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Editorial

Memory formation: Its changing face

'*The two offices of memory are collection and distribution*' Samuel Johnson (1759)

Attempts to understand the neurobiological basis of memory are overwhelmed by the enormity of the task. The practical response is to divide the topic up into more and more manageable chunks. On the face of it there are numerous ways of dividing up memory processes, for example, by type of learning (classical conditioning, recognition memory, spatial learning, motor skills, to name but a few), by focussing on the neural and molecular properties of key brain structures thought to be especially critical for aspects of learning, or by contrasting memory across species or even phyla of animals. A division that subsumes all of the above approaches is that between memory formation ('collection') and memory retrieval ('distribution'). The attraction of targeting memory in this way is that it helps to reveal common features related to memory formation across different species, different brain sites, and different classes of learning. The drawback of trying to examine just 'memory formation' is that this concept is increasingly being replaced by a much more dynamic vision that blurs the distinctions between various memory processes and, at the same time, reveals a growing constellation of factors that moderate consolidation processes. These discoveries have forced a re-appraisal of what is meant by memory formation. This Special Issue of Neuroscience & Biobehavioral Reviews provides novel insights to this changing face of memory formation.

Any consideration of memory formation must acknowledge the paradox that retrieval mechanisms are inevitably affected by the quality of the initial representation of that event (Craik and Rose, 2012). Thus, in one sense, memory formation and memory retrieval are inextricably linked. While acknowledging this conceptual problem, it had become traditional to talk about distinct processes of encoding, consolidation and retrieval, and then placing them in a standard temporal relationship so that one follows the other. This simplistic notion is undermined by research into memory consolidation and reconsolidation. That is, the realisation that some memories (or some aspects of some memories) are labile and vulnerable to change long after initial memory formation. The possible boundary conditions for reconsolidation are discussed (Finnie and Nader, 2012) and related to the concept of metaplasticity, i.e., molecular mechanisms that regulate the efficacy of neuronal plasticity. Pursuing the theme of memory consolidation and subsequent transformation, Nadel et al. (2012) argue that a fundamentally different set of concepts are now needed to embrace this far more dynamic, and far more complex, view of memory formation that appears to lack specific time-frames.

It is perhaps not surprising that several reviews in this Special Issue focus on the properties of the medial temporal lobe, despite memory formation in its broadest sense being a property of essentially all of the brain. This focus on the medial temporal lobe reflects the involvement of this region in those forms of memory most readily brought to our conscious mind, i.e., our memory for day to day events (episodic memory) and our memory for facts (semantic memory). Consequently these memories have a unique personal status that creates our sense of individuality. The hippocampus is thought to occupy an especially important role for the formation of episodic memories, and new syntheses of findings from rodent research are provided to understand how the hippocampus may function with parahippocampal areas to bring together 'what' and 'where' information (Eichenbaum et al., 2012). Further new ideas about how contextual and spatial learning by rats may relate to acquiring new episodic memories are discussed (Stella et al., 2012) and new computational approaches outlined. The complex issue of how to relate findings across species, in particular from rodents to humans, is further explored (Battaglia et al., 2012) by contrasting computational algorithms for memory with those for linguistics.

Adjacent to the hippocampus within the temporal lobe is the amygdala. The amygdala is centrally involved in the modulation of memory formation for an event when this event has heightened emotional valence (McIntyre et al., 2012). Details are provided giving insights into the multiple, complementary mechanisms that enable this emotional modulation of memory formation. It is also known that the amygdala, in conjunction with other areas, has a critical role in fear conditioning. A key clinical issue relates to the persistence of inappropriate fear memories and the factors that may alter the rate of extinction of those same memories. The significance of this topic to the present Special Issue emerges as it is appreciated that extinction is itself a form of memory formation (Orsini and Maren, 2012), which despite its enormous importance as a form of learning has often been overlooked. A closely related topic concerns the ways in which stress affects memory formation, where once again the amygdala, along with other medial temporal structures have central roles (Schwabe et al., 2012). Glucocorticoids are known to be key moderating factors in memory formation during heightened emotion and stress (McIntyre et al., 2012; Schwabe et al., 2012), and the role of glucocorticoids has been extended to examine the complex issue of memory for social interactions (van der Kooij and Sandi, 2012).

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A vital goal in delivering more sophisticated descriptions of memory formation is to encompass the ways in which this process captures multiple interactions across structures. This concept is given prominence in those reviews on memory modulation by emotion and stress (e.g., McIntyre et al., 2012; Schwabe et al., 2012), and is further developed in a specific consideration of the interactions between the hippocampus and the medial prefrontal cortex for episodic memory (Kroes and Fernandez, 2012). Once again, the emphasis is on dynamic interactions, both across brain sites and across time. These hippocampal–medial prefrontal connections comprise one of a group of three distinct networks of hippocampal pathways, each distinguished by different patterns of efferents that have been defined in the primate medial temporal lobe by Aggleton (Aggleton, 2012). The identification of these various networks both reinforces the notion that the hippocampus has multiple functions and also moves the spotlight onto the importance of the subiculum for memory formation (Aggleton, 2012).

Another dimension to be considered is how memory formation changes with the development of an individual across their lifetime. It has long been appreciated that babies and infants have longer and more intense sleep. It is now emerging that these changes in sleep pattern may interact with memory consolidation in ways that are different to those in the adult brain (Wilhelm and Born, 2012). As we mature there appear to be further changes in episodic memory formation that relate to prefrontal–temporal lobe interactions, as well as changes within the medial temporal lobe (Ofen, 2012). These changes are paralleled by increased semantic knowledge, which brings about schema-based alterations in memory. This consideration of developmental aspects of memory formation concludes with a review of memory encoding, aging, and senescence (Craik and Rose, 2012) where issues related to altered semantic processing and changes in neuroplasticity are examined. The concept of ‘brain fitness’ is also considered (Craik and Rose, 2012).

The rationale behind this special issue is to highlight the complex, diverse array of factors that affect memory formation. A repeated theme is the way in which memory encoding cannot be located in a given place or a given time, and that the move to much more dynamic models is a necessity that brings with it numerous challenges. Indeed, the very term ‘memory formation’ becomes increasingly outmoded as these reviews spell out how the divisions between different aspects of memory have become increasingly eroded as we gain more sophisticated insights into what is, in one sense, the prime purpose of the brain–memory formation.

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