brain research in this area is based on existing cognitive theories. The consensus at present is that true bilingualism in the sense that neither language has preferential status, does not exist. Instead one language is always chosen as the base (the 'mother tongue') and this is processed in universally similar regions mainly of the left hemisphere. On the other hand, it is possible that brain areas used by representation of a second language differ somewhat from person to person. Bilingual studies show that grammar needs to be learned young, whereas the semantics and vocabulary of a language can be delayed and go on throughout life (Neville & Bavelier, 1998). Teaching programmes of the future might be able to build on exemplary systems in efficient learners. Research still needs to establish whether a sensitive period exists for second language learning, which will indicate optimal learning conditions.

2.5 Enriched Environments and Synaptic Growth

A fundamental characteristic of the brain is that it is organised through a process of interaction between the organism and its environment. In other words, experience drives the developmental process. Neurobiological research has shown that experience affects brain development in at least two ways. Firstly, 'experience-expectant' development involves age-specific neural readiness for information normally available in the (speciestypical) environment, and often involves overproduction and selective elimination of synapses. Secondly, 'experience-dependent' development refers to those aspects of experience that are unique to the individual and may be acquired at a wide range of ages; learning and memory appear to be experience-dependent processes; experience-dependent processes appear to involve active synapse formation and modification in response to experience. Thus learning and memory can be viewed as the most education-relevant aspect of a general adaptive process that updates the organisation of the brain on the basis of the organism's experience.

2.5.1 Rich and poor environments for rats

Neurobiological research involving rats is often cited as evidence for the importance of enriched, stimulating early childhood environments. Early studies showed that laboratory rats raised in an 'enriched' environment, with wheels to spin, ladders to climb on, and other rats to play with, have up to 25% more synapses per neuron in brain areas involved in sensory perception than 'deprived' rats, raised alone in a lab cage with no 'playmates' or toys. Furthermore, the rats raised in complex environments perform learning tasks better than deprived rats. In addition to neural consequences, experience also affects other aspects of brain cellular structure. The capillary system is driven in the extent of its perfusion of the brain by physical activity and exercise, whether or not learning is involved.

In subsequent studies, Greenough and his colleagues showed that the brains of adult rats form new synapses in response to new experiences and toys (Greenough et al., 1987). So, research on rats suggests that experience can also shape the *adult* brain. Therefore, unlike critical-period phenomena, the ability to create synapses in response to new experiences seems to persist throughout life. Although the effects of complex environments occur more readily in younger animals, they endure throughout life.

In these experiments, the 'enriched' environment in the laboratory was actually more like the normal environment of a rat in the wild. So, rather than showing that extra stimulation leads to an increase in synaptic connections, it might be more accurate to say that a more 'normal' environment leads to more synaptic connections than a deprived environment. In terms of human babies, the research does not imply that parents should provide special 'enriching' experiences to children beyond those that they experience in everyday life. It is unlikely that children brought up in any 'normal' species-specific environment could be deprived of sensory input. This implies that there is a threshold of environmental richness below which a deprived environment could harm a baby's brain.

2.5.2 Adopted babies from deprived orphanages

Recent studies have demonstrated that Romanian babies reared in severely deprived conditions, with poor nutrition, ill-health, little sensory or social stimulation, are more likely to have delayed development of skills such as walking and talking, and impaired social, emotional and cognitive development (O'Connor et al., 1999). However, the recovery of these functions and the resilience of the deprived children in these studies was striking. So although it is clearly damaging to deprive a baby and length of deprivation relates to extent of adverse effects, this research does suggest that even very deprived babies can recover to a large extent if given remedial stimulation and care.

2.6 The brain basis of cognitive development of pre-school children

For a brief review of the developmental psychology research on sensory, cognitive, emotional and educational development, a recent report on Early Years Learning may be consulted (see www.parliament.uk/post/home.htm or contact S.-J.B. for copy of report). Currently, studies of the brain basis of cognitive development are lacking, mainly because of ethical and technical considerations of scanning children's brains. The recent advances in fMRI technology, for example the ability to scan the brain in less time at lower magnetic field strengths, mean that children can be scanned. We expect studies on the development of sensory capacities, cognition and emotion in the brain will be carried out in the near future. Existing psychological and educational research will guide such studies.

2.7 Mapping the brain in childhood

A group of researchers recently used MRI to obtain brain scans from children of ages 3 to 15 years. The researchers scanned the children's brains at intervals ranging from two weeks to four years, which allowed them to follow changes in their brains and construct 'growth maps' of the children's brain development (Thompson et al, 2000). Thompson and colleagues found that the children's brains develop in a specific pattern, with a spurt of growth that starts in the front of the brain from ages 3 to 6. Between the ages 6 and 13, the researchers found that the pattern of rapid growth moves from the front to the back, toward the areas of the brain that are specialised for language skills. The researchers found that there is a sharp cut-off in the growth of the language areas of the brain after age 13. Another finding from the imaging study was that from age 13 to 15 about 50% of the brain tissue that controls motor skills are pruned away.

These findings will need to be replicated and related to changes in learning. They may have implications for teaching. For instance, language learning and activities that require motor skills, such as playing an instrument or a sport, may have a critical period in which it is particularly easy to acquire these skills.

Thus, brain imaging could in theory give a biological underpinning to concepts of critical/sensitive periods. In particular, it may be possible that research using diffusion tensor imaging will tell us about the development of myelination, connectivity, etc. and that this may relate to optimal windows for learning performance. However, if this type of brain research is to have an impact on education, it will need to be designed and carried out in active collaboration with educational researchers.

2.8 Summary

The young brain is very flexible, sensitive and plastic, has predispositions for learning in certain domains (e.g. language, social interaction), and is influenced by events in the outside world. Sensory areas of the brain develop optimally when the environment contains a variety of sensory stimuli - visual stimuli, textures and sounds. Although babies' brains undergo a large amount of change in the first few years of life, parts of the human brain continue to develop well into adolescence and beyond. It is therefore difficult to make direct links from the neuroscientific evidence to specific early childhood environments, experiences and early child-care policies. There is no suggestion from the experiments that 'the richer the environment the better'. Instead these experiments suggest that each species requires a certain amount of environmental stimulation. There appears to be a threshold so that a very low level of environmental stimulation will be damaging.

Developmental psychology research has demonstrated that children's main learning achievements before formal schooling starts come naturally in the course of activities such as play, exploration, everyday talk and social interaction with peers and siblings. Already well researched and integrated into policy development is the area of early years learning based on a coherent theoretical and practical programme covering care and education. In the future, inputs from brain, cognitive and social sciences may enhance this programme.

2.9 Seven research questions relating to childhood learning

In theory, neuroscience should be able to tell us what is good and bad for young brains. Is 'hot-housing' useful or damaging?

Research on the timecourse of brain development and critical periods has implications for the optimal times for introducing material in the school curriculum. Is it better to concentrate in the early years on music and language, and only later on more abstract things like maths concepts/metalinguistic awareness, for instance?

It is important to make the distinction between *critical period* as the duration and quality of the stimulus needed for imprinting, and *sensitive period* as the 'window of opportunity' for the imprinting to take place. Is it important to catch the window of opportunity? How can it be established that the window is open and closed?

Are the 'windows' for learning specific things due to unalterable physiological processes or can they be extended by teaching? Can neurological changes underlying learning be speeded up by teaching?

If specific aspects of neurological development and learning can be speeded up - does it have a deleterious effect? Does encouraging development in one brain area have a positive effect on whole brain development?

What are the limits of plasticity? Does the brain rewire so that certain taught abilities take over to the detriment of other abilities (e.g. social and emotional development)? For instance, if formal teaching of reading, writing and maths occurs earlier, is there rewiring that detracts from other types of learning?

It is not clear what the effect on brain development might be of chronic emotional disturbances. If there were long-term neurological changes they would certainly have consequences in the classroom. Studies on, for example, the children of mothers who suffered post-natal depression, could give an indication of the educational and psychological outcomes of early maternal incapacity. This would indicate whether such children would benefit from remedial teaching early on.

3 Life long learning

Teaching and learning applies to all ages and includes cultural knowledge in different domains as well as emotional, social, communication and motor skills. Neuroscientific ideas and findings are of potential relevance in all these domains, but the achievements of brain research in these areas are still sparse.

3.1 Plasticity in the adult brain

Changes in the brain generally occur as a function of use of the brain. In other words the brain continuously adapts to its environment. Research on plasticity in the adult brain has benefited from brain imaging techniques such as fMRI and PET. However, studies on recovery from brain damage are also relevant.

3.1.1 Learning to be a London taxi driver

The hippocampus is a structure deep inside the brain that is essential for spatial navigation and spatial memory. Research on rats has demonstrated that so-called 'place cells' in the hippocampus fire at specific locations, suggesting that the hippocampus creates and stores maps of space (see Burgess & O'Keefe, 1996). Recent functional imaging studies have confirmed that the hippocampus stores spatial memories in humans. In one recent experiment, subjects were scanned while navigating round a virtual town. Prior to the experiment subjects had learned the layout of town. In the scanner subjects had to locate objects in virtual town by remembering where they were located. The researchers found that hippocampus activity increased with accuracy of navigation (Maguire et al., 1996).

The hippocampus is known to remain plastic well into adult life. The hippocampus in birds changes in size, especially in birds who parasitise other birds' nests, so have to know and remember where things are. Hippocampus size is related to how much parasitising bird does. Thus it seems that the hippocampus can change in size according to how much the bird uses it to remember where nests are located.

Recently, researchers have scanned the brains of people who are expert navigators. London taxi drivers, whose spatial memory of the layout of London has to be extremely advanced, were scanned while they reported a complex route they would take to get from one area of London to another. The area that was activated by this navigation task was the hippocampus (Maguire et al., 1997). In addition, the researchers compared the structure of the taxi drives' brains with that of non-taxi drivers. There were significant differences between the hippocampus size of the London taxi drivers and the non-taxi drivers. The posterior hippocampus was larger in taxi drivers. Furthermore, its size was related to the time the person had been driving taxis, suggesting that its size depends on how much a person uses their spatial memory (Maguire et al., 2000). However there was also a decrease in anterior hippocampus size, which also correlated with length of driving taxis. This suggests that there might be costs when one part of the brain develops and grows through experience.

3.1.2 Learning to be a musician

Some research has suggested that doing something well might require less, not more brain cells. However, this was contradicted by a study of skilled musicians. The part of the brain that processes sound (the auditory cortex) in highly skilled musicians was enlarged by about 25% compared with control subjects who had never played an instrument. Enlargement was correlated with the age at which musicians began to practice. This work indicates that the reorganisation of the auditory cortex is usedependent (Pantev et al., 1998).

Pascual-Leone and colleagues used TMS to study the role of plastic changes of the human motor system in the acquisition of new fine motor skills. Non-piano playing adults learned a five-finger exercise on the piano for two hours a day over the course of five days. The area of the brain responsible for finger movements enlarged and became more active in these subjects compared with control subjects who had not learned the piano exercise. This study demonstrates that in just five days the adult brain can adapt according to how it is used (Pascual-Leone et al., 1995).

3.1.3 *Just how plastic is the brain?*

The adult brain remains flexible and capable of a remarkable amount of change and relocation of function, depending on how it is used. It is important to point out that this type of plasticity is a baseline state – it is occurring all the time in the brain, whenever a new memory is laid down or a new face is seen.

How the extent of flexibility at different ages and in different contexts be investigated further? TMS is a technique that is well suited to this pursuit. TMS can be used to temporarily disrupt attention and learning in adult volunteers. Learning could be studied under experimentally controlled and reversible adverse conditions and different teaching methods could be compared.

3.2 Types of learning

Perhaps the most important implication from neuroscience for education is that it may be possible to identify and modify the neural structures that underlie different learning processes. It is unlikely that there is one single type of learning for everything. In terms of brain structures involved, learning maths differs from learning to read, which differs from learning to play the piano.

From research on brain damaged patients and functional imaging we know that there are multiple memory systems in the brain. Episodic memories (memories of episodes) are stored in different brain areas from semantic memories (memories of facts). Thus, people with profound amnesia cannot remember episodes (what has happened to them a few minutes ago) but can retain their semantic knowledge and can still talk. Different regions of the prefrontal cortex are used in memory encoding (left prefrontal cortex) and memory retrieval (right prefrontal cortex) (Fletcher et al., 1988a; 1998b). It has been shown by psychologists and neuroscientists that learning can be implicit or explicit, and these different types of learning take place in different brain areas. Implicit memory is typically seen when we experience a vague sense of familiarity. Moreover, objects identified as familiar are also preferred. We will briefly highlight some of this research, and its possible implications for education. In the future it should be possible to establish a systematic programme of research in which different types of learning at different ages and the effects of different types of teaching are made visible in the brain.

3.2.1 The power of implicit learning

Many years of research on implicit learning have shown that people are able to learn information in the absence of awareness. People can learn complex rules by being exposed to sequences that adhere to the rules, without having any explicit notion of the rules or having learned them (Berns et al., 1997). Berns et al (1997) mapped brain regions responsive to novelty without awareness using PET. Subjects performed a simple reaction-time task in which all stimuli were equally likely but, unknown to them, they actually followed a complex sequence. Subjects' behavioural performance indicated that they learned the sequences even though they were unaware of the existence of any order. Once the subjects were trained, a subtle and unperceived change in the nature of the sequence resulted in increased blood flow in a network comprising the left premotor area, left anterior cingulate, and right ventral striatum. Blood flow decreases were observed in the right dorsolateral prefrontal and parietal areas. The time course of these changes suggests that the ventral striatum is responsive to novel information, and the right prefrontal area is associated with the maintenance of contextual information, and both processes can occur without awareness.

3.2.2 Acquiring knowledge

What does implicit/explicit mean in terms of knowledge acquisition? Does any index of knowledge mean that that knowledge is explicit? It is clear that children know tacitly something about things before they can talk about them. In adults too some knowledge appears to be implicit. People are organising and categorising the world before they are able to introspect about it. Some categories may be acquired more easily than others, and some individuals may thrive more on explicit learning than others. Teaching often involves making procedural knowledge declarative. How do teachers know when to make rules explicit? Does a reciprocal dialectic between implicit learning and explicit teaching aid learning? Can explicit teaching replace missing implicit learning? Is a degree of prior implicit learning always helpful?

3.2.3 Skills learning

Learning a skill, that is procedural learning, differs from the acquisition of declarative knowledge (Bechara et al, 1995). It is well known that amnesic patients who have hippocampal damage have severely impaired declarative memory – they are unable to learn and retain new facts. However, they are able to learn new skills and they retain skills they acquired before their brain damage. For example, a severely amnesic patient who used to be a pianist has no memory for events that happened more than five minutes earlier, but is nonetheless able to play the piano as perfectly as he could before damage to his hippocampus occurred. Amnesic patients are also able to acquire new skills, despite not explicitly remembering being taught the skill. It is proposed that such patients' basal ganglia, which are intact, are capable of procedural learning and execution and maintaining previously acquired skills. Patients with Parkinson's disease, whose basal ganglia function abnormally, have good memory for episodes and facts, but they are unable to learn new skills. In other words, there seems to be a dissociation between declarative and procedural learning, confirmed by recent functional imaging studies (Gabrieli et al., 1998). For purposes of teaching it might be important to know that learning facts, such as mathematical equations and historical dates, relies on different brain regions than learning to do sport or play a musical instrument. A possible research question is whether the two kinds of learning can occur in parallel rather than each having to be taught separately. For instance, can teaching usefully combine counting and skipping?

3.2.4 Doing two things at once

People often have to carry out more than one task at a time and this makes demands on working memory, typically requiring the switching between information appropriate for one or other task. Patients with frontal lesions tend to be disproportionately impaired at dual versus single task performance (McDowell et al., 1997) suggesting a frontal role in these aspects of working memory. D'Esposito et al. (1995) compared brain activity when participants performed two tasks concurrently with activity when each task was performed alone. Neither of the two tasks, a spatial rotation task and a semantic judgement task, produced significant activation of dorsolateral prefrontal cortex when performed alone; only when they were combined was significant activation of this area observed. However, this result has not been replicated by all dual-task studies (e.g. Klingberg, 1998). Since the frontal lobes are later maturing structures of the brain, it may be possible to adjust task demands during teaching according to the neurological maturity during adolescence.

3.3 Natural/artificial learning

Distinctions have been made between skills such as walking, talking and emotional understanding, which develop naturally in almost all children and skills such as reading, writing and maths, which are cultural accomplishments and require teaching. It has been argued that failure to recognise the differences between these conceptually and developmentally distinct domains of learning and teaching has led to the development of flawed early years learning policy and arrangements (Ball, 1994). Whether this is an important and useful distinction requires investigation. One question is whether teaching is actually desirable for naturally programmed mental functions that develop with a 'good enough' amount of environmental stimulation. More may not be better. In contrast culturally important knowledge which needs to be taught might require that prior development of skills whose learning is pre-programmed. This is an empirical question.

3.4 Methods of learning

3.4.1 Rote learning

Does rote-learning have its own brain basis? Studies on memory have shown that a phonological code and rehearsal is important to memorise and store verbal information. Two functional imaging studies investigating the effect of rehearsing items to be recalled on brain activity implicate left inferior parietal cortex (BA 40) in storage of material, and left inferior frontal cortex (BA 44) in rehearsal (Awh et al., 1996; Paulesu et al., 1993). A common suggestion (Jonides et al., 1996) is that the areas activated during maintenance of verbal material, (left premotor cortex, supplementary motor cortex and right cerebellum, left inferior frontal cortex), comprise a network involved in speech production. This is consistent with the proposal that rehearsal of rote learned stimuli uses articulatory codes (Baddeley,1986).

The role of rote learning in education has long been controversial. While rote learning does not teach how to relate disparate pieces of information, it is clearly useful, e.g., for learning new vocabularies. Knowing one's times-tables off-by-heart is useful for dealing with everyday arithmetical problems, even if it does not make one any better at understanding mathematics. Individuals who lack the neuronal circuitry necessary to memorise detailed information may have a difficult time learning poetry or prose by heart. However, if sufficiently motivated, they will be able to learn, perhaps by alternative routes using other types of learning. Brain imaging can reveal if this is the case. It is likely that individual differences in rote memory capacity exist. However, the consequences for other cognitive functions are not known.

3.4.2 Imitation

What is the role of observation, imitation, imagination and modelling in human learning and development? Imitation – observing how others do things, and then trying to do the same thing oneself – is a well-established learning strategy. Human babies seem to be born with the ability and the disposition to imitate the communicative gestures of those around them. They will copy facial expressions when only a few days old, and by ten weeks are mimicking such basic emotions as happiness and anger (see Harris 1989). This early imitation is likely to have a different brain basis from later imitation.

There is evidence that observing someone making an action activates a component of the brain's motor system without inducing an overt movement. Neurons in the premotor cortex (an area involved in movement control) of monkeys 'fire' when the monkey observes someone grasping an object, while the monkey makes no movements itself ('mirror neurons'; Rizzolatti et al., 1990). There are cells that respond both to a specific grasping movement of the hand, and to the sight of a goal-directed action, in the absence of any overt movement. Neuroimaging techniques have shown the same kinds of correspondences in human beings. When human subjects observe someone making a movement, without making any movements themselves, a component of their brain's motor system is activated (Iacoboni et al., 1999). Imitation might play a role in understanding other people's intentions and desires from their motor actions. Human beings naturally imitate other people's gestures, facial expressions and actions, and imitation seems to play an important role in learning about other people (Meltzoff, 1999). Iacoboni et al (1999) proposed that the motor plans necessary for imitating an action may be based on a mechanism that directly matches the observed action onto an internal motor representation of that action.

What is the role of imitation in formal school-based learning? How is it distinct from orienting one's behaviour relative to a role model? Is implicit imitation of peers different from imitation of the behaviour of adults? Social psychology studies suggest that there are massive effects of peer groups. A deeper understanding of imitation, its role in learning and its brain basis might enable us to understand how it can be exploited for beneficial learning, or controlled in the case where it might be harmful.

As with all neuroscientific studies, it is important to emphasise the difference between the tasks employed to investigate imitation in the brain and the type of imitation relevant to education. In education, imitating attitudes, mentalities and emotions may be more important than imitating simple movements. However brain imaging studies on imitation so far have only involved scanning subjects' brains while they imitate extremely simple movements, such as finger tapping. The need for interdisciplinary studies, involving social psychologists, anthropologists and educationers, cannot be emphasised enough to tease out paradigms for experimentation that might be relevant in the classroom.

3.4.3 Visual imagery

In many ways the opposite of imitation, visual mental imagery, involves 'seeing with the mind's eye' regardless of what is seen in the world. For example, when calculating how many windows there are in one's living room, most people report that they visualise the room, scan this image, and count the windows. Of course, this is only an introspective report and does not reveal what process is actually used by the brain. Over the past 25 years a large amount has been learned about the nature and functions of imagery, and the neural mechanisms underlying it are now beginning to be understood. Four empirical findings are particularly relevant to our understanding of the relation between imagery and emotion. First, neuroimaging studies have revealed that at least two-thirds of the same brain areas are activated during visual imagery and visual perception, even when the stimuli and task are very different (Mellet et al., 2000). Mental images of objects and events can engage much of the same processing that occurs during the corresponding perceptual experience. Second, people differ dramatically in their abilities to form and use imagery. Moreover, these differences are specific to individual aspects of imagery. For example, the ability to imagine objects rotating is not necessarily related to the ability to scan over objects in images or to the ability to form vivid images. Third, visualising aversive stimuli (such as burned bodies) causes skin conductance changes and changes in heart-rate. Thus, mental images affect the body. Fourth, visualising aversive stimuli activates some brain areas more than does visualising neutral stimuli (such as a lamp or chair). Among the areas activated is the anterior insula, which is known to be involved in registering the state of autonomic activity in the body (Kosslyn et al., 1996). Thus, visualising aversive events not only affects the body, but these events appear to be registered by the brain.

These findings confirm the long-held belief that people can alter their emotional state by forming specific mental images. Some researchers have claimed that such procedures can affect a host of bodily functions, including those of the endocrine and immune systems. However, the efficacy of imagery in modulating emotional state depends in part on a person's abilities to form and use imagery. It is not yet clear whether practice or training can alter the efficacy of imagery in such self-regulation. For example imagery (of, say, winning or losing) can increase or decrease testosterone. Increased levels of testosterone aids spatial navigation (Silverman et al., 1999). Thus, it might be possible to aid spatial navigation by imagery. Emotional imagery could be used to modulate stress, which is known to affect learning.

3.4.4 Mental exercise

Experimental psychology has long established the value in mental exercise for (motor) learning. Imagining making movements in the absence of any overt behaviour is possible, and this mental activity can have detectable consequences. First, mental practice of various motor tasks can lead to a significant improvement in subsequent performance (see Feltz and Landers, 1983 for review). Mental training affects various outcomes of motor performance such as muscular strength (Yue and Cole, 1992), movement speed (Pascual-Leone et al., 1995) and temporal consistency (Vogt, 1995). Second, prolonged performance of tasks in the imagination can lead to significant physiological changes. Subjects who performed or mentally simulated leg exercise had increased heart rates and respiration rates in both conditions (Decety et al., 1991). Third, changes in brain activity associated with movements made in the imagination can readily be detected using brain imaging techniques. Decety et al. (1994) asked subjects to imagine grasping 3D objects presented to them. Stephan et al. (1995) compared execution of a sequence of joystick movements with imagining making such a sequence. These studies showed that the brain regions activated during motor imagery are a subset of those activated during motor execution.

Jeannerod (1994) has argued that motor imagery is closely related to motor preparation. Preparing to make a movement and holding it in readiness while waiting for a signal to release the movement engages the same processes as those involved in imagining making that movement. Functional neuroimaging studies of motor preparation and motor imagery highlight activity in anterior cingulate cortex (ACC), anterior supplementary motor cortex (SMA), inferior lateral premotor cortex and inferior parietal lobe (Decety *et al.*, 1994; Stephan *et al.*, 1995). Since these areas are engaged by motor preparation and motor imagery, it is proposed that they are involved with representations of intended and predicted movements.

3.5 Learning through therapy

Cognitive behaviour therapy (CBT), which is generally successful at treating problems such as phobias and obsessions, is derived from learning studies in animals. When behavioural therapy is used to treat phobias it is believed that the phobic had an initial negative experience with the phobic objects, and that the avoidance of that object helps to maintain the phobia. From research on aversive conditioning in animals it is known that avoiding the aversive object maintains the aversion while encountering it (as non-aversive) reduces the aversion. Thus behavioural therapies often involve the phobic having to confront the phobic object and re-learn that it is not harmful.

Cognitive therapy (CT) re-trains people in the way they think about a particular issue. Parallels might be found between CT techniques in teaching new ways of thinking in depressives or phobics and techniques in teaching mathematics, language or life skills. Brain imaging studies are beginning to be done to show the brain changes that accompany recovery during rehabilitation therapy. Using functional neuroimaging Mayberg et al. (2000) found that recovery from depression is associated with a decrease in orbitofrontal cortex activity. Similar studies could be carried out during different phases of learning and teaching in normal development.

3.6 Context of learning

The individual person and individual brain cannot be studied in isolation. Educators and psychologists have a long and distinguished track record in illuminating this question. However, neuroscience can also offer insights about how context affects learning. Context includes biological as well as social factors, and factors that are intrinsic to the task being learned.

3.6.1 An effect of culture on the brain

Paulesu et al. (2000) demonstrated that skilled readers in Italian and skilled readers in English have different patterns of brain activation during reading. Both reader groups activated the same brain system in the left hemisphere, with three main components: inferior basal temporal areas, anterior regions of the frontal gyrus, and superior temporal gyrus. This latter region, associated with sound-to-letter-decoding, was more strongly activated by Italian readers, while English readers activated more strongly the former regions, associated with word meaning. Paulesu et al. attributed this difference to differences in the consistency and transparency of the orthography, which is high in Italian, low in English. The theoretical claim was that English relies more heavily on semantics because of the existence of irregular words, which need to be identified before they can be pronounced. Although, in the experiment reported, no irregular words were presented, the English readers engaged more areas associated with word identity rather than sound-letter decoding. The conclusion is that culture, as manifested by the acquisition of orthographic systems, permanently affects brain physiology. Thus, subtly different brains are built in different cultures, and different teaching methods may be optimal in different places.

3.6.2 Drugs and learning

Neurobiological and neuropharmacological factors influence learning. There are drugs that enhance memory directly, drugs that treat behavioural disorders which influence learning, and stimulants such as caffeine, alcohol, smoking/nicotine, glucose, etc. which may facilitate or impair learning. Neuropharmacological tools such as Ritalin and 'smart' drugs might enable the brain to become more responsive in the learning environment. One day we might be able to take a drug to improve our learning and memory. Alternatively, different types of teaching styles might have the same effects as taking a drug in terms of the chemical systems in the brain.

3.6.3 Memory consolidation and sleep

It has long been believed that sleep is important for learning. There is evidence that during certain components of sleep, certain regions of the brain are active, and this activity might represent the consolidation of events that occurred during the previous day. Rapid eye movement (REM) sleep, in which dreaming occurs, is now known to be important for acquisition of novel skills. It has been proposed that material recently acquired through experience may be consolidated and stored during REM sleep or that forgetting of unnecessary material occurs in this state (Crick & Mitchison, 1983). Behavioural research in rats shows that periods of learning are associated with increased REM sleep, whereas REM sleep deprivation impairs memory for previously learned material (Hennevin et al., 1995).

The hippocampus, a structure that is important for episodic memory, is thought to be important in the consolidation process during REM sleep in animals (Poe et al., 2000) and humans (Maquet et al., 2000). Maquet et al (2000) showed that subjects' performance on a simple reaction time (SRT) task improves after practice and overnight. They used PET to compare brain activity in a group of subjects who had and those who had not learned the SRT task prior to sleep. They found that in REM sleep-specific areas of the brain were more active in the trained than in the non-trained subjects. These brain areas are a subset of those used to learn such a task during wakefulness. These results support the notion that an important part of learning continues well after teaching, and without conscious awareness.

3.6.4 Emotion and memory

It is known that negative emotional events are better remembered than non-emotional events. Both animal and human investigations have shown that the amygdala, an important part of the brain's limbic system, is involved with the formation of enhanced long-term memory associated with events arousing fear and sadness. For example, people were scanned while viewing and remembering emotionally arousing films (Cahill et al., 1996). Activity in the amygdala while viewing the emotional films was highly correlated with the number of emotional (but not the number of neutral) films recalled. This suggests that the amygdala is crucial for memory of emotionally salient events, which are better recalled than neutral events. The same group of researchers has shown that the amygdala interacts with the hippocampus, part of the brain that stores non-emotional memories. It seems that the amygdala is particularly involved in fear conditioning, which may be a type of one-trial learning. In contrast the hippocampus is responsible for remembering neutral events.

3.6.5 Reward and risk

In animals, ascending dopaminergic systems, including the amygdala, basal ganglia and prefrontal cortex, have been shown to be critically involved in responses to various intrinsically pleasurable stimuli, including food and drugs of abuse. Reward learning in humans has been studied less extensively. However, functional imaging studies using infusions of nicotine (Stein et al., 1998) or cocaine (Breiter et al., 1997) have associated the rewarding effects of these drugs with neural responses in regions including nucleus accumbens, brainstem, amygdala, and prefrontal cortices. Other functional imaging studies have associated financial reward with activation of ventral striatum, midbrain, thalamic, and prefrontal regions (Thut et al., 1997).

In humans, the nonspecific excitement engendered by risk-taking behaviour may be as important in maintaining these behaviours as the potential rewards, but it has not been clearly established how these nonspecific effects are expressed in the human brain. Neuropsychological studies suggest that ventral prefrontal regions may be an important interface between cognitive and emotional components of risk-taking behaviours (Damasio, 1994). Furthermore, patients with lesions to ventromedial prefrontal regions show pronounced impairments on gambling tasks and fail to show normal task-related autonomic changes (Bechara et al., 1996).

Elliott et al (2000) used fMRI to measure neural responses to rewards while subjects performed a simple gambling task. Correct and incorrect responses were associated with financial rewards and penalties, and the researchers assessed the relationship between the level of accumulated gain or loss and brain activity. The results demonstrated neural sensitivity of midbrain and ventral striatal regions to financial rewards and hippocampal sensitivity to financial penalties. Furthermore, the authors showed that neural responses in globus pallidus, thalamus, and subgenual cingulate were specific to high reward levels occurring in the context of increasing reward. Responses to both reward level in the context of increasing reward and penalty level in the context of increasing penalty were seen in caudate, insula, and ventral prefrontal cortex. These results demonstrate dissociable neural responses to rewards and penalties that are dependent on the psychological context in which they are experienced.

The basal ganglia are also activated by various aspects of reinforcement, including reward. It has been suggested that through their direct anatomical connections with the limbic system (including the amygdala), the basal ganglia are responsible for linking the reward-related information processed in limbic structures with behavioural responses (Everitt et al., 1992).

Thus the brain has a powerful, widely distributed system in which behaviour is initiated and modulated according to the reward. For research on learning and teaching information on factors that modulate this system would be highly relevant.

3.6.6 Reward and punishment

It is known that better learning occurs under a certain level of stress. Learning can be very fast for a noxious stimulus. This type of learning is important for survival. The brain systems that respond to punishment have been mainly evaluated in animals.

Schoenbaum et al (1998) have reported that in rodents, which were learning an olfactory discrimination task, neurons in both amygdala and orbitofrontal cortex (OFC) are involved in associative learning of positive and negative outcomes. Patients with OFC damage do not respond in gambling tasks to differential levels of reward and punishment, unlike normal volunteers (Damasio, 1994). Damasio has suggested that the OFC might be responsible for monitoring somatic markers related to reward and punishment encoded by the amygdala. Processing information that conveys the amount of success or failure in an ongoing activity is crucial to adjust behaviour and achieve a goal. Skin conductance normally increases in anticipation of reward or punishment. This response seems to depend on the amygdala being intact. Bechara et al (1999) have shown that people with damage to their amygdala do not respond in the normal way to reward and punishment (winning or losing money) in terms of their behavioural response (performing optimally on a gambling task), or their physiological response, for example, skin conductance.

Zalla et al (2000) studied brain responses to reward and punishment when the outcome of a task depended on the subjects' performance. Subjects were instructed to detect a stimulus that appeared on a screen as fast as they could. After detecting the target they were told whether they were faster ('WIN') or slower ('LOSE') than their (non-existent) 'opponent'. The experimenters manipulated the percentage of trials in which subjects obtained WIN and LOSE outcomes, and found that activity in the left amygdala was related to the frequency of reward while activity in the right amygdala was related to the frequency of punishment. As previously mentioned, the amygdala is strongly connected with areas of the brain responsible for learning, for example the hippocampus. Reward and punishment have a clear effect on learning, presumably via these connections. It is difficult at present to relate this research to research in an educational context, but the factors touched on are highly important to learning and cannot be ignored, including those that relate to stress and lack of reward/punishment.

3.7 Seven research questions related to lifelong learning

Does evidence from brain changes during learning suggest age-related teaching in which methods of teaching are changed according to the age of the learner, in nursery, throughout school and beyond into adulthood?

What are the costs to the brain of acquiring a new skill or improving an old skill? Does enhancement of certain brain regions compromise other regions? Does getting better at one skill mean taking away space from another skill? What brain systems are involved in transfer of learning and can they be boosted?

Are there verbal and spatial/pictorial learning styles and how do they relate to brain differences? What is the effect of verbalisation on tasks that can be done non-verbally, and what is the effect of visualisation on verbal tasks?

Some things are easy to learn because of a natural predisposition for learning built up through evolution. For example, phobias of snakes and spiders are easier to acquire than phobias of harmless objects (Ohman et al., 1975), which are not 'pre-wired' into the brain circuits by evolution. It is possible to override such 'prepared' learning, for example by behavioural therapy. How do these types of learning differ?

Is it necessary to learn implicitly first, then explicitly? Can explicit learning happen when intuitive grasp is lacking? What does it mean to teach so that implicit learning is facilitated?

What is the difference between imitation of actions performed by peers and those performed by remote role models? Does brain activation differ?

There are many unanswered questions about the importance of sleep for learning in adults and children. A programme of research on 'sleep as a teacher' could be set up to consider effects such as timing, delay and interference between different tasks. Are time of day learning effects related to sleep patterns?

4 Individual differences and learning difficulties

Processes that are involved in normal teaching and learning, can be elucidated by studying what happens when the system is challenged. The three-level framework (section 1) was originally designed to explain the effects of neurobiological abnormalities on the development of cognition and on subsequent impairments in behaviour. However, explanations of why something goes wrong, entail hypotheses about why something goes right. Thus, the framework is well suited to consider the effects of teaching and learning given different types and degrees of challenge. Biologically caused abnormalities that lead to mild or severe developmental disorders (e.g. dyslexia, dyscalculia, ADHD, autism spectrum disorders) occur in a sizeable proportion of individuals, conservatively estimated at 5%. The differences in brain and mental functions that are consequences of these disorders can be considered in the same way as individual differences in ability and personality in the normal population.

4.1 Individual differences in learning and the brain

Neuroscience can help identify individual differences in strategies and aptitudes in problem solving as well as specific deficits in individuals. An ultimate goal could be to devise educational/psychological/psychophysical tests for such conditions.

Little is known about individual differences in the brain. Brain research tends to look for similarities, not differences, between brains. Consequently, brain research on individual differences has hardly been done. In the future, such knowledge may help us to access each child's personality, ability and learning needs. This may then lead to a more personalised, adequate and efficient way of teaching and learning.

We do not know how great the individual differences are in brain structure and function, or in brain development at various ages or how they are influenced by factors outside the individual. Differences in the course and timing of brain development are important especially during those periods when children are being selected (for further education etc.) on the basis of exams. Currently the major selection procedures (for secondary education/ A levels/ University) take place when children's brains are undergoing more changes than at any later time. These selections probably mould a child's future more than anything else; yet, unfairly, some children's brains will be more mature than others when they take place. If great individual differences exist, then this could fuel research into how educational selection could be 'staggered'. For instance, it might be possible to ensure that each child can make crucial decisions (and takes important exams) when they are ready rather than when they reach a certain age.

4.1.1 Gender differences

Research on gender differences in the brain has demonstrated clear differences between male and female brains. However, many of the results are equivocal and there is little agreement as to what the differences mean. Even less is known about the timing of the development of any neurological gender differences. One of the most consistent findings is that male brains are more voluminous in the anterior temporal lobes, including the amygdala and anterior hippocampus, and this has recently been replicated in a large study investigating morphological differences between the sexes (Good et al., 2000). Good and colleagues also found that the anterior cingulate cortex is more voluminous in women. Each of these regions has strong involvement in emotional sensitivity of social and non-social content. However, the implications of these findings are unknown.

In terms of functional differences between male and female brains, a fairly consistent finding is that the left planum temporale (a language area) is more highly activated during language tasks in men than in women. One still controversial possibility is that men are more lateralised (or asymmetrical) than women, who use both hemispheres during language tasks (Shaywitz et al., 1995). This might correspond to reported sex differences in verbal tasks: several researchers have found that women outperform men on verbal tasks. In contrast, men seem to be better at spatial tasks than women. These sex differences have been linked with hormonal differences. Hampson investigated spatial abilities in women during their monthly hormonal cycles (Hampson, 1990; 1995). She found that women's spatial ability was inversely related to the level of oestrogen. Similarly, Saldanha et al. (1999) has found that testosterone improves spatial memory and increases hippocampus size in male and female birds.

Research on cognitive and brain differences between the sexes might have repercussions in the teaching of skills that involve spatial or verbal skills, for example maths and languages, respectively. Maths involves spatial manipulation, which might explain why boys often outperform girls on maths, and girls do better at languages than boys in exams (Gallagher et al., 2000). However, whether these differences are biological or socially caused is unknown. Knowledge of gender differences in cognition could inform education research into questions such as should girls be taught some things at a different time from boys?

4.2 Recovery after brain injury

One important task for teaching is enhancing learning in people who have lost skills because they have suffered brain injury. Major difficulties are the very challenging behaviours that can arise as a result of the injury, where the usual behaviour modification techniques fail. However, the problems may be similar with youngsters, whose challenging behaviours are difficult to ascribe either to the brain injury or to going through a difficult time (e.g. being a teenager). The link between clinical practice and scientific findings in this area is still at a preliminary stage. However, acquired sociopathy, acquired dyslexia etc. all have developmental equivalents which may sometimes not have been diagnosed.

4.3 The mathematical brain and dyscalculia

Recent experimental advances have clarified how numeracy develops in young children and how it can fail to develop due to neurodevelopmental disorder.

In the adult brain, lesion and brain-imaging studies indicate that the left and right intraparietal area, which is involved in visuo-spatial processing, is associated with knowledge of numbers and their relations ('number sense'). Firstly, parietal lesions can lead to dyscalculia. Secondly, the parietal lobe is activated by arithmetic (Deheane et al., 1999). This fits with the notion that calculation contains a spatial element. It is believed that this quantity representation system is present, at least in a rudimentary form, very early on in development and even in evolution because behavioural studies have revealed number perception, discrimination, and elementary calculation abilities in infants (Spelke, 1994) and animals (see Dehaene et al., 1998).

It has been proposed that our ability to make sense of number concepts rests on this non-verbal representational system located in the parietal lobe (Dehaene et al., 1999). Deheane suggests that during development and education the quantity system becomes progressively linked to other representations of numbers, either visually in the form of strings of Arabic digits (e.g. 85), or verbally in the form of strings of words (e.g. eighty-five). Indeed recent evidence suggests that exact calculation is language-dependent, while approximation relies on nonverbal visuo-spatial brain networks. Deheane and colleagues trained bilingual subjects to make both exact calculations and estimations in one of their two languages. The researchers then tested the subjects in both languages. Performance on the exact problems was faster in the teaching language than in the untrained language. In contrast, approximations performance was equivalent in both languages. The functional imaging evidence supported these behavioural results: the bilateral parietal lobes showed greater activation for approximations than for exact calculations. Additional activation was found during the exact calculations in the brain's language areas.

Fluency in arithmetic in adults is likely to depend on a constant interplay between quantity, visual, and verbal representations of numbers. For instance, rote calculations are performed largely using the verbal system, while approximations of calculations are made using the quantity system. According to Deheane's analysis, developmental dyscalculia and/or innumeracy can arise for several reasons. First, one of the three cardinal modules may be impaired or fail to develop properly because of early brain damage or genetic disorganisation of the underlying neural circuitry. Some children seem to suffer from an early deficit of the parietal quantity representation, and some totally lack an intuition of quantity. Second, the linkages between the modules may fail to develop fluently. For instance, a child may learn the subtraction algorithm by rote, yet fail to connect it to his or her intuitions of quantity, resulting in gross errors (e.g. 53-19=56). In both cases, education strategies informed by psychological and neuroscience studies of number processing could perhaps help in circumventing or rehabilitating those deficits.

Many studies have shown that there are gender differences in mathematical ability. However, if they exist, these differences are clearly not purely biological. There are variations in the size of the gender effect between cultures. While there are sex differences in both China and USA, the girls in China perform better than the boys in USA. This is not a biological difference between the Chinese and the Americans – when Chinese girls are taught in the USA their mathematical ability declines to the level of the American girls. If there are sex differences, there is also a great degree of overlap between boys and girls – many girls are better than boys at maths. Thus, cognitive rehabilitation should not be by gender, but for anyone who falls below a certain threshold.

4.4 The literate brain and dyslexia

Literacy is a paradigm example of an artificially taught activity that has profound consequences for shaping of the human brain. The consequences of literacy for our social, political and economic lives are enormous, and much has been written about it. Here we just highlight the consequences of being literate for a neurocognitive function other than reading. We also briefly consider the burden of dyslexia in a literate society.

An unusual brain imaging experiment compared literate and illiterate brains while listening to and repeating real words and nonsense words (Castro-Caldas et al., 1998). Portuguese women, now in their sixties, who through historical circumstances, were illiterate, were compared with other women from the same social background, who had acquired a modicum of literacy. The brain areas activated for word repetition were similar in the two groups, but the areas activated for nonsense word repetition differed. The literate brain treated these stimuli like other words, activating language areas, while the illiterate brain instead activated the memory retrieval system of the frontal regions of the brain. This parallels the behavioural finding that illiterate women, when repeating the nonsense words, often turned them into real words. This experiment demonstrates that the effect of literacy on the brain also affects spoken language processing.

In dyslexia research, as in research on dyscalculia, a vast bridge spanning genetics, brain anatomy and physiology, cognitive psychology and education, is already being sketched out. The neuropsychology of dyslexia has made great strides in the last decade. In particular, a consensus has been reached to view dyslexia as a developmental disorder with a basis in the brain and in the genes, where the interaction of genetic and environmental factors is taken for granted.

This is despite the fact that, so far, no unique physical biological marker for dyslexia exists. Nevertheless, we already have some knowledge of the underlying brain abnormalities which are visible in abnormal activation patterns in the brains of dyslexic individuals, during certain tasks that involve spoken and written language processing. For instance, Brunswick et al. (1999) found that during reading dyslexics had reduced activations in the major components of the reading system of the left hemisphere of the brain. In particular, the posterior inferior temporal cortex was activated less strongly, an area associated with semantics and highly automated word retrieval processes. This region is particularly important in reading English (see section 3.6.1). Thus, English dyslexics, have greater difficulties learning to read and write and remain less accurate than Italian dyslexics even after years of compensatory learning.

One theory proposes that normal start-up mechanisms are not operating so that fast track learning of speech sound and sound-to-letter decoding is not possible; nevertheless, slow learning remains an option (Frith, 1999). If this theory is correct, then it would follow that normal teaching to facilitate normal learning of literacy is inappropriate for dyslexic individuals. Teaching procedures are required that allow abnormal slow learning to be facilitated, in contrast to those that facilitate normal fast learning. Research can establish whether it is beneficial to use different kinds of teaching methods for dyslexic children. A similar case can be made for other genetically based developmental disorders, given that they can be explained in terms of faulty start-up mechanisms.

The progress of learning to read can be traced in performance, by self-evaluation, and it can also be traced in terms of changes in brain activation. Reading research can in principle be done without input from neuroscience. However, without such input, the understanding of how written language is learned by normal and dyslexic children is incomplete. Likewise, it is incomplete if environmental factors, such as the complexity of English orthography, or the quality of schooling, are ignored.

4.5 Seven research questions related to individual differences and learning disabilities

How do individual differences as manifested in neurological structure and function interact with learning progress and outcome? Can anyone become a Mozart given appropriate teaching?

Does brain-washing exist? What can brain science tell us about deliberate and directed learning and forgetting? What can it tell us about the consequences on quite different skills after a new skill is acquired? For example, what is the effect of literacy and numeracy on other cognitive functions?

Imagery in different modalities as an aid to learning and teaching (including remedial teaching) be monitored through brain scanning and manipulated through TMS. Are there individual differences? What type of imagery is most effective for learning?

The brain's limbic (emotional) system is different from brain systems that process academic abilities, but they are strongly connected. Does learning skills such as reading and writing and maths affect emotional development and vice versa?

Learning disorders are estimated to affect at least 5% of the population. Much more research is needed if we are to understand its biological underpinnings and possibilities for remedial teaching.

Research programmes on mathematical learning and teaching would benefit from links to neuroscience research. Previously intractable questions can now be tackled. Are there sensitive periods for maths in which the brain is particularly responsive to learning maths? Do these differ for different kinds of mathematical ability, for example exact calculation versus approximation? Can a motivation for maths be embedded early on? Does avoiding maths lead to a deterioration in mathematical ability?

Does knowing about the brain aid learning? Should children and adults (pupils, teachers and parents) be taught about their brains and learning? These are questions amenable to empirical research. Are there differences between teachers who are aware of neuroscience/psychology and teachers who are not? For example, are there differences in their methods or success? If teachers know about how the brain learns do they behave differently towards children? Would they change their class size, teaching or testing methods?

5 Conclusions and recommendations

Our selective review suggests that neuroscience research does have relevance to research in teaching and learning. Indeed it has the potential to generate new research questions and to galvanise research in a new interdisciplinary science of learning.

There are a number of caveats, which temper this optimistic evaluation. It seems most likely that the main impact of neuroscience on education will be felt in the field of learning disorders. Research to date has implications for what to do when the brain goes wrong. The implications are less clear for what to do when brains function normally or how to improve normal functioning. Even psychology studies designed to answer questions of teaching and learning do not always have applications, because lab-based experiments rarely take into account the culture of the classroom or individual differences.

Learning experiments conducted by cognitive psychologists have taught us a lot about how we process information, about different ways of encoding information, about how to make encoding more efficient, and about the application of skills that enhance learning, such as mnemonics and imitation. Results from these experiments have implications for education as well as for neuroscience research.

We strongly believe that to continue discovering how the brain learns and how to facilitate this learning, an interdisciplinary 'learning science' is needed. The evolution of such an approach, with convergence from brain scientists, psychologists, and educationers, would probably need five to ten years. A continuous forum for neuroscientists and educationers, with cognitive psychologists as mediators, could be a way forward. This would allow a common vocabulary to emerge and research questions to be discussed and elaborated.

Within such a forum, a number of workshop and research projects could be organised, as well as a web-page discussion group. A charismatic individual needs to be found to lead such an enterprise, and the members should consist of scientists and practitioners with fresh ideas.

An important prerequisite to generate research in teaching and learning is the dissemination of findings from neuroscience, possibly via cognitive psychology. Currently there is little information about neuroscience research that is accessible to educationers and teachers. Literature (books, journals, magazines), videos, CD ROMS, cassettes that explain basic findings from brain science and cognitive psychology would be a useful tool.

However, the interaction should not comprise a one-way flow of information in which educationers learn about neuroscience. The goal of developing an interdisciplinary 'science of learning' cannot be usefully pursued by one or other of the disciplines taking the lead, but depends on each challenging the other with ideas and hypotheses to test.

Most importantly, there should be transference from both sides so that neuroscientists and educationers together can design and perform experiments on learning that are empirical, quantitative and that are relevant to real life teaching and learning.

6 References

Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppe, R. A., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory. *Psychological Science* 7, 25-31.

Baddeley, A. D. (1986). Working Memory. Oxford: Oxford University Press.

Ball, C. (1994). *Start Right: the Importance of Early Learning*. London: Royal Society for the Encouragement of Arts, Manufactures & Commerce.

Bechara A, Tranel D, Damasio H, Adolphs R, Rockland C, Damasio AR (1995). Double dissociation of conditioning and declarative knowledge relative to the amygdala and hippocampus in humans. *Science* 269, 1115-8

Bechara A, Tranel D, Damasio H, Damasio AR (1996) Failure to respond autonomically to anticipated future outcomes following damage to the prefrontal cortex. *Cerebral Cortex* 6, 215-225.

Bechara A, Damasio H, Damasio AR, Lee GP. (1999). Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. *Journal of Neuroscience* 19(13), 5473-81.

Beck, J (1996). A meeting of minds between neuroscientists and educators is first step in improving America's schools. *Chicago Tribune* Section 1, p. 23.

Berns GS, Cohen JD, Mintun MA (1997). Brain regions responsive to novelty in the absence of awareness. *Science* 276(5316), 1272-5.

Breiter HC, Gollub RL, Weisskoff RM, Kennedy DN, Makris N, Berke JD, Goodman JM, Kantor HL, Gastfriend DR, Riorden JP, Mathew RT, Rosen BR, Hyman SE. (1997). Acute effects of cocaine on human brain activity and emotion. *Neuron* 19(3), 591-611.

Bruer, J. T. (1999). Education and the brain: A bridge too far. *Educational Researcher* 26 (8), 4-16.

Brunswick N, McCrory E, Price CJ, Frith CD & Frith U (1999). Explicit and implicit processing of words and pseudowords by adult developmental dyslexics: A search for Wernicke's Wortschatz? *Brain* 122(10), 1901-17

Burgess, N & O'Keefe, J. (1996). Neural computation underlying the firing of place cells and their role in navigation. *Hippocampus* 6(6). 749-62.

Cahill L, Haier RJ, Fallon J, Alkire MT, Tang C, Keator D, Wu J, McGaugh JL. (1996) Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proceedings of the National Academy of Sciences (USA)*. 93(15), 8016-21

Castro-Caldas A, Petersson KM, Reis A, Stone-Elander S, Ingvar M. (1998). The illiterate brain. Learning to read and write during childhood influences the functional organization of the adult brain. *Brain* 121(6), 1053-63.

Chow, K.L. & Stewart, D. L. (1972). Reversal of structural and functional effects of long-term visual deprivation in cats. *Experimental Neurology* 34: 409-433.

Cragg, B. G. (1975). The development of synapses in the visual system of the cat. *Journal of Comparative Neurology* 160: 147-166.

Crick, F. & Mitchison, G. (1995). REM sleep and neural nets. *Behavioural Brain Research* 69(1-2), 147-55

Damasio, A.R. (1994) Descartes' error. New York: Putnam.

Decety, J., Jeannerod, M., Germain, M. & Pastene, J. (1991). Vegetative response during imagined movement is proportional to mental effort. *Behavioural Brain Research* 42, 1-5.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J.C. & Fazio, F. (1994). Mapping motor representations with PET. *Nature* 371, 600-602.

Dehaene S, Dehaene-Lambertz G, Cohen L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neuroscience* 21(8), 355-61. Review.

Dehaene S, Spelke E, Pinel P, Stanescu R, Tsivkin S. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science* 284(5416), 970-4.

D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., & Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature* 16, 279-281.

Elliott, R., Friston, K.J. & Dolan, R.J. (2000) Dissociable Neural Responses in Human Reward Systems. *Journal of Neuroscience* 20(16), 6159-6165

Everitt B.J., Robbins T.W. (1992) Amygdalaventral striatum interactions and reward-related processes. In: *The amygdala* (Aggleton J.P., ed). New York: Wiley.

Feltz, D.L. & Landers, D.M. (1983). The effects of mental practice on motor skill learning and performance. A meta-analysis. *Journal of Sport Psychology* 5, 27-57

Fletcher PC, Shallice T, Dolan RJ. (1998a). The functional roles of prefrontal cortex in episodic memory. I. Encoding. *Brain*. 121(7), 1239-48.

Fletcher PC, Shallice T, Frith CD, Frackowiak RS, Dolan RJ. (1998b). The functional roles of prefrontal cortex in episodic memory. II. Retrieval. *Brain* 121(7), 1249-56.

Frith, U. (1999). Paradoxes in the definition of dyslexia. *Dyslexia: an International Journal of Research and Practice* 5, 192-214

Gabrieli, JD, Brewer, JB & Poldrack, RA. (1998). Images of medial temporal lobe functions in human learning and memory. *Neurobiology of Learning and Memory* 20(1-2), 275-83

Gallagher AM, De Lisi R, Holst PC, McGillicuddy-De Lisi AV, Morely M, Cahalan C (2000). Gender differences in advanced mathematical problem solving. *Journal of Experimental Child Psychology* 75(3), 165-90.

Good, C.D., Johnsrude, I., Ashburner, J., Henson, R.N.A., Friston, K. & Frackowiak, R.S.J. (2000). Voxel-based morphometry analysis of 465 normal adult human brains. *Neuroimage* 11(5), S607

Goldman-Rakic, P. S. (1987). Development of cortical circuitry and cognitive function. *Child Development* 58, 601-622.

Greenough, W. T., Black, J. E., & Wallace, C. S. (1987). Experience and brain development. *Child Development* 58: 539-559.

Hampson, E. (1990). Variations in sex-related cognitive abilities across the menstrual cycle. *Brain and Cognition* 14(1), 26-43.

Hampson, E. (1995). Spatial cognition in humans: possible modulation by androgens and estrogens. *Journal of Psychiatry Neuroscience* 20(5): 397-404

Harris, P. (1989). Children and emotion. Blackwell, UK.

Hennevin E, Hars B, Maho C, Bloch V. (1995). Processing of learned information in paradoxical sleep: relevance for memory. *Behavioural Brain Research* 69(1-2), 125-35.

Henson, R.N.A. (in press). Neural working memory: applications of the Working Memory model to neuropsychology and neuroimaging. In Andrade, J. (Ed.) *Working Memory: a work in progress*. London: Routledge.

Huttenlocher, P. (1990). Morphometric studies of human cerebral cortex development. *Neuropsychologia* 28(6): 517-527.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C. & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science* 286, 2526-8

Jeannerod, M. (1994). The Representing Brain - Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences* 17, 187-202.

Jonides, J., Reuter-Lorentz, P. A., Smith, E. E., Awh, E., Barnes, L. L., Drain, M., Glass, J., Lauber, E., Patalano, A. L., & Schumacher, E. (1996). Verbal and spatial working memory in humans. In D. Medin (Ed.) *The Psychology of Learning and Motivation* (pp. 43-88). London: Academic Press.

Klingberg, T. (1998). Concurrent performance of two working memory tasks: potential mechanisms of interference. *Cerebral Cortex* 8(7), 593-601.

Kosslyn SM, Shin LM, Thompson WL, McNally RJ, Rauch SL, Pitman RK, Alpert NM. (1996). Neural effects of visualizing and perceiving aversive stimuli: a PET investigation. *Neuroreport* 7(10), 1569-76.

Kuhl, P.K. (1998). The development of speech and language. In *Mechanistic relationships between development and learning*, ed. T.J. Carew, R. Menzel & CJ Shatz (pp. 53-73). New York: Wiley.

Maguire, E.A., Frackowiak, R.S. & Frith, C.D. (1996). Learning to find you way around: a role for the human hippocampal formation. *Proceedings for the Royal Society of London (B): Biological Sciences* 263, 1745-50.

Maguire, E.A., Frackowiak, R.S.J. & Frith, C.D. (1997). Recalling routes around London: activation of the right hippocampus in taxi drivers. *Journal of Neuroscience* 17(18), 7103-10

Maguire, E.A., Gadian, D.S., Johnsrude, I.S., Good, C.D., Ashburner, J., Frackowiak, R.S. & Frith, C.D. (2000). Navigation related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences (USA)* 97(8): 4398-403.

Maquet, P., Laureys, S., Peigneux, P., Fuchs S., Petiau, C., Phillips, C., Aerts, J., Del Fiore, G., Degueldre, C, Meulemans, T., Luxen, A., Franck, G., Van Der Linden, M., Smith C., Cleeremans, A. (2000). Experience-dependent changes in cerebral activation during human REM sleep. *Nature Neuroscience* 3(8), 831-6.

Mayberg, H.S., Brannan, S.K., Mahurn, R.K., Jerabek, P.A., Brickman, J.S., Tekell, J.L., Silva, I.A., McGinnis, S., Glass, T.G., Martin, C.C. & Fox, P.T. (2000). Cingulate function in depression: a potential predictor of treatment response. *Neuroreport* 8(4), 1057-61.

McDowell, S., Whyte, J., & D'Esposito, M. (1997). Working memory impairments in traumatic brain injury: evidence from a dual-task paradigm. *Neuropsychologia* 35(10), 1341-53.

Mehler J., Jusczyk P., Lambertz G., Halsted N., Bertoncini J. & Amiel-Tison C. (1988). A precursor of language acquisition in young infants. *Cognition* 29(2), 143-78.

Mellet E, Tzourio-Mazoyer N, Bricogne S, Mazoyer B, Kosslyn SM, Denis M (2000). Functional anatomy of high-resolution visual mental imagery. *Journal of Cognitive Neuroscience* 12(1), 98-109

Meltzoff, A.N. (1999). Persons and representation: why infant imitation is important for theories of human development. In: *Imitation in infancy*. (Eds. J. Nadel & G. Butterworth). pp9-35, Cambridge: Cambridge University Press.

Mitchell, D.E. (1989). Normal and abnormal visual development in kittens: insights into the mechanisms that underlie visual perceptual development in humans. Canadian Journal of Psychology 43(2):141-64. Review.

Morton, J. and Frith, U. (1995). Causal Modelling: A Structural Approach to Developmental Psychopathology. In: Cicchetti, D. & Cohen, D.J. (Eds.), *Manual of Developmental Psychopathology*. Volume 1. New York: Wiley, p. 357-390.

Neville, HJ & Bavelier, D. (1998). Neural organization and plasticity of language. *Current Opinion in Neurobiology* 8(2), 245-8.

O'Connor, T.G., Bredenkamp, D. & Rutter, M. (1999). Attachment disturbances and disorders in children exposed to early severe deprivation. *Infant Mental Health Journal* 20(10), 10-29.

Ohman A., Erixon G. & Lofberg I. (1975). Phobias and preparedness: phobic versus neutral pictures as conditioned stimuli for human autonomic responses. *Journal of Abnormal Psychology* 84(1), 41-5.

Pantev C., Oostenveld R., Engelien A., Ross B., Roberts L.E. & Hoke M. (1998). Increased auditory cortical representation in musicians. *Nature* 392, 811-4.

Pascual-Leone A., Nguyet D., Cohen L.G., Brasil-Neto J.P., Cammarota A. & Hallett M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of Neurophysiology* 74(3), 1037-45.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature* 362, 342-344.

Paulesu E., McCrory E., Fazio F., Menoncello L., Brunswick N., Cappa S.F., Cotelli M., Cossu G., Corte F., Lorusso M., Pesenti S., Gallagher A., Perani D., Price C., Frith C.D. & Frith U. (2000). A cultural effect on brain function. *Nature Neuroscience* 3(1), 91-6.

Pinker, S. (1994). The language instinct. New York: Morrow.

Poe, G.R., Nitz, D.A., McNaughton, B.L. & Barnes, C.A. (2000). Experience-dependent phase-reversal of hippocampal neuron firing during REM sleep. *Brain Research* 855(1), 176-80.

Rakic, P. (1995). Corticogenesis in human and nonhuman primates. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (pp. 127-145). Cambridge MA: MIT Press.

Rizzolatti, G., Gentilucci, M., Camarda, R.M., Gallese, V., Luppino, G., Matelli, M. & Fogassi, L. (1990). Neurons relating to reaching-grasping arm movements in the rostral part of area 6 (area 6a beta). *Experimental Brain Research* 82, 337-350.

Saldanha, CJ, Clayton, NS, Schlinger, BA. (1999). Androgen metabolism in the juvenile oscine forebrain: a cross-species analysis at neural sites implicated in memory function. *Journal of Neurobiology* 40(3), 397-406.

Schoenbaum, G, Chiba, AA, Gallagher, M (1998). Orbitofrontal cortex and basolateral amygdala encode expected outcomes during learning. *Nature Neuroscience* 1(2):155-9

Shaywitz BA, Shaywitz SE, Pugh KR, Constable RT, Skudlarski P, Fulbright RK, Bronen RA, Fletcher JM, Shankweiler DP, Katz L, et al. (1995). Sex differences in the functional organization of the brain for language. *Nature* 373(6515), 607-9.

Silverman I, Kastuk D, Choi J, Phillips K (1999). Testosterone levels and spatial ability in men. *Psychoneuroendocrinology* 24(8):813-22

Spelke, E. (1994). Initial knowledge: six suggestions. Cognition 50(1-3), 431-45

Stein EA, Pankiewicz J, Harsch HH, Cho JK, Fuller SA, Hoffmann RG, Hawkins M, Rao SM, Bandettini PA, Bloom AS. (1998). Nicotine-induced limbic cortical activation in the human brain: a functional MRI study. *American Journal of Psychiatry* 155(8), 1009-15.

Stephan, K.M., Fink, G.R., Passingham, R.E., Silbersweig, D., Ceballos-Baumann, A.O., Frith, C.D. & Frackowiak, R.S.J. (1995). Functional anatomy of mental representation of upper extremity movements in healthy subjects. *Journal of Neurophysiology* 73, 373-386.

Thompson, P.M, Giedd JN, Woods RP, MacDonald D, Evans AC, Toga AW. (2000). Growth patterns in the developing brain detected by using continuum mechanical tensor maps. *Nature* 204, 190-193.

Thut G, Schultz W, Roelcke U, Nienhusmeier M, Missimer J, Maguire RP, Leenders KL. (1997). Activation of the human brain by monetary reward. *Neuroreport* 8(5):1225-8.

U.S. Department of Education (1996) *Building knowledge for a nation of learners: A framework for education research 1997*. Washington, DC: U.S. Department of Education, Office of Educational Research and Improvement.

Vogt, S. (1995). On relations between perceiving, imagining and performing in the learning of cyclical movement sequences. *British Journal of Psychology* 86, 191-216.

Wiesel, T. N., & Hubel, D. H. (1965). Extent of recovery from the effects of visual deprivation in kittens. *Journal of Neurophysiology* 28: 1060-1072

Yue, G. & Cole, K.J. (1992). Strength increases from the motor program. Comparison of training with maximal voluntary and imagined muscle contractions. *Journal of Neurophysiology* 67, 1114-1123.

Zalla T, Koechlin E, Pietrini P, Basso G, Aquino P, Sirigu A, Grafman J. (2000). Differential amygdala responses to winning and losing: a functional magnetic resonance imaging study in humans. *European Journal of Neuroscience* 12(5), 1764-70.

Appendix 1: Functional Neuroimaging Methods

The relationship between neuronal activity and cerebral blood flow

When a population of brain cells (neurons) becomes activated it requires an increased supply of blood flowing to it to replenish the supply of oxygen and glucose, which the neurons depends on for energy. This tight coupling between neuronal activity and the associated local cerebral glucose metabolism and therefore blood flow is the principle underlying functional neuroimaging. Functional neuroimaging techniques measure brain activity by detecting changes in blood flow in human subjects. There are many types of functional neuroimaging, the main two techniques being PET and fMRI. In both PET and fMRI the volunteer lies inside the scanner and performs some cognitive or sensorimotor task while the scanner images regional blood flow (or flow-related phenomena) in his or her brain.

Positron Emission Tomography (PET)

In PET cerebral blood flow is imaged by following a radioactive tracer injected into the bloodstream as it flows through the brain. The tracer is introduced into the blood stream via an intravenous injection. The subject lies in the scanner and the radiation detector positioned around his or her head detects whereabouts in the subject's brain the radiation – and therefore the blood – flows to while the subject performs a particular task.

Functional Magnetic Resonance Imaging (fMRI)

In MRI the subject is exposed to a large magnetic field. Different structures in the brain (white matter, grey matter, cerebrospinal fluid and bone, for example) have different magnetic properties and therefore appear different in the MRI image. fMRI can be used to trace blood flow in the brain because the magnetic properties of blood depends on how much oxygen it contains. When neurons become active they require a supply of oxygen to be carried to them in the blood. It is this oxygen carried in the blood that the fMRI scanner detects.

Comparison of PET and fMRI

There are several advantages of fMRI over PET. Firstly, fMRI does not involve exposing the subject to ionising radiation. Therefore subjects can be scanned with fMRI on numerous occasions, and subjects can be of all ages. This is unlike PET, which because it involves exposing the subject to ionising radiation, cannot be used to scan women of child-bearing age or children. Secondly the temporal and spatial resolutions of fMRI are higher than PET. PET measures blood flow on a spatio-temporal scale of about 6mm and at least 30 seconds. fMRI has a spatio-temporal scale of about 1-3mm and one or more seconds. Thirdly, a PET scan takes significantly longer than an fMRI scan: approximately two hours compared to 30 minutes respectively. However, fMRI is very loud and earplugs must be worn by the subject to protect his or her hearing. In addition, the MRI scanner is more enclosed than the PET scanner, so can be a problem for claustrophobic subjects. FMRI images are susceptible to artifacts, especially in the temporal lobes, which makes PET more suitable for some studies.

Appendix 2: Diagram of the human brain

