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## Levels of processing: A view from functional brain imaging

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This paper briefly reviews two central assumptions of the levels-of-processing framework in the light of findings from recent PET and fMRI studies: First, to address the suggestion that memory traces can be seen as records of analyses carried out for the purposes of perception and comprehension, studies on encoding-retrieval overlap in brain activation patterns are considered. Second, to address the suggestion that deeper, more semantic, processing results in more durable traces, studies of how encoding activity relates to processing depth and subsequent memory performance are examined. The results show that some of the sensory regions that are activated during initial perception are subsequently reactivated during retrieval, and activity in frontal and medial-temporal brain regions is related to depth of processing and level of memory performance. Collectively, these results provide support for central components of the levels framework.

In their classical paper on levels of processing, Craik and Lockhart (1972) suggested that memory traces can be seen as records of analyses carried out for the purposes of perception and comprehension, and that deeper, more semantic, processing results in more durable traces. In the present review, these suggestions will be discussed in the light of findings from recent PET and fMRI studies. First, findings from studies on encoding-retrieval overlap in brain activation patterns will be considered. If a memory trace is a record of processes recruited during initial perception and comprehension, then the activation of a trace during subsequent retrieval should involve reactivation of processes that were engaged during the original experience. Accordingly, encoding-retrieval overlap in brain activation patterns is expected. Second, studies of brain activity associated with deeper, more semantic, processing will be considered. If there are different levels of processing, then the activity in some brain regions should vary as a function of the depth of processing. Moreover, given that deeper processing results in more durable traces, activity in regions

associated with deeper processing should predict subsequent memory performance.

### ENCODING-RETRIEVAL OVERLAP IN BRAIN ACTIVITY

Several recent PET and fMRI studies have examined the relation between brain activity during initial encoding/acquisition and subsequently during episodic memory retrieval (see Nyberg, 2002). Collectively, these studies provide converging evidence that some of the brain regions that are activated during encoding are reactivated during retrieval. As summarised in Table 1, overlap is observed in different brain regions depending on the specific type of event information. However, regardless of type of information, the emerging view is that only a subset of the encoding-related activation pattern is reactivated during retrieval, and the sites where overlap is observed tend to be in secondary rather than in primary areas (Nyberg, 2002; see also Wheeler, Petersen, & Buckner, 2000).

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TABLE 1  
Functional brain imaging studies of episodic encoding–retrieval overlap

Type of event information	Select overlap sites
<i>Auditory information</i>	
Nyberg et al. (2000)	Bilateral auditory responsive cortex (BA 21/22)
Wheeler et al. (2000)	Left superior temporal cortex (BA 22)
<i>Visual information</i>	
Roland & Gulyás (1995)	Precuneus & angular gyrus
Wheeler et al. (2000)	Precuneus (7) & left fusiform cortex (19)
<i>Spatial information</i>	
Köhler et al. (1998)	Right inferior parietal cortex (BA 39/40)
Moscovitch et al. (1995)	Right inferior parietal cortex (BA 39/40)
Persson & Nyberg (2000)	Bilateral inferior parietal cortex (BA 39/40)
<i>Motor information</i>	
Nyberg et al. (2001)	Left ventral motor cortex (BA 4/6)

BA = Brodmann area

In several of the studies on encoding–retrieval overlap, reactivation of encoding-related activity has been demonstrated when the test required the subjects to retrieve specific perceptual information. For example, Persson and Nyberg (2000) contrasted retrieval of spatial event information (trying to remember if centrally presented stimuli had appeared on the left or right side of the computer screen at encoding) with conditions that did not involve retrieval of spatial information. It was found that regions in the dorsal visual stream were differentially activated during retrieval of spatial information. These regions overlapped with regions that were activated when subjects tried to memorise location information. While such findings of encoding–retrieval overlap provide some support that memory traces can be seen as records of analyses carried out for the purpose of perception and comprehension, there is also evidence that the act of directing one's attention to a certain modality can lead to activation of brain regions that are engaged during real perception (see Cabeza & Nyberg, 2000). Therefore, in order to provide strong evidence that it is the actual process of remembering that accounts for the reactivation pattern, it is critical to control for potential confounding effects of selective attention. This has been done in several studies.

One example comes from an experiment by Nyberg, Habib, McIntosh, and Tulving (2000) on "incidental reactivation". In that study, subjects encoded single visual words and visual words paired with sounds. Subsequently, they were given yes/no recognition tests of visually presented words. It was found that recognition of words that

had been encoded in the context of auditory sounds was associated with increased activity in auditory regions of the temporal lobes. This was so despite the fact that there was no demand to try to remember auditory information (hence the term "incidental"). These and related findings (e.g., Nyberg et al., 1995) provide strong evidence that perceptual information is part of memory traces and that the brain regions where such information is stored are spontaneously reactivated at retrieval.

Findings that sensory brain regions are recruited during episodic memory tests can be related to the original proposal in the levels-of-processing framework that "there is usually no need to store the products of preliminary analyses" ( Craik & Lockhart, 1972, p. 675). "Preliminary analyses" referred to analyses of various sensory features (e.g., brightness and loudness). However, subsequent studies showed that records of sensory information can persist to affect later performance over a long retention interval (e.g., Conway & Gathercole, 1987). Indeed, in later developments of the framework, it was concluded that "sensory or surface aspects of stimuli are not always lost rapidly as we claimed in 1972" (Lockhart & Craik, 1990, p. 98). Thus, functional brain imaging findings of activation of sensory brain regions during standard episodic memory tests are consistent with the levels framework.

## LEVELS OF BRAIN ACTIVITY

The preceding discussion concerned recruitment of sensory brain regions during encoding. In

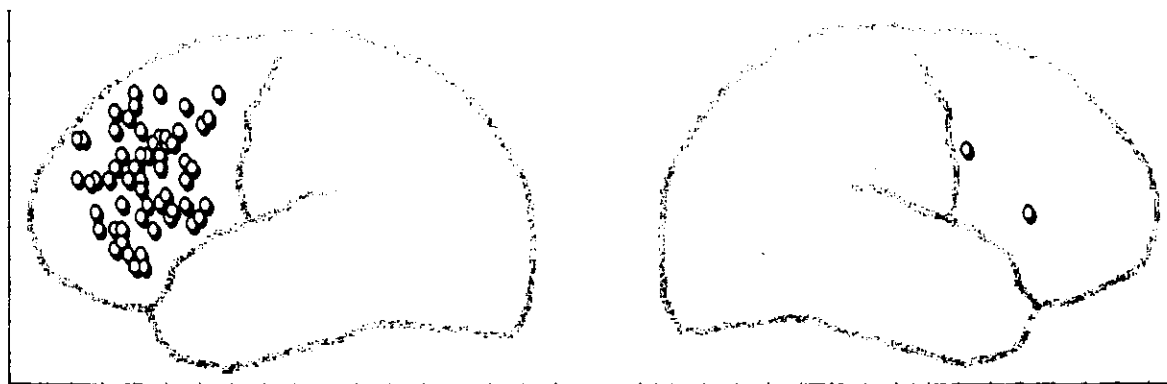
addition, a number of PET and fMRI studies have found that intentional as well as incidental encoding processes are associated with prefrontal brain regions. In an early study (Kapur et al., 1994), brain activity associated with semantic processing (living/nonliving classification) was contrasted with activity associated with a more shallow processing task (detecting the presence or absence of the letter a). It was found that deeper, semantic processing was associated with increased activity in left prefrontal regions (BAs 10, 45, 46, 47). Similar findings have been observed in a number of studies (e.g., Grady, McIntosh, Rajah, & Craik, 1998; Kapur et al., 1996, for reviews, see Buckner, Logan, Donaldson, & Wheeler, 2000; Cabeza & Nyberg, 2000), and it has been suggested that encoding processes are more strongly associated with the left than the right frontal lobe (Nyberg, Cabeza & Tulving, 1996, 1998; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994; see Figure 1). It should be noted, however, that regions of the right frontal lobe have been engaged during encoding of nonverbal information such as unfamiliar faces (e.g., Kelley et al., 1998).

In their early study on neuroanatomical correlates of the levels-of-processing effect (Kapur et al., 1994), Kapur, Craik and colleagues proposed that increased activity in left inferior frontal regions leads to more readily retrievable memory traces. This proposal was supported by the results from an event-related fMRI study (Wagner et al., 1998). In that study, brain activity was measured while subjects made semantic decisions (abstract or concrete word?). After a retention interval, they were given a recognition memory test. The event-related design permitted identification of

brain regions that showed increased activity during encoding of words subsequently remembered compared with those subsequently forgotten. It was found that correct recognition that was accompanied by high confidence was associated with increased activity in several left prefrontal regions, and also in left temporal regions (parahippocampal/fusiform gyri). The results of a related event-related fMRI study on encoding of indoor and outdoor scenes provided additional support that level of prefrontal and medial temporal (parahippocampal) activity predicted subsequent memory performance (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998). In the latter study the frontal activation was right-lateralised and the temporal activity was bilateral, which likely reflected the nonverbal nature of the stimuli. These event-related fMRI findings provide strong support that increased activity in frontal regions leads to more readily retrievable memory traces.

## CONCLUSION

In conclusion, functional brain imaging studies have identified neuroanatomical correlates of two central components of the levels-of-processing framework; that memory traces are records of analyses related to perception and comprehension, and that deeper semantic processing yields more durable records. Specifically, brain-imaging findings suggest that input from frontal regions to medial temporal regions affects the binding of sensory information into memory traces (cf., Buckner et al., 2000). Clearly, levels-of-processing has proven to be a useful framework not only



**Figure 1.** Results from published PET and fMRI studies of intentional and incidental encoding (based on Cabeza & Nyberg, 2000). Each circle represents the result of one experimental contrast. Only frontal peaks are plotted. Courtesy of Roberto Cabeza.

for memory research but also for cognitive neuroscience.

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