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Stress and the control of remembering: balancing hippocampal and striatal forms of memory retrieval

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Memory can be controlled by multiple brain systems that may compete for control of behavior. It is by now well established that acute stress can bias this competition and favor dorsal striatum-dependent 'habit' learning over hippocampus-dependent 'cognitive' learning. Recent evidence in humans suggests that stress modulates the preferential engagement of multiple memory systems not only during memory formation but also at retrieval, after both hippocampal and dorsal striatal memory traces have been formed. The nature of this stress-induced shift of the brain systems guiding retrieval appears to depend on the intensity of initial training and may promote efficient responding during stressful encounters.

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Introduction

In the first half of the past century, the basal ganglia were mainly implicated in motor behavior [1]. Subsequent research challenged the view of the basal ganglia as a pure motor system and revealed that the basal ganglia are involved in a variety of cognitive functions, ranging from learning and memory to attentional processes or the building of action plans [1–3]. In particular, the dorsal striatum, composed of caudate nucleus and putamen, was shown to be relevant for a form of learning, often referred to as 'habit' learning, in which rather rigid stimulus-response (S-R) associations are incrementally built [1,4,5]. This putative dorsal striatal S-R 'habit' memory system has been dissociated from a flexible but cognitively more demanding ('cognitive') memory system that processes the relationship between multiple cues to build a cognitive map and depends mainly on the hippocampus [4,6]. These dorsal striatal and hippocampal memory systems operate in parallel [7] but may lead to distinct responses and compete for control of behavior [8,9]. A key question thus concerns the factors that determine which of these memory systems gets the upper hand and can thus guide behavior.

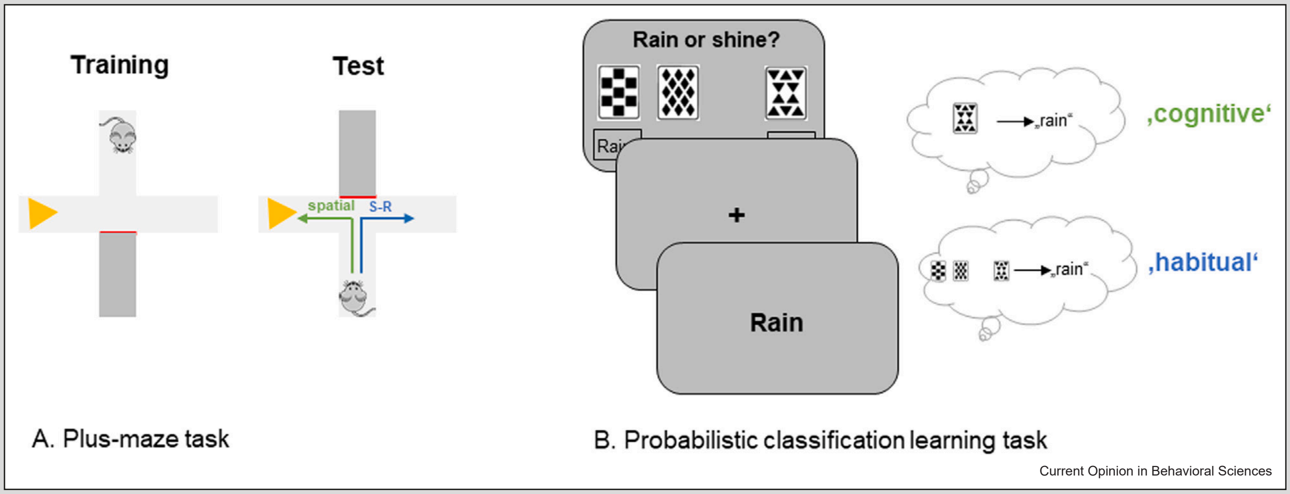
Research over the past two decades demonstrated that arousal or stress may bias the preferential engagement of striatal and hippocampal memory systems [10–12]. Stressful events have been known for long to be a powerful modulator of learning and memory [13,14]. Although major stress mediators, such as glucocorticoids and noradrenaline, were initially thought to act primarily on medial temporal and prefrontal areas, more recent evidence suggests that these stress mediators impact also striatal processes [15–17]. Beyond its effects on the functioning of a single memory system, stress has been shown to modulate the balance of multiple memory systems. Most of the research in this area focused on the preferential recruitment of hippocampal 'cognitive' memory and dorsal striatal 'habit' memory during learning. I will briefly summarize these findings in the first part of this review. Recent research revealed that stress may modulate, in addition to its effects on the engagement of multiple memory systems during learning, the preferential recruitment of coexisting hippocampal and dorsal striatal memory traces during remembering. I will focus on these recent discoveries in the second part of this review. Finally, I will suggest that modulatory effects of stress on the acquisition and expression of 'cognitive' vs. 'habitual' memories can be found across domains of memory, pointing to a general mechanism that may facilitate adaptation to stressful events.

Stress-related shift from hippocampal to dorsal striatal memory formation

Using dual-solution tasks that can be acquired by hippocampus-dependent spatial (cognitive) and dorsal striatum-dependent S-R (habit) memory (Box 1), initial studies in rodents showed that stress shortly before training may favor habit over cognitive learning [18,19]. These findings were important as they demonstrated that acute stress affects not only how much is learned or

Box 1 Dissociating hippocampal and dorsal striatal memory.

In order to separate hippocampus-based and dorsal striatum-based memory system, rodent studies used mainly spatial navigation tasks, in which a goal location could be learned using the relationship between multiple cues (i.e. a spatial or 'cognitive' strategy) or by learning the association with a single proximal cue or simple motor response (i.e. a response or 'habit' strategy). In a subsequent test trial, the proximal cue was relocated or the starting position changed to probe whether animals had learned a S-R association or a spatial location. For instance, in a plus maze task (A), animals were trained to find a food reward placed in the west arm. During training, they always started from the north arm. To dissociate hippocampal cognitive from dorsal striatal habit learning, a probe trial was administered in which animals started from the south arm. In this test, turning right was indicative of a habitual response strategy and turning left of a more cognitive spatial strategy [29]. Similar setups were used in cued versions of a water maze [18] or in a circular hole board task [19]. Inspired by these rodent experiments, human studies used similar dual-solution navigation tasks, mainly in virtual environments, to separate hippocampal spatial from dorsal striatal response learning [5,21,22]. In addition to these navigation tasks, human studies used probabilistic classification learning tasks in which participants learn based on trial-by-trial feedback how to categorize different patterns of stimuli (B). Neuropsychological studies in patients with amnesia or Parkinson's disease as well as fMRI studies in healthy participants showed that these classification tasks can be supported by the hippocampus and by the dorsal striatum [9,51]. At the behavioral level, the contributions of these systems manifest in cognitive and habitual learning strategies that can be identified by mathematical modeling [52].



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memorized in a situation but also what is learned and how a task is approached. Subsequent research provided insights into the underlying mechanisms. Specifically, injection of an anxiogenic drug directly into the basolateral amygdala was sufficient to induce the bias toward habit memory [20], suggesting a key role of the amygdala in the shift from cognitive to habit learning. Furthermore, pharmacological manipulations showed that noradrenergic arousal and glucocorticoids acting via the mineralocorticoid receptor are involved in the bias from hippocampal to dorsal striatal learning [19,20].

These rodent data were subsequently translated to humans. As in rodents, stress before training in dual-solution tasks favored dorsal striatal S-R memory also in humans, at the expense of hippocampal spatial memory [21,22]. Neuroimaging studies linked this stress-induced shift to reduced hippocampal and increased dorsal striatal activity [23,24] but also to an opposite pattern of amygdala connectivity with the hippocampus and dorsal striatum, respectively [24–26]. Whereas amygdala–hippocampus connectivity was reduced by stress, amygdala–dorsal striatum connectivity increased, in line with rodent data suggesting that the amygdala orchestrates the stress-related shift in the preferential engagement of hippocampus and dorsal striatum during learning. A recent study that combined functional magnetic resonance imaging (fMRI) with a virtual navigation task further revealed that a stress-related reduction in behavioral flexibility was associated with reduced neural replay of future locations in the spatial environment [27••]. In striking parallel to the rodent studies, the shift to habit learning after stress was linked to noradrenergic arousal [24] and glucocorticoids acting through the mineralocorticoid receptor [26]. Blockade of the mineralocorticoid receptor abolished the shift toward dorsal striatal memory and genetic variants linked to mineralocorticoid receptor expression could explain interindividual differences in the sensitivity to the stress-induced shift from hippocampal to dorsal striatal learning [26,28]. In sum, findings across tasks and species showed that stress or major stress mediators promote a shift in the memory system preferentially engaged during learning, from hippocampal cognitive to dorsal striatal habit memory.

Stress-induced modulation of hippocampal and dorsal striatal control of retrieval

Under nonstressful conditions, hippocampus-dependent cognitive and dorsal striatum-dependent habit memory systems can contribute equally to task acquisition, depending on the extent of practice. Hippocampal memory develops typically early during training, whereas dorsal striatal memory emerges typically only after more extended training [5,9,29]. The emergence of dorsal striatal activation is thought to coincide with the shift from cognitive to more habitual learning strategies [30], and this shift appears to be accelerated by stress [31]. At the end of training, both hippocampal and dorsal striatal memory traces should have evolved. If multiple memory traces coexist, the question arises which of these is used at subsequent retrieval. Can stress bias, in addition to its impact on the engagement of hippocampal and dorsal striatal learning strategies, also the preferential recruitment of already-established hippocampal and dorsal striatal memory traces at retrieval?

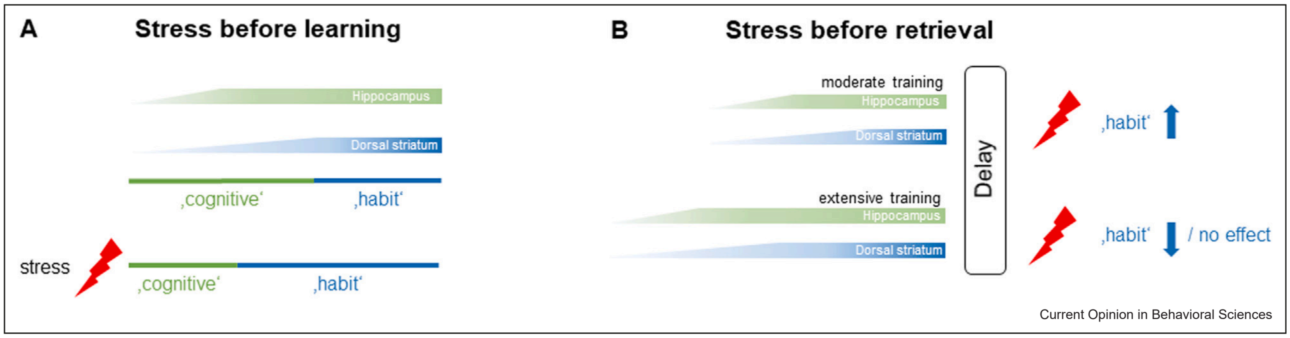
Although habit memory formation and retrieval appear to involve distinct mechanisms [32•], an initial rodent study suggested that stress might also induce a preference for habitual over cognitive memory retrieval. In this study, intra-amygdala infusion of an anxiogenic drug before memory retrieval led to a bias toward habit memory [33]. However, although stress effects on retrieval processes within hippocampal or dorsal striatal memory systems are well established [16,34], investigation into the influence of stress on the balance of hippocampal and dorsal striatal memory at retrieval has only recently begun, in particular in humans. A recent study revealed that stress-induced elevations of cortisol shortly before retrieval favor habit over cognitive memory [35••]. Using fMRI, this study further showed that stress and cortisol increased dorsal striatal activity during retrieval but reduced amygdala–hippocampus connectivity, thus suggesting that stress promotes habit memory retrieval. In sharp contrast to these findings, another study indicated that administration of glucocorticoids or the α2-adrenoceptor antagonist yohimbine, leading to increased noradrenergic stimulation, reduced the shift toward habit memory retrieval relative to placebo [36]. The glucocorticoid-related reduction in the engagement of the efficient habit memory system was further accompanied by impaired retrieval performance. Similarly, another recent study showed that stress before retrieval resulted in a preference for cognitive memory compared with nonstressed controls and that this stress effect was abolished by the β-adrenergic receptor antagonist propranolol [37]. How can these seemingly discrepant results be reconciled?

All of these studies showed consistently a practice-dependent shift from cognitive to habit learning strategies during training, in line with earlier findings [5,9,30]. However, one critical difference between these studies was the extent of training. While training was moderate in the study that showed a stress-induced shift toward habit memory retrieval [35••], initial training was rather extensive in the two studies that obtained a stress-related bias toward cognitive memory retrieval [36,37]. Could the intensity of initial training and by implication the initial strength of the hippocampal and dorsal striatal memory traces impact the nature of the modulatory effect of stress on the memory system recruited at retrieval? A recent study tested this hypothesis [38•]. Participants completed either 100 trials or 200 trials of a classification learning task that can be solved by the hippocampus or by the dorsal striatum (Box 1). Twenty-four hours later, participants underwent a stress or control manipulation before they performed a retention test. The results of this study showed that stress led to a bias toward habit memory retrieval in participants that underwent moderate training but had no effect in those who underwent extensive training. Together, there is accumulating evidence that stress may not only modulate the preferential engagement of hippocampal and dorsal striatal memory systems during learning but also the relative recruitment of established hippocampal and dorsal striatal memory traces at retrieval, with the nature of these effects depending on the strength of the initial memory traces (Figure 1).

Stress-induced modulation of multiple memory systems across domains

Differential contributions of multiple memory systems are not limited to spatial navigation or classification learning tasks but can be observed in various domains of learning and memory. For instance, hippocampal and dorsal striatal contributions can also be distinguished in motor learning [39]. Moreover, ‘cognitive’ memory systems that depend on the hippocampus or prefrontal cortex (PFC) and ‘habitual’ memory systems depending on the dorsolateral striatum or the amygdala have been described in threat learning and instrumental or reinforcement learning [40–42]. Interestingly, in all of these domains, stress has been shown to shift the balance of these memory systems toward the habitual systems, pointing to a general cognitive mechanism under stress. In motor learning, stress induced a shift from hippocampal–cortical networks to sensorimotor regions [43•]. Likewise, in fear learning, stress favors amygdala-dependent cue- and delay-conditioning, at the cost of hippocampal context- and trace-conditioning [44–46]. Moreover, in instrumental learning, stress may shift behavioral control from PFC-dependent goal-directed or model-based systems toward dorsolateral striatum-dependent habitual or model-free systems [47•-49]. Virtually, all of these studies induced stress before learning.

Figure 1



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Stress effects on the preferential recruitment of hippocampal and dorsal striatal memory systems during learning and retrieval. **(a)** In dual-solution tasks, hippocampal memory is built up early in training, whereas dorsal striatal memory is only established later during training. Once dorsal striatal memory is fully developed, behavioral response strategies shift from hippocampus-dependent ‘cognitive’ to dorsal striatum-dependent ‘habit’ memory. Stress is assumed to accelerate this shift and favor ‘habit’ over ‘cognitive’ memory. **(b)** When both hippocampal and dorsal striatal memory traces have been established, stress may affect which of these memory traces predominates during retrieval. The nature of the stress effect appears to depend on the extent of initial training, with stress before retrieval promoting habit memory after moderate training but leaving the mode of retrieval unaffected or even reducing habit memory after extensive training.

However, one study on instrumental learning exposed individuals to a stressor before a retention test and revealed that stressed individuals showed a bias toward habitual responding [50], in line with the findings described above that suggest that stress may bias the recruitment of multiple memory systems also at retrieval.

Concluding remarks

Findings across species, tasks, and domains of learning and memory indicate that stress before learning may bias the recruitment of multiple memory systems in favor of rather simple, reflexive systems, such as the dorsal striatum, at the expense of more flexible but cognitively more demanding systems, such as the hippocampus. This stress-induced shift from ‘cognitive’ to ‘habit’ learning appears to be adaptive for coping with an ongoing stressor as this bias allows intact performance under stress, while its (pharmacological) blockade is associated with performance deficits [19,26]. Recent evidence suggests that the modulatory influence of stress on the preferential engagement of multiple memory systems is not limited to memory formation but can also be found at retrieval, when multiple memory traces are available. Whether stress before retrieval promotes ‘habit’ or ‘cognitive’ memory appears to depend on the extent of training in the specific task. The stress-induced bias toward ‘habit’ memory retrieval after moderate training might be adaptive as the use of this less-demanding system may enable individuals to leverage well-established routines that allow efficient responding and free cognitive resources for coping with the stressor. The functional relevance of a potential stress-related bias toward more cognitive memory retrieval after extensive training remains less clear (and it is to be noted that this was not consistently found, see [38•]). Possibly, hippocampal memory traces are stronger after extended training, making them more robust and effective under stress. This, however, remains speculative and there is evidence suggesting that the bias toward ‘cognitive’ memory retrieval after extended training is associated with impaired performance [37]. Moreover, as in all studies testing stress effects on either encoding or retrieval, stress selectively before retention testing results in a different state during encoding and retrieval, which might also impact memory performance as well as the preferential memory system engagement (for a discussion of the issue of state dependency, see [33]). Elucidating the functional relevance of the stress-induced modulation of multiple memory systems at retrieval as well as the exact mechanisms involved herein is a challenge for future research. A better understanding of how stress may bias the preferential engagement of multiple memory systems at retrieval may have important clinical implications, for instance, related to the prevention of relapse to dysfunctional routines in stress-related mental disorders.

Declaration of Competing Interest

None.

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