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Review

Behavioral facilitation after hippocampal lesion: A review

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HIGHLIGHTS

- Hippocampal damage cannot only lead to deficits but also to behavioral facilitation.
- Such facilitatory lesion effects can be attributed to the loss of interference between hippocampal and basal ganglia mechanisms.
- Facilitatory lesion effects are typical for tasks dependent on implicit or procedural information processing.

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ABSTRACT

When parts of the brain suffer from damage, certain functional deficits or impairments are the expected and typical outcome. A myriad of examples show such negative consequences, which afford the daily tasks of neurologists, neuropsychologists, and also behavioral neuroscientists working with experimental brain lesions. Compared to lesion-induced deficits, examples for functional enhancements or facilitation after brain lesions are rather rare and usually not well studied. Here, the mammalian hippocampus seems to provide an exception, since substantial evidence shows that its damage can have facilitatory behavioral effects under certain conditions. This review will address these effects and their possible mechanisms. It will show that facilitatory effects of hippocampal lesions, although mostly studied in rats, can be found in many mammalian species, that is, they are apparently not species-specific. Furthermore, they can be found with various lesion techniques, from tissue ablation, to neurotoxic damage, and from damage of hippocampal structure itself to damage of fiber systems innervating it. The major emphasis of this review, however, lies on the behavioral effects and their interpretations. Thus, facilitatory effects can be found in several learning paradigms, especially active avoidance, and some forms of Pavlovian and instrumental conditioning. These will be discussed in light of pertinent theories of hippocampal function, such as inhibition, spatial cognition, and multiple memory systems theories, which state that facilitatory effects of hippocampal lesions may reflect the loss of interference between hippocampal spatial and striatal procedural cognition. Using the example of the rat sequential reaction time task, it will also be discussed how such lesions can have direct and indirect consequences on certain behavioral readouts. A final note will advocate considering possible functional facilitation also in neurologic patients, especially those with hippocampal damage, since such a strategy might provide new avenues for therapeutic treatments.

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1. General introduction

This review will focus on the phenomenon of functional facilitation after hippocampal lesion. It consists of the following parts: After a brief overview of hippocampal anatomy and its presumed functions, brain lesions as such will shortly be addressed regarding their general role in neuroscience, as well as critical limitations, which have to be considered when trying to interpret their outcomes. Then, facilitatory effects, mainly from humans, will shortly be addressed with respect to lesions outside the hippocampus, followed by a historical account of hippocampal lesion effects. In more detail, the roles of species, lesion techniques, and behavioral tests will be outlined and discussed in light of prevalent theories of hippocampal function. Here, active avoidance will receive special attention, since tests of active avoidance learning have provided the classical facilitatory effects. Other Pavlovian and instrumental tests will then be described, showing that facilitatory effects can actually be found in rather different paradigms, which makes it difficult to relate the consequences of hippocampal lesions to a unique mechanism. Special emphasis will be given to our own work with an instrumental serial reaction time task in rats, where we studied facilitatory effects of hippocampal lesions in detail, addressing factors such as instrumental versus sequential learning, post-reinforcement pauses, extinction, and action-outcome relationships. Compared to the rich evidence obtained in experimental animals, similar knowledge in human subjects is almost entirely lacking. Nevertheless, the facilitation issue might deserve more clinical attention in the future, since some facilitated function, possibly due to enhanced impacts of undamaged and learning-relevant brain structures (such as in the basal ganglia), might also be useful to help compensate for hippocampal losses in humans.

2. Brief introduction into hippocampal structure and function

Since this review anatomically focusses on the hippocampus, some basic knowledge of it will be presented in the following:

In the current scientific literature, the term “hippocampus” is used in a somehow inconsistent way. Classically, it refers to the three layers of the cornu ammonis, namely CA1, CA2 and CA3, which are often summarized as hippocampus proper. However, it has become rather popular to embrace several brain areas under the term hippocampus, namely hippocampus proper, dentate gyrus, subiculum, and entorhinal cortex, all of which are also termed “hippocampal formation” (for details see [6]). In the present review, the term hippocampus will be used in the more popular sense that is, including hippocampus proper and the adjacent structures mentioned above. Also, one can differentiate between different major parts of the hippocampus proper. In rats, it has a rather bent shape, with a dorsal, intermediate, and ventral part. Since most of the studies reviewed here were done with rats, these terms (especially dorsal) will continue to be used.

Regarding its basic circuitry, the hippocampus, mainly via the entorhinal cortex, receives inputs from various neocortical regions. Through the perforant pathway, projections from entorhinal cells reach the dentate gyrus. Its granule cells send axons (termed mossy fibers) to innervate the pyramidal cells of the CA3, which send projections (termed Schaffer collaterals) to the CA1. These, in turn, project to the subiculum (and entorhinal cortex), and from there to structures outside the hippocampus, especially cortical ones. Also, several fiber bundles funnel information to and from, and within or between the hippocampi of both hemispheres (for details see [1]). Out of these, only the fimbria-fornix pathway will receive specific attention in this review, which connects the hippocampus with areas in the brainstem, thalamus, hypothalamus, septum, and nucleus accumbens.

Regarding its functions, the hippocampus has undergone several stages and levels of interpretation, depending on methodological developments, critical experiments and findings (for older examples [70,119,138]). Discussing these complex issues in great detail goes far beyond the scope of this review, but the reader can be referred to an excellent paper by Morris [107]. Nevertheless, some theoretical hallmarks have to be provided which are of relevance here: Currently, the prevailing theories state that the hippocampus plays a critical role in memory, especially its formation. Here, one major research line, originally based on findings in humans with brain lesions, emphasizes its role in declarative memory [147,153], especially events and facts that can be consciously recalled. Although such kind of conscious memory cannot be tested directly in non-human animals, several monkey or rodent tests are considered to somehow model declarative memory [29,148], especially recognition memory, like the rodent object place-recognition test [58], which is often taken as a tool to measure episodic memory [154]. The other major research line, which apart from various brain manipulation techniques and the development of specific behavioral tests (e.g. [110,111], is largely based on cell recordings in rodents, emphasizes the hippocampal role in spatial cognition and memory, that is, the formation and use of spatial maps [63,120]. Somehow related theories [30,75,150] state that the hippocampus is important to form and use stimulus configurations and relations, and examples for that are space, context and their details. Also, it was suggested that the hippocampus may resolve conflicts between competing approach and avoidance tendencies, that it processes novelty, or regulates stress via control of the HPA-axis (e.g. [69,70]). Regarding functional localization, the major anatomical parts along the hippocampal longitudinal axis have been associated differentially with behavioral functions, since spatial learning and memory has been linked primarily to the dorsal

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