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Review

Recollection and familiarity in the human thalamus

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ABSTRACT

Recollection and familiarity are two distinct forms of recognition memory that differ in terms of the associative richness of the memory experience. In recollection, exposure to a previously encountered item cues the recollection of a number of contextual, temporal and other associative information. In the case of familiarity, instead, the item is recognized as previously encountered, but it does not cue any associative information. According to the dual-process theory, the memory processes that underlie recollection and familiarity are qualitatively different and this distinction is reflected in the existence of different neural substrates underlying the two processes. Thus far, research has primarily focused on distinct regions of the medial temporal lobe as implicated mostly in recollection (hippocampus) or familiarity (perirhinal cortex). Aggleton and Brown (1999) suggested extending the neuroanatomical distinction to other cortical and subcortical areas of the brain, including the thalamus. In particular, they proposed the existence of two reciprocally independent neural circuits for recollection and familiarity. The former would include the hippocampus, the fornix, the mammillary bodies and the anterior thalamic nuclei. The second would involve the mesial magnocellular portion of the mediodorsal nucleus connected to the perirhinal cortex through the ventroamygdalofugal pathway. Here we review neuropsychological evidence in experimental animals and brain-damaged individuals and functional neuroimaging evidence in healthy humans that supports Aggleton and Brown's model at the level of the thalamus. The evidence substantially supports the functional relationship between recollection processes and integrity of the thalamic anterior nuclei. Additional evidence, not predicted by the model, has been provided in favour of the reliance of recollection on the integrity of the lateral portion (parvocellular) of the mediodorsal nucleus. Finally, there is sparse and controversial evidence in support of the reliance of familiarity on the integrity of the mesial portion of the mediodorsal nucleus, possibly due to neuroimaging methodological limits which did not satisfactorily distinguish between the medial and lateral portions of the mediodorsal nucleus.

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1. Role of the human thalamus in declarative memory: an overview

The role of the human thalamus in memory functioning has been known for a long time (Schulman, 1964; Taylor, 1964). It has commonly been related to the close anatomical connections between regions in the mesio-temporal lobe (MTL), particularly the hippocampus proper, and diencephalic structures including some thalamic nuclei. In this regard, Delay and Brion (1969) proposed the existence of a memory circuit that starts from the hippocampal formation in the MTL and reaches the mammillary bodies (MB) via the subiculum-fimbria-fornix complex. The MB are connected through the mammillo-thalamic tract (MTT) to the anterior thalamic nuclei (AN), which in turn project to limbic cortical areas (anterior and posterior cingulum and retrosplenial cortex). According to Aggleton and Saunders (1997), a lesion at any level of this circuit could be responsible for an anterograde amnesic syndrome whose characteristics are clinically indistinguishable from those of classical hippocampal amnesia.

Particularly instructive in this regard has been the description of amnesic patients with isolated or predominant damage to the mesial regions of the thalamus. Historically, the first condition in which a clinically relevant declarative memory disorder was associated with pathological alterations of the thalamus was the alcoholic Korsakoff syndrome, a chronic stage of acute Wernicke's encephalopathy (Kopelman et al., 2009). It has long been debated whether the amnesic syndrome characteristic of these patients (generally associated with a relevant deficit of frontal functions) is mainly related to the neuronal loss at the level of the MB or directly affecting the AN or to the mediodorsal (MD) thalamic nucleus. The neuroimaging of Korsakoff's syndrome (see Jung et al., 2012) provides little in vivo evidence of the intrathalamic localization of lesions responsible for memory deficits. Most recent neuropathological evidence supports, however, a close relationship between AN damage and memory dysfunction (Harding et al., 2000).

Lacunar infarcts at the level of the anterior mesial regions of the thalamus are the second condition of a primary thalamic disease able to simulate a hippocampal amnesic syndrome. In this case, apart from some early neuropathological studies (Castaigne et al., 1981), most of the available evidence about the intrathalamic localization of the critical damage is provided by in vivo neuroimaging studies. In a detailed analysis of the relevant literature, Carlesimo et al. (2011) were able to review 41 papers (published between 1983 and 2009) for (with) a total of 83 patients who had suffered a thalamic ischaemic stroke in the territories supplied by the tuberothalamic and/or paramedian arteries (17 patients had right-sided lesions, 25 left-sided lesions and 41 bilateral lesions). The main results of that review can be synthesized as follows: (i) similar to amnesic patients with mesio-temporal lobe damage, patients with vascular thalamic amnesia display a prevalent deficit of declarative anterograde memory, a less severe deficit of retrograde memory and substantially normal short-term and implicit memory; (ii) unlike mesio-temporal lobe patients, vascular thalamic amnesics frequently present dysexecutive and behavioural deficits similar to those observed in patients with

frontal damage; (iii) the presence of amnesia in patients with thalamic lacunar infarcts is strongly predicted by involvement of the MTT. Indeed, 95% of patients with MTT damage, but only 46% without MTT involvement, had amnesia. Conversely, the involvement of neither the MD nucleus or the intralaminar nuclei significantly predicted the presence of a memory disorder. Damage to the MTT in thalamic vascular amnesic patients is consistent with the supposed role of the AN in the genesis of the memory deficit in Korsakoff patients. Indeed, this tract conveys the main contingent of hippocampal projections to the AN complex via the MB (a much smaller contingent reaches the AN via a direct access from the fornix).

Since the 2011 review, no crucial new evidence (either single cases or group studies) has been provided regarding the prevalence or the qualitative characteristics of cognitive deficits in individuals with anterior thalamic lesions. Only two studies merit citation, both relating the location of thalamic infarcts to the anatomically connected frontal and MTL cortical areas. In particular, Nishio et al. (2014), using a tractography procedure, demonstrated that the MTT and the anterior and inferior thalamic peduncles are disrupted in amnesic patients with anterior thalamic infarction. Instead, Serra et al. (2013), comparing the connectivity pattern of a pure amnesic patient with that of a patient with additional executive deficits, documented that only the second patient's lesions were located within nuclei that were highly connected with the prefrontal cortical areas.

In summary, there is wide clinical and experimental evidence of involvement of the thalamus in declarative memory functioning. The bulk of the evidence demonstrates that lesions at the level of the AN and the connected MTT play the most crucial role in the rise of thalamic amnesia, in tight relation to their anatomical connections with the hippocampus. There is, however, some indication (mainly deriving from the neuropathological literature on Korsakoff's patients) of involvement of the MD thalamic nucleus in some aspects of declarative memory.

2. Different components of recognition memory: the contribution of recollection and familiarity

2.1. Two routes to recognition: recollection and familiarity

Recognition memory is a form of declarative episodic memory retrieval in humans (other forms of episodic retrieval are free recall and cued recall). Recognition memory consists of remembering having previously received information or experienced an event to which one is currently exposed. It is widely agreed that the subjective experience of recognition may assume two different aspects depending on the associative richness of the memory experience. In one case, exposure to a previously encountered item cues the recollection of a number of contextual, temporal and other associative information that makes the experience of retrieval vivid, like reliving the event with the eyes of the mind. In other cases, instead, the item is recognized as previously encountered but it does not cue any associative information, so the act of remembering manifests just as a feeling of familiarity. These two modalities

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