The neural bases of haptic working memory

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Introduction

When deciding which kiwi fruit or pear needs eating first or which drink has the right temperature to be consumed on a warm day, we are likely to explore and compare hardness or temperature using our hands. The process that enables us to keep the relevant information active for task performance over a short period of time is called 'working memory' (WM) [1]. WM allows us to hold stimulus characteristics on-line to guide behaviour in the absence of external cues or prompts [2]. Without active WM, initial percepts decay quickly with different time constants for different input modalities (Box 1).

The neural basis of *haptic WM* is usually studied indirectly in sequential discrimination paradigms, when information from one stimulus has to be retained for comparison with a second stimulus. In an attempt to avoid confounds due to hand and finger movements, passive stimulus presentation prevails over the more natural active exploration of tactile object features such as shape and texture.

Haptic perception can be decomposed into *tactile* and *kinaesthetic perception* [3]. Functionally, the tactile (cutaneous) sense provides awareness of stimulation of the outer surface of the body, whereas the kinaesthetic sense provides us with an awareness of static and dynamic body posture. The term *tactual perception* was coined to refer to all perceptions mediated either by cutaneous sensibility and/or kinaesthesis. Haptic perception (and therefore haptic memory) is more than the sum of kinaesthetic and passive tactile processing. While passive tactile stimulation and isolated *kinaesthesia* produce tactual sensations, only active exploration allows for the perception of objects in space [4,

Box 1. Sensory memory

After a stimulus has ceased, some sensory information is retained independently of active rehearsal or interference. This 'ultra' short-term form of memory has been explored most intensively for visual (*iconic memory*) and auditory stimuli (*echoic memory*). In both modalities, sensory memory is considered to be very short lived, in the order of a few hundreds of ms. However, a study by Melzack and Eisenberg [71] indicates that somatosensory 'afterglows' can persist over minutes when the lip was stimulated with nylon monofilaments. Nevertheless, it might be prudent not to generalise these results to other body sites and kinds of tactile stimuli. Results from Gilson and Baddeley [8], Millar [19] and Sinclair et al. [13] indicate that some information that is robust against interference persists for 5–10 s for the location of touch, three-dimensional shapes and vibrotactile frequency. Results from Harris et al. [14, 15] point to two different processes within the initial seconds following vibrotactile stimulation, the first one lasting up to 1 s. This would be in line with other modalities. It is safe to assume that the exact characteristics of tactile sensory memory are not yet thoroughly explored and might differ for the wide variety of tactual features.

Box 2. A cognitive model of working memory

In 1974, Baddeley and Hitch [72] introduced a multicomponent model of WM that has remained influential until today. The theory proposes two *slave systems* (the *phonological loop* for verbal material and the *visuo-spatial scratch-pad* for visual information) that are responsible for short-term maintenance of information. Although Baddeley [73] acknowledged the possibility of additional slave systems for other kinds of information (e.g. tactile) no further slave systems were added in later elaborations (Fig. 1).

A *central executive* is responsible for directing attention to relevant information, suppressing irrelevant information and inappropriate actions, and for coordinating cognitive processes when more than one task must be done at the same time.

WM allows for temporal storage and manipulation of a limited amount of information and thereby supports human cognitive processes by providing an interface between perception, long-term memory and behavioural response [6, 70]. Only task relevant features of the initial memory trace (Box 1) are retained, and maintenance of this information is susceptible to interference (Box 3). The upper capacity limit of WM has been estimated at four so-called ‘chunks’, but capacity is reduced when information is not merely maintained but also manipulated [36] (Box 3).

How does working memory relate to other memory systems?

A well-know taxonomy of human memory systems makes a distinction between explicit memory which is consciously accessible and implicit memory which is not [74]. Implicit (nondeclarative) memory is related to perceptual and motor skills. Implicit memory has been related to structures in the neocortex, striatum, amygdala, cerebellum and reflex pathways. Explicit (declarative) memory contains factual knowledge of people, places and things as well as their meaning. It has been subdivided in episodic memory, for events and personal experiences, and semantic memory, for facts. The initial stages of explicit long-term memory are thought to be mediated by structures in the medial temporal lobe, including the hippocampus, perirhinal, enthorhinal and parahippocampal cortex. The association areas in parietal, frontal and temporal cortex are believed to be the ultimate repositories of distributed explicit memory traces. WM is required for encoding and recall of explicit knowledge, and perhaps for some types of implicit knowledge as well. However, not all information processed in WM enters long-term memory.

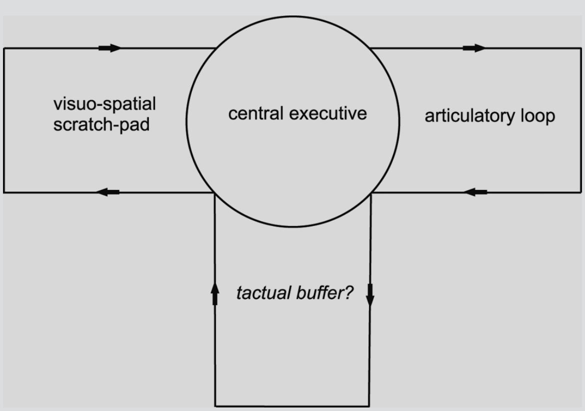

Figure 1. WM
A WM model, adapted from Baddeley [70]. Is there enough evidence to assume a discrete buffer for tactual information along with its own neural network?