The concept of working memory is ubiquitous in research concerned with temporary storage and on-line processing in humans and animals. The replacement by Baddeley and Hitch (1974) of the concept of short-term memory focused largely on retention of word lists, with the broader concept of a multiple component working memory, was remarkable in redefining a major area of scientific endeavour. It has been remarkable in stimulating substantial lines of research yielding insight into verbal and visuo-spatial temporary storage through behavioural studies of healthy and brain damaged human adults and children. Recent years have seen genuine progress in the understanding of executive functions, previously consigned to a largely intractable homunculus. It has also been remarkable in its resilience over more than three decades of scientific interrogation, and of robust declarations of its demise (Crowder 1982; Ruchkin et al., 2003). To mark 30 years of this resilience, the Second International Conference on Working Memory was held in Kyoto, Japan in 2004, and papers in this Special Issue were inspired (although not exclusively so) by some of the contemporary research presented at that conference. This followed on from the first such International Conference on Working Memory held in 1994 in Cambridge, UK to mark 20 years since the landmark paper.

From the 2004 Kyoto conference, it was clear that the working memory concept has survived very successfully like all powerful ideas because of its relative simplicity and its combination of predictive and explanatory power. However, like the memes of Dawkins (1976), working memory as an idea has evolved into several variations (reviewed in Miyake and Shah, 1999); the original trio of phonological loop, visuo-spatial scratchpad and central executive is now a quartet with the addition of an episodic buffer (Baddeley, 2000) included to account for temporary retention of integrated representations which are multi-sensory and have semantic content. In contrast is the concept of a domain general working memory (e.g., Daneman and Merikle, 1996; Kane and Engle, 2002) with a focus on individual differences in mental ability. Other approaches have developed computational models of overall working memory function (Barnard, 1999; Lovett et al., 1999) or of domain specific functions (review in Burgess and Hitch, 2005). The 2004 Kyoto Conference also reflected the exponential rise in the use of measures of brain activity to track the time course and the neuroanatomical networks associated with working memory function. However, whether functional imaging studies with PET, fMRI, ERP or MEG will help assess the relative utility of the range of working memory theories on offer any more effectively than behavioural studies remains a topic of some debate (Coltheart, 2006; Henson, 2005; Page, 2006). The papers in this Special Issue on “Working Memory in the Brain” address this issue directly.

Marklund et al. (2007, this issue) employ a mixed blocked and event-related design in an fMRI study of episodic, semantic and working memory contrasted with sustained attention. This approach identified transient activity, particularly in the left dorsolateral prefrontal cortex (DLPFC) that appears to reflect the operation of working memory during retrieval from long-term memory. It also identified sustained activity in more ventro-lateral PFC that appears to reflect maintenance of attention. Raye et al. (2007, this issue) provide fMRI evidence for left DLPFC activation associated with participants “refreshing” (simply thinking about) the visual appearance of a recently presented word. In contrast, more anterior areas of the left PFC appear associated with initiating a mental process of a physical button press, while subvocal rehearsal of a single word was associated with left ventro-lateral PFC. The pattern of activation for verbal rehearsal is certainly consistent with previous studies linking Broca’s area with rehearsal in the absence of a substantive verbal memory load (e.g., Logie et al., 2003; Paulesu et al., 1993). The approach also offers a means to explore whether the differential activation patterns reported by Raye et al. (2007, this issue) reflect rehearsal versus refreshing or a verbal rehearsal function versus a visual rehearsal function – a possible dissociation identified both from recent behavioural studies (e.g., review in Logie, 2003) and in brain imaging studies (e.g., D’Esposito et al., 1998).

Takeda and Funahashi (2007, this issue) identify groups of neurons in the dorso lateral prefrontal cortex of the monkey brain that show sustained activation during a delay between presentation of a visual cue and saccades to that cue. Moreover, this activation appears to be
specific to the direction of the planned saccade which indicates that these neurons might be associated with temporary memory for the location of the cue rather than just some form of general anticipation of a future action. These results are neatly complemented by the McCollough et al. (2007, this issue) paper which reports lateralised ERP data from human volunteers associated with a delay period between presentation and test (change detection) of a target array in the contralateral visual hemifield. Like the Takeda and Funahashi (2007, this issue) results, the directional sensitivity of the human ERP data points to temporary retention of the visual information rather than some form of preparation for response. Moreover, McCollough et al. (2007, this issue) demonstrate that the ERP signal is sensitive to the size of the visual memory load and not to overall task difficulty. One complication is that the human contralateral ERPs appear in more posterior areas, and Takeda and Funahashi (2007, this issue) focused on neurons in the DLPFC.

Watanabe et al. (2007, this issue) offer further insight into possible involvement of PFC neurons in the monkey (single cell recording) and in the human (fMRI), in retention of information about an anticipated event. In the case of the monkey, they report increased firing in anticipation of receiving a preferred reward compared to a non-preferred reward. This points to a representation held in working memory rather than a general anticipatory process. Watanabe et al. (2007, this issue) go further in arguing that this increased firing linked with preferred rewards indicates a neural response akin to emotion, and they identify orbito-frontal cortex as host to a “working memory for emotion”.

What was originally referred to as the central executive of working memory has become much more tractable both theoretically and empirically in recent years through identification of a range of executive functions. For example, using latent variable analysis with behavioural data, Miyake et al. (2000, 2001) identified memory updating, task shifting and inhibition as three different cognitive functions, all of which are typically considered to be executive processes. The PET study reported in this volume by Collette et al. (2007, this issue) focuses on three different memory updating tasks and identifies a complex network of activation involving prefrontal and parietal cortex and the cerebellum. They suggest that the updating process also may involve different neuroanatomical networks for different updating tasks, rather than there being a generaliseable updating function. Of course, it might be in the nature of executive processes that they involve rather more complex networks of activation than do temporary storage tasks. Moreover, Collette et al. (2007, this issue) use memory tasks that are likely to involve rather different temporary memory functions, namely consonants, categorized word lists, and tones of different pitches, each of which is conceptually distinct from behavioural studies and associated with activation of different areas of the brain from the neuroimaging literature. Hence it is possible that updating may operate on similar principles but involve different networks in the brain to support the updating function according to the type of material and temporary memory system that is being updated. This raises the interesting challenge as to whether other executive functions might operate in a similar fashion – that is, delivering the same kind of function (e.g., updating, task shifting, inhibition) in different ways according to the specific task, and the strategies that participants choose to perform those tasks. For example, Emerson and Miyake (2003) demonstrated that control of task switching can be implemented using subvocal rehearsal, often not considered to be an executive function.

An analogous theme is taken up in the paper by Sala and Courtney (2007, this issue) in which they argue that binding of two or more features (e.g., object identify and object location) in an integrated representation could be implemented in a variety of ways – for example by activation of domain specific areas for objects and for locations, or by a new network that does not necessarily involve separable cortical areas. It is striking from the behavioural data that performance levels do not differ according to whether only one feature or both features of a stimulus have to be retained. Even more striking is that there appeared to be no increase in activation in ventral and dorsal areas of the prefrontal cortex when both features had to be retained compared with one or the other feature. Indeed, they argue that there is an overall lower level of activation in the “remember both” condition. They offer the novel and intriguing account that there are cells common to dorsal and ventral areas of the PFC that are activated for both features through excitatory connections between the areas. Moreover, these areas are different from those cells that are specialised for location in the dorsal PFC and objects in the ventral PFC. The more specialised cells are therefore not activated in the “both” condition, leading to an overall reduction in the activation observed, and the retention of integrated objects rather than separate features. This conclusion is consistent with behavioural data on binding cited by the authors.

A more direct link between theory based on experimental, behavioural studies and brain imaging, this time using PET, is made in the paper by Beaman et al. (2007, this issue). In a review of some recent studies they note that there appear to be two forms of processing associated with effects of irrelevant speech in verbal working memory tasks. As noted by the authors, there has been an ongoing debate for over two decades (e.g., Salamé and Baddeley, 1982; Larsen and Baddeley, 2003) as to whether irrelevant speech disrupts verbal short term
memory performance because it has direct access to the phonological loop of working memory, or because the changing state of irrelevant speech and other varying auditory inputs disrupts an a-modal memory system that tags items according to their sequential order. Beaman et al. (2007, this issue) describe PET data linked with neuroanatomical and empirical arguments that irrelevant speech may be having two quite separate effects: one that has an impact on speech processing and the functioning of verbal short-term memory in the left superior temporal gyrus as a result of irrelevant speech presented to the right ear; another that has an impact on non lexical and non phonological processing in the right hemisphere following presentation of irrelevant speech or changing state auditory input to the left ear. This is a neat example of the use of neuroimaging techniques to help resolve a debate arising from behavioural studies, and also points to possible behavioural studies that could move the debate forward.

The papers considered thus far have been concerned largely with the healthy brain in younger adults. The final four papers are concerned with working memory in the damaged brain and in the healthy older brain. Newsome et al. (2007, this issue) used fMRI techniques to explore activation patterns in traumatic brain injury (TBI) patients while undertaking n-back tasks. These are often thought to measure the storage and updating processes in working memory. With a low memory load, the TBI patients showed less activation in frontal cortex than did a group of patients who had suffered orthopaedic injuries but with no record of head injury. In contrast, the TBI patients showed greater activation in more posterior areas compared with the non brain injured group. With a higher memory load, the differences between the groups in activation patterns were less clear. There were no clear differences in memory performance between the groups despite the differences in activation patterns. The results point to possible alternative strategies for task performance in the TBI group, particularly for relatively low storage loads, that might compensate for the cognitive impact of the damage sustained. However this topic clearly points to a fruitful line of research that might include ERP as well as fMRI studies to track the time course as well as the location of processing in TBI patients, and additional studies with TBI patients showing clear cognitive impairments and possible longer term follow up with those patients that show cognitive recovery in the weeks and months following the onset of the brain trauma.

Hamilton and Martin (2006) offer a powerful and detailed single case study of a patient with a specific deficit of semantic short-term memory. These kinds of patients are relatively rare in the neuropsychological literature and they offer significant insight into the role of semantic knowledge in short-term memory tasks. The pattern of impairment arises from an enhanced sensitivity to the build up of proactive interference. The authors argue that control processes in working memory, in particular the inhibition of previously presented material may account for the difficulty in this patient rather than a deficit in working memory capacity.

The final two papers consider working memory in the healthy older brain. Rypma et al. (2007, this issue) use fMRI linked with accuracy and response time data in delayed response tasks to explore the activation patterns in older people that are associated with better or poorer behavioural performance. Their intriguing result is that activity in the PFC increases in older adults when they have shorter response times and more accurate retrieval performance, but activity in the same areas decreases in healthy younger adults when they perform well on the behavioural task. Results are taken to support the influential view that most if not all cognitive changes in old age may be attributed to cognitive slowing. This result is consistent with the report by Logie et al. (2007, this issue) that older adults are slowed differentially compared with younger adults when asked to perform a memory task and a response time task concurrently. However, the notion that cognitive slowing with age affects all cognitive tasks is undermined by the finding that the slowing in the older people occurred only when the response time task was coupled with the retrieval phase of the memory task. When combined during the encoding phase of the memory performance, but not response time was affected more in the older people. Moreover, as these authors note, previous studies by this group have shown that when a memory task is combined with perceptuo-motor tracking instead of a response time task, then there is no clear evidence that healthy older people have any particular difficulty under dual task conditions, providing single task performance is equated between younger and older groups.

Papers in this Special Issue arose from spontaneous submissions of manuscripts that were subject to the normal exacting review standards of Cortex. In this sense it is intended to be a sample rather than a comprehensive collection of some of the best experimental and brain imaging studies of working memory in healthy and brain damaged adults. Nevertheless, the science reported here reflects some of the major fruitful approaches to conceptual understanding of working memory as well as its relationship with brain function. Working memory, age 32, appears to be alive and in remarkably robust health.

REFERENCES

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