

*Descriptive Account***Correlates between bioscience students' experiences of higher education and the neurobiology of learning**Poppy Turner<sup>1</sup> and Andrew Curran<sup>2</sup><sup>1</sup> *Dept of Education, University of Bath, Claverton Down, Bath, BA2 7AY and*<sup>2</sup> *Dept of Neurology, Alder Hey Hospital, Liverpool, L12 2AP**Date received: 23/03/2006**Date accepted: 12/05/2006***Abstract**

*There is growing interest amongst educationalists in the relationship between education and neuroscience; for example, the Society for Research into Higher Education (SRHE) recently hosted an event entitled 'Bridging the gap between neuroscience and education'. While students' quotations are informative about what promotes or facilitates their learning, and what inhibits it, they do not reveal anything about the neurobiology that underlies their construction of knowledge and understanding. In this article, qualitative data from bioscience students on their undergraduate learning experiences are considered in the light of insights into the structure and function of the brain, which neuroscience can provide, in order to enrich our understanding of learning and teaching. Consideration of the neurobiology of learning demonstrates that the way in which students experience their learning environments can significantly alter their ability to learn by affecting the neurobiological capabilities of their brains.*

**Keywords: Undergraduate learning, students' experiences, neuroscience****Introduction**

In this article, the authors seek to inform the education-neuroscience debate by using neuroscientific knowledge (of brain structure and function) to interpret statements that university students have made about their undergraduate learning. Quotations are selected from a study involving 70 bioscience students, from four cohorts, who studied Molecular and Cellular Biology between 1994 and 2005 (Turner, 2005). In this qualitative study, the researcher entered into open dialogue with students (face-to-face and by email), allowing students to reveal what they found significant about their learning situations. There are, of course, many ways in which to analyse empirical data from students about their learning experiences. The illustrative comments used in this paper were initially analysed from an educational viewpoint. In this paper we speculate that the very different perspective of neuroscience may be able to make a useful addition to our understanding of learning and how to optimise it in our students.

Learning, at its most fundamental level, is a process of neurochemical and neuroanatomical change resulting in permanent or semi-permanent changes

in cerebral architecture (Damasio, 1990; Kirkwood & Bear, 1994; McClelland *et al*, 1999; Merzenich & Sameshima, 1993; Rodriguez *et al*, 1999; Skrebitsky & Chepkova, 1998). The effectiveness with which our brains learn new information or adjust previous information to fit new circumstances depends on our degree of engagement with the learning environment in which we find ourselves (Aosaki *et al*, 1994; Hollerman *et al*, 2000; Kahkonen *et al*, 2002; Ljungberg *et al*, 1992; Nieoullon, 2002; Posner & Petersen, 1990; Schultz *et al*, 1995). In this paper hypotheses from the neurobiological literature are employed to shed light on comments made by students in undergraduate learning situations and to explore why some circumstances enhanced the learning process whilst others inhibited it. Students' comments fell naturally into clear categories; we have used these firstly to illustrate students' experiences of their learning environments and then to consider neurobiological explanations for how these may have enhanced or inhibited their learning; these comments are a guide to the reader and, of necessity, a simplification of what is, in reality, highly complex.

### **Promoters of learning**

The following quotations came from undergraduates who were spending their third year of a four year sandwich degree on work placements in a variety of institutions.

#### **1. Attention**

- "Learning comes from putting into practice what I've learnt about academically but didn't quite understand until I actually did it."
- "Working on your own project makes you think through what you are doing and why you are doing it ... helps cement knowledge into your head."
- "I gained more understanding and knowledge as I had my own project ... greater interest to look into my work and its background."

It is perhaps self evident that paying attention to a stimulus to be learned facilitates the process of learning. The comments above reflect this observation and suggest that students found that the combination of attention and cognition enhanced their learning experience.

#### **2. Independence**

- "Quite challenging as I had to do almost all the work on my own, after I had been shown how to do it."
- "The work became more challenging as the project progressed and I was left to my own initiative."
- "Huge plus point [is] independence. I don't just know the technique I am doing, I understand it inside out."

These comments again demonstrate the importance of cognition, of the students having to think about their projects, and of gradually developing self confidence and independence. They also contain comments relating to attention (i.e. "Quite challenging", "More challenging").

### 3. Emotional connection

- Good placement supervisors were seen as “friendly”, “helpful”, “approachable” or “enthusiastic”. “This enthusiasm is then passed on to you.”
- “It was fantastic [on placement] being with people who were so enthusiastic about their subject and brimming with energy all the time. It is very easy to be swept up in the excitement.”
- “Have learnt so, so much since I have been here through working with truly talented and intelligent people who explain things in depth and detail ... almost like having a second family! Fantastic learning experience.”
- “Listening to colleagues talking about antibodies all the time ... it’s a bit like doing GCSE Spanish and moving to Spain. You just pick it up subconsciously.”
- “Very relaxed atmosphere ... people are so friendly, it makes you want to go to work and do the best you can, not just for yourself but so you don’t let the others in the team down.”
- “The people I worked with were very chilled and relaxed and I found this was the best way to get work done”.

Students reported that emotional involvement with the process of learning, and with good supervisors, promoted their learning. All the statements above have a strong emotional flavour, e.g. “excitement”.

#### ***The neurobiology***

The quotations above suggest that three elements of students’ experiences came together to enhance their learning: attention and cognition; the development of independent thought; and emotional connection. From a neurobiological viewpoint, it is this emotional connection with a topic and the neurochemical dopamine that act as the unifying factors in successful learning.

Dopamine is arguably the single most multi-functional neurochemical in our brains, with a wide range of diverse and complex actions. The cell bodies of dopamine neurones are located mainly in the pars compacta of the substantia nigra and the medially adjoining ventral tegmental area (Schultz, 1999). Their axons project to the striatum (the caudate nucleus and putamen), the ventral striatum, including the nucleus accumbens, and the frontal cortex (dorsolateral, ventrolateral and orbital prefrontal cortex). This very widespread distribution enables dopamine neurones to influence most of the core functions of the brain.

The control of dopamine release in the brain is predominantly under the auspices of the limbic system (Ljungberg *et al*, 1992; Mirenowicz & Schultz, 1994; Phillips, 1984; Schultz, 1998; Schultz & Romo, 1990; Schultz *et al*, 1995). The limbic system is responsible for our emotional responses (Blood *et al*, 1999; Hariri *et al*, 2000; Joseph, 1992). Emotional connection with a topic therefore enhances dopamine release widely throughout the brain and, as stated above, dopamine has various interrelated and complementary functions throughout the brain.

**1. Attention and cognition.** Dopamine is centrally involved in both attentional and cognitive processes (Kahkonen *et al*, 2002; Knutson *et al*, 2004; Nieoullon, 2002; Overtoom *et al*, 2003). The attentional system is hypothesised to contain a posterior subconscious component, situated in the right posterior parietal lobe (Posner & Petersen, 1990), and an anterior conscious component, also in the right hemisphere. When perceptual information is recognised as having biological value by associative and limbic areas (i.e. via the posterior attentional system), it converges on the prefrontal cortex where the anterior cingulate and medial orbitofrontal cortex (the anterior attentional system) are involved in evaluating the importance of the information, i.e. whether it is novel, potentially rewarding or harmful, and whether it is worthy of attention and response (Posner & Petersen, 1990).

Dopamine is also released extensively throughout the frontal cortex where higher cognition occurs (Arnsten *et al*, 1994; Goldman-Rakic, 1998; Henze *et al*, 2000). This duality of function, where dopamine is required for the attentional processes that focus on a stimulus and for the facilitation of cognitive processes needed to think about that stimulus, allows the same stimulus both to attract attention and to facilitate reflection, by higher centres, on the nature of the stimulus and to plan responses to it.

**2. Learning.** Having paid attention to and thought about a stimulus, we are also able to learn from the experience and dopamine is central to learning (Baddeley *et al*, 2000; Beninger, 1983). Learning involves creating synaptic links between neuronal cells to establish 'hard wired' patterns of neuronal firing called Hebbian Assemblies (Bailey *et al*, 2000; McClelland *et al*, 1999; Skrebitsky & Chepkova, 1998). The first step in this process is the establishment of sustained levels of neuronal excitation or depression known as long term potentiation (LTP) and long term depression (LTD) (Bliss & Collingridge, 1993; Martinez & Derrick, 1996). Once these two neurophysiological events have occurred in the hippocampus and the corpus striatum (Bliss & Collingridge, 1993; Silkis, 2001), they stimulate neurones to grow dendritic connections with each other. These dendrites making contact with neighbouring neurons and firing at the same time obey the Hebbian rule; 'nerves that fire together wire together'. Dopamine is essential to all levels of this process from the establishment of LTP and LTD to the final growing of synaptic connections (Goldman-Rakic, 1998; Kerr & Wickens, 2001; Silkis, 2001).

**3. Response to the stimulus.** Finally, dopamine is required for the corpus striatum to function (Chase *et al*, 1998). The corpus striatum is a sub-cortical structure that receives input from all of the frontal cortex (Smith *et al*, 1998). It sub serves cognition (in the caudate nucleus), emotional context (in the nucleus accumbens), and sensori-motor and motor functions (in the putamen). By ensuring normal functioning in the corpus striatum, dopamine therefore facilitates all aspects of the response of the individual to a stimulus.

To summarise this section, dopamine is centrally involved in the most important functions of the brain. Its release firstly switches on our attentional

system to a particular stimulus (as described by Posner (Posner & Petersen, 1990)) and then facilitates cognitive activation through its release in the frontal brain (Arnsten *et al*, 1994; Goldman-Rakic, 1998; Groenewegen & Uylings, 2000) before finally facilitating the passage of relevant information throughout the brain (Calabresi *et al*, 2000; Conti *et al*, 2001; Hollerman *et al*, 2000), establishing learning (Calon *et al*, 2000; Kerr & Wickens, 2001; Ljungberg *et al*, 1992; Myslivecek, 1997) and facilitating the responses to the stimulus. Undergraduates' comments on what enhanced their learning all arguably focus around successful engagement of their emotional attention, which facilitated dopamine release and enhanced their learning.

### ***Inhibition of learning***

In this section we will look first at those experiences which students felt inhibited their learning and then discuss the concept of reward and how that fits with the neurobiology of learning as described above. Once again the quotations came from undergraduates spending their third year of a four year sandwich degree away from university on placements.

#### **1. Lack of challenge, lack of emotional engagement**

- “Bioinformatics isn’t all that interesting so I’m finding it quite hard to understand and retain any information.”
- “Pretty dull! I haven’t felt at all challenged ... frustrated.”
- “Very mundane. I haven’t really learnt anything ... just one method I now know ... I have no motivation to learn anything more about it ... You just think ‘What’s the point’.”
- “Needed more mental stimulation.”
- Routine work “Depressed me immensely [and] didn’t allow me to develop concepts and link information.”

Students failed to learn from activities and environments with which they failed to engage. In these environments they were clearly not experiencing any reward from their work, subsequently disengaged from the process and consequently failed to learn much from it. The work had lost their attention.

#### **2. Poor supervision**

- “I really needed someone who knew about [the research] to tell me if the data was good.”
- “I knew I was making unnecessary mistakes.”
- “My learning was hindered by my supervisor as I felt he used me almost as cheap labour ... I would generally have to do what I was told.”
- Another supervisor “Refused to give me a project of my own ... I found myself less motivated to work for him.”
- “My boss was a nightmare ... all sweetness and light one minute then really nasty and snappy the next ... My main task every day was to do everything in my power to avoid my boss.”

Students failed to learn where supervision was poor and made “unnecessary mistakes”. In this situation there was a failure of engagement and consequent failure of cognition. Note that confidence is important in learning because of the concept of reward, which will be discussed below.

### 3. Poor communications or environment

- “People assume I know how to do something ... don't explain very well ... hard to feel able to ask questions.”
- “No kind of team work and even less communication. Group meetings were to bitch at each other ... typically scientific - big egos, ambitious people who want to be famous in their field ... big divides and communication problems ... never want to work in a lab ever again and has probably put me of science for life.”

Students reported learning little in situations where they lacked helpful dialogue and interaction with colleagues and where they felt isolated or uncomfortable. Once again there was a failure of reward in these situations.

#### ***The neurobiology***

It has been stated above that reward has a role in the neurobiology of learning. That role is, in fact, central to the entire process of learning. It is through reward, or the anticipation of reward, that the limbic brain is stimulated to produce dopamine (Mirenowicz & Schultz, 1994; Schultz, 1998; Schultz *et al*, 1995) and thus sets in chain the events which lead eventually to successful learning. In all the above environments reward was missing.

The concept of reward is complex. Reward, or rather what is perceived as reward, can differ widely across species and individuals. Higher mammals have more complex perceptions of rewards as those rewards become based on cognitive representations. They concern such objects and constructs as novelty, challenge, acclaim, power, money, territory, and security (Schultz, 1999). Schultz (1999) defines rewards as having three basic functions:

1. They elicit approach and consummatory behaviour and serve as goals for voluntary behaviour. Because of this, rewards can interrupt ongoing behaviour and change the priorities of behavioural actions to enable the organism to better achieve reward.
2. Rewards have positive reinforcing effects i.e. they encourage the organism to ‘come back for more’. Interestingly, learning proceeds when rewards occur unpredictably and slows as rewards become more predicted (Rescorla & Wagner, 1972).
3. Rewards induce subjective feelings of pleasure and positive emotional states.

Dopamine is central to the processing of information relating to rewards (Schultz, 1997). Rewards activate areas of the brain involved in appetite and sexual satisfaction, such activation is prevented by lesions that damage dopamine delivery (Beninger, 1983; Robbins & Everitt, 1996). Reward is intimately linked with learning and, through learning, with adjusting behaviours.

The concept of reward is not simple when dealing with higher functioning primates, and especially in humans. Reward must also be associated with attention; one can, by and large, only achieve reward by being attentive to the environment in which such a reward may occur. Complex rewards (such as acclaim and power) must also involve cognitive processes to plan for and anticipate initially, and then to perceive if the planning has been successful in achieving the imagined reward.

Students' comments suggest that they found learning more difficult when they did not perceive reward in their environment. However, the fact that humans are also able to look ahead to the eventual goals of an activity means that students are able to learn enough to achieve their desired exam results, even if their environment fails to facilitate their learning.

### ***Learning and stress***

The final section in this paper looks at the effects of stressful situations on students' ability to learn. This was a particular problem for the students in their final year at university, as illustrated by the following quotations:

- "In the first three days I was set nine tasks and that was just scary ... panic."
- "It was hard to cope, anxiety mostly ... I am OK if I have one thing to concentrate on but, if there's lots I don't know where to start! Horrible feeling knowing that you have so much to do ... extremely stressful."
- "Very down lately ... I'll be glad when this term is over and I can catch up on some reading ... The worst thing was getting a bad mark for [an exam] that made me feel I have a huge mountain to climb ... Finding it tough going and running out of steam."
- Some students stopped doing any background reading "Simply because I don't have time to do it. If I tried to do it, I would stress myself out."
- "I'm just so scared!" before giving a seminar presentation and, afterwards, "They were quite tough on the presentations ... had no positive comments, only criticisms, which made us all feel like crap".
- Another respondent confirmed the effect of negative feedback by saying that students felt "Torn apart".

A workload which students found burdensome resulted in high levels of stress and this, coupled with negative feedback in the form of poor exam results or criticism of their presentations, left them struggling emotionally. Under these circumstances learning was "tough going" and some students abandoned background reading altogether.

### ***The neurobiology***

The stress response consists of a series of coordinated behavioural and physiological manifestations that promote survival (Gold, 2005). To a large extent these manifestations are orchestrated by the amygdala, which drives cognitive programmes away from those that are complex, sequence dependent and integrative to those that are well-rehearsed, acquired during previous experiences of danger, and encoded to emerge readily in subsequent life-threatening situations (Fuster, 1991; LeDoux, 1995). In short,

the stress response inhibits prefrontal cortical activity (Gold, 2005) and moves the individual's behaviours towards simple, immediate responses to the environment. This primitive, survival based response system is also triggered by social stress such as that described by students above (LeDoux *et al*, 1989). During stress reactions, the individual will also set aside the propensity for complex behavioural and cognitive programs that may require concentration (Gold, 2005). Over-stressed students are therefore less able to concentrate and to assimilate new information. They are also less able to create flexible patterns of thinking and their planning ability is impaired. Excessive stress is, therefore, counterproductive of learning.

## Conclusion

This article had limited objectives but has, hopefully, demonstrated that there are neuroscientific reasons for seeking and taking seriously students' perceptions of their learning experiences. The way in which students experience their learning environments can significantly alter their ability to learn by affecting the neurobiological capabilities of their brains. In short, it matters whether or not students are provided with interesting activities, with which they can engage, and whether or not they are happy or over-stressed. It matters because engagement and emotions impact on the neurobiology of learning. Neuroscience and education are very different disciplines and come from very different paradigms; one is a physical science, in which research tends to involve laboratory conditions or randomised controlled trials, and the other is a social science where research is often qualitative and conducted in naturalistic settings. Yet both can make a useful contribution to our understanding of undergraduate learning. There is, it seems, a richness of understanding to be gained from debating education in the light of neuroscientific knowledge, and perhaps also from debating neuroscience in the light of current educational theories.

**Communication author:** Dr Andrew Curran, Dept of Neurology, Alder Hey Hospital, Liverpool. Email: [Andrew.Curran@rlc.nhs.uk](mailto:Andrew.Curran@rlc.nhs.uk)

## References

- Aosaki, T., Tsubokawa, H., Ishida, A., Watanabe, K., Graybiel, A., & Kimura, M. (1994) Responses of tonically active neurons in the primates striatum undergo systematic changes during behavioural sensorimotor conditioning. *Journal of Neuroscience*, 14(6), 3969-3984
- Arnsten, A. F., Cai, J. X., Murphy, B. L., & Goldman-Rakic, P. S. (1994) Dopamine D1 receptor mechanisms in the cognitive performance of young adult and aged monkeys". *Psychopharmacology (Berl)*, 116(2), 143-151
- Baddeley, A., Bueno, O., Cahill, L., Fuster, J. M., Izquierdo, I., McGaugh, J. L., Morris, R. G., Nadel, L., Routtenberg, A., Xavier, G., & Da Cunha, C. (2000) The brain decade in debate: I. Neurobiology of learning and memory. *Brazilian Journal of Medical Biological Research*, 33(9), 993-1002
- Bailey, C. H., Giustetto, M., Huang, Y. Y., Hawkins, R. D., & Kandel, E. R. (2000) Is heterosynaptic modulation essential for stabilizing Hebbian plasticity and memory? *Nature Review of Neuroscience*, 1(1), 11-20
- Beninger, R. J. (1983) The role of dopamine in locomotor activity and learning. *Brain Research*, 287(2), 173-196
- Bliss, T.V.P. & Collingridge, G.L. (1993) A synaptic model of memory - long-term potentiation in the hippocampus. *Nature*, 361, 31-39
- Blood, A. J., Zatorre, R. J., Bermudez, P., & Evans, A. C. (1999) Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience*, 2(4), 382-387
- Calabresi, P., Centonze, D., & Bernardi, G. (2000) Electrophysiology of dopamine in normal and denervated striatal neurons. *Trends in Neuroscience*, 23(Suppl), 57-63
- Calon, F., Hadj, T. A., Blanchet, P. J., Morissette, M., Grondin, R., Goulet, M., Doucet, J. P., Robertson, G. S., Nestler, E., Di Paolo, T., & Bedard, P. J. (2000) Dopamine-receptor stimulation: biobehavioral and biochemical consequences. *Trends in Neuroscience*, 23(10) Suppl, 92-100
- Chase, T. N., Oh, J. D., & Blanchet, P. J. (1998) Neostriatal mechanisms in Parkinson's disease. *Neurology*, 51(2) Suppl 2, 30-35
- Conti, G., Blandini, F., Tassorelli, C., Giubilei, F., Fornai, F., Zocchi, A., & Orzi, F. (2001) Intra-striatal injection of D1 or D2 dopamine agonists affects glucose utilization in both the direct and indirect pathways of the rat basal ganglia. *Neuroscience Letters*, 309(3), 161-164
- Damasio, A. R. (1990) Synchronous activation in multiple cortical regions: a mechanism for recall. *Neuroscience*, 2, 287-297
- Fuster, J. M. (1991) The prefrontal cortex and its relation to behavior. *Progress in Brain Research*, 87, 201-211
- Gold, P. W. (2005) The neurobiology of stress and its relevance to psychotherapy. *Clinical Neuroscience Research*, 4(5-6), 315-324

- Goldman-Rakic, P. S. (1998) The cortical dopamine system: role in memory and cognition. *Advances in Pharmacology*, 42, 707-711
- Groenewegen, H. J. & Uylings, H. B. (2000) The prefrontal cortex and the integration of sensory, limbic and autonomic information. *Progress in Brain Research*, 126, 3-28
- Hariri, A. R., Bookheimer, S. Y., & Mazziotta, J. C. (2000) Modulating emotional responses: effects of a neocortical network on the limbic system. *Neuroreport*, 11(1), 43-48
- Henze, D. A., Gonzalez-Burgos, G. R., Urban, N. N., Lewis, D. A., & Barrionuevo, G. (2000) Dopamine increases excitability of pyramidal neurons in primate prefrontal cortex. *Journal of Neurophysiology*, 84(6), 2799-2809
- Hollerman, J. R., Tremblay, L., & Schultz, W. (2000) Involvement of basal ganglia and orbitofrontal cortex in goal-directed behavior. *Progress in Brain Research*, 126, 193-215
- Joseph, R. (1992) The limbic system: emotion, laterality, and unconscious mind. *Psychoanalytical Review*, 79(3), 405-456
- Kahkonen, S., Ahveninen, J., Pekkonen, E., Kaakkola, S., Huttunen, J., Ilmoniemi, R. J., & Jaaskelainen, I. P. (2002) Dopamine modulates involuntary attention shifting and reorienting: an electromagnetic study. *Clinical Neurophysiology*, 113(12), 1894-1902
- Kerr, J. N. & Wickens, J. R. (2001) Dopamine D-1/D-5 receptor activation is required for long-term potentiation in the rat neostriatum in vitro. *Journal of Neurophysiology*, 85(1), 117-124
- Kirkwood, A. & Bear, M. F. (1994) Hebbian synapses in visual cortex. *Journal of Neuroscience* 14(3, Pt 2), 1634-1645
- Knutson, B., Bjork, J. M., Fong, G. W., Hommer, D., Mattay, V. S., & Weinberger, D. R. (2004) Amphetamine Modulates Human Incentive Processing. *Neuron*, 43(2), 261-269
- LeDoux, J. E. (1995) Emotion: clues from the brain. *Annual Review of Psychology* 46, 209-235
- LeDoux, J. E., Romanski LM, & Xagraris A.E. (1989) Indelibility of subcortical emotional memories. *Journal of Cognitive Neuroscience*, 1, 238-243.
- Ljungberg, T., Apicella, P., & Schultz, W. (1992) Responses of monkey dopamine neurons during learning of behavioural reactions. *Journal of Neurophysiology* 67, 145-163
- McClelland, J. L., Thomas, A. G., McCandliss, B. D., & Fiez, J. A. (1999) Understanding failures of learning: Hebbian learning, competition for representational space, and some preliminary experimental data. *Progress in Brain Research*, 121, 75-80
- Martinez, J. L., Jr. & Derrick, B. E. (1996) Long-term potentiation and learning. *Annual Review of Psychology*, 47, 173-203
- Merzenich, M. M. & Sameshima, K. (1993) Cortical plasticity and memory. *Current Opinion in Neurobiology*, 3(2), 187-196

- Mirenowicz, J. & Schultz, W. (1994) Importance of unpredictedness for reward responses in primate dopamine neurons. *Journal of Neurophysiology*, 72, 1024-1027
- Myslivecek, J. (1997) Inhibitory learning and memory in newborn rats. *Progress in Neurobiology*, 53(4), 399-430
- Nieoullon, A. (2002) Dopamine and the regulation of cognition and attention. *Progress in Neurobiology*, 67(1), 53-83
- Overtoom, C. C. E., Verbaten, M. N., Kemner, C., Kenemans, J. L., Engeland, H. v., Buitelaar, J. K., van der Molen, M. W., van der Gugten, J., Westenberg, H., Maes, R. A. A., & Koelega, H. S. (2003) Effects of methylphenidate, desipramine, and -dopa on attention and inhibition in children with Attention Deficit Hyperactivity Disorder. *Behavioural Brain Research*, 145(1-2), 7-15
- Phillips, A. G. (1984) Brain reward circuitry: a case for separate systems. *Brain Research Bulletin*, 12(2), 195-201
- Posner M.I. & Petersen S.E. (1990) The attention system of the human brain. *Annual Review of Neuroscience*, 13, 25-42
- Rescorla R.A. & Wagner A.R. (1972) A theory of pavlovian conditioning: variations in the effectiveness of reinforcement and nonreinforcement. In *Classical Conditioning II: Current Research and Theory*, eds Black, A.H. & Prokasy, W.F. pp 64-99. New York, USA: Appleton Century Crofts
- Robbins, T. W. & Everitt, B. J. (1996) Neurobehavioural mechanisms of reward and motivation. *Current Opinion in Neurobiology*, 6(2), 228-236
- Rodriguez, E., George, N., Lachaux, J.-P., Martinerie, J., Renault, B., & Varela, F. J. (1999) Perceptions shadow: long-distance synchronization of human brain activity. *Nature*, 397, 430-433
- Schultz, W. (1997) Dopamine neurons and their role in reward mechanisms. *Current Opinion in Neurobiology*, 7(2), 191-197
- Schultz, W. (1998) Predictive reward signal of dopamine neurons. *Journal of Neurophysiology*, 80, 1-27
- Schultz, W. (1999) The Reward Signal of Midbrain Dopamine Neurons. *News in Physiological Science*, 14, 249-255
- Schultz, W. & Romo, R. (1990) Dopamine neurons of the monkey midbrain: contingencies of responses to stimuli eliciting immediate behavioural reactions. *Journal of Neurophysiology*, 63, 607-624
- Schultz, W., Romo, R., Ljungberg, T., Mirenowicz, J., Hollerman, J. R., & Dickinson, A. (1995) Reward-related signals carried by dopamine neurons. In *Models of information processing in the basal ganglia*, eds Houk, J. C., Davis, J. L. & Beiser, D. G., pp 233-248. Cambridge, MA, USA: MIT Press
- Silkis, I. (2001) The cortico-basal ganglia-thalamocortical circuit with synaptic plasticity. II. Mechanism of synergistic modulation of thalamic activity via the direct and indirect pathways through the basal ganglia. *Biosystems*, 59(1), 7-14

- Skrebitsky, V. G. & Chepkova, A. N. (1998) Hebbian synapses in cortical and hippocampal pathways. *Review of Neuroscience*, 9(4), 243-264
- Smith Y, Shink, E., & Sidibe, M. (1998) Neuronal circuitry and synaptic connectivity of the basal ganglia. In *Surgical treatment of movement disorders*, eds Bakay, R.A.E., Mayberg, M.R. & Winn, H.R., pp 203-223. Philadelphia, PA, USA: W.B. Saunders Company, Philadelphia
- Turner, P. (2005) Undergraduate learning at programme level: an analysis of students' perspectives. PhD thesis, University of Bath