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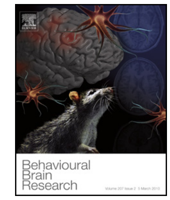

Review

The neural bases of crossmodal object recognition in non-human primates and rodents: A review

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HIGHLIGHTS

- Multisensory integration (MSI) is essential to everyday behavior.
- The neural substrates of MSI are poorly understood.
- We review non-human studies of MSI using crossmodal object recognition tasks.
- This research reveals roles for various cortical regions and neurochemical systems.

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ABSTRACT

The ability to integrate information from different sensory modalities to form unique multisensory object representations is a highly adaptive cognitive function. Surprisingly, non-human animal studies of the neural substrates of this form of multisensory integration have been somewhat sparse until very recently, and this may be due in part to a relative paucity of viable testing methods. Here we review the historical development and use of various "crossmodal" cognition tasks for non-human primates and rodents, focusing on tests of "crossmodal object recognition", the ability to recognize an object across sensory modalities. Such procedures have great potential to elucidate the cognitive and neural bases of object representation as it pertains to perception and memory. Indeed, these studies have revealed roles in crossmodal cognition for various brain regions (e.g., prefrontal and temporal cortices) and neurochemical systems (e.g., acetylcholine). A recent increase in behavioral and physiological studies of crossmodal cognition in rodents augurs well for the future of this research area, which should provide essential information about the basic mechanisms of object representation in the brain, in addition to fostering a better understanding of the causes of, and potential treatments for, cognitive deficits in human diseases characterized by atypical multisensory integration.

Contents

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1. Introduction

At any given moment, our brains are inundated with stimuli arriving through distinct, highly specialized sensory channels. Despite the relative segregation of early sensory pathways in the brain, our experience of and interactions with the outside world are shaped by multimodal constructs resulting from the integration of information across sensory systems. Although seemingly effortless, the importance of multisensory integration is likely derived from the adaptive value conferred upon recognition processes. For instance, when faced with the potential presence of a predator, the ability to rapidly select the appropriate behavioral response relies on an efficient assessment of the situation. It is often in these circumstances that visual information alone is not sufficient to adequately guide behavior, as lighting may be poor or the predator obscured from view. Therefore, accurate recognition of a potential threat would be greatly enhanced by the amalgamation of sensory stimuli which in isolation may not sufficiently evoke concern, but when integrated would indicate the presence of an imminent danger.

This is just one example of the influence that multisensory object representation can have over behavior. In many subtler ways, our ongoing behavior is driven by our reactions to the multisensory features of the everyday objects we encounter. Moreover, it is becoming increasing apparent that various human cognitive disorders (e.g., schizophrenia, autism, Alzheimer's disease) are associated with atypical multisensory integration abilities. Considering the adaptive behavioral influence of multisensory integration, these deficits could be at the root of many of the other cognitive symptoms displayed by patients with these conditions, and a better understanding of multisensory brain mechanisms could reveal novel insight into basic object representation functions, as well as strategies for treating cognitive impairment.

The current review will focus on a relatively neglected area of multisensory research, the use of non-human primates and rodents to study "crossmodal object recognition", or the ability to recognize objects across sensory modalities. Despite receiving substantial interest from behavioral neuroscientists in the 1960s, 1970s, and 1980s, work in this area trailed off for several years. However, crossmodal object recognition research appears to be gaining traction once again with the recent development of novel rodent tests that have clearly been influenced by the earlier, predominantly non-human primate, paradigms. This is a promising development given the relative ease with which such tasks can be applied to non-human studies, which remain an important source of information about the neurobiological bases of behavior. This work has great potential to help uncover the neural substrates of complex object representation, as well as helping to better characterize mechanisms of multisensory integration, which is relevant to many vital cognitive functions, such as attention, emotion, perception, learning, and memory. We will first review the historical development of crossmodal object recognition tasks for non-human primates and rodents. Next, we will survey the literature regarding the neurobiological bases of performance in these tasks. Finally, we will discuss the relevance of crossmodal object recognition tasks to human cognitive disorders.

2. Development of crossmodal object recognition tasks for non-human primates

Early work on crossmodal cognition originated from studies exploring crossmodal transfer of responses. In such tasks, learning in one modality is aided by previous learning of a similar task in a different modality. In one such study, rats learned to produce a habitual motoric behavior in the presence of either an auditory or visual stimulus. Reward was contingent upon returning to a feeding area via one of two return alleys. Once a return alley was selected, rats were required to change behavior and traverse the alternate alley if presented with a light stimulus. In subsequent trials, the stimulus was switched from visual to auditory, and transfer of responses across modalities was inferred as rats learned this task faster than experimentally naïve rats learning about the auditory cue for the first time [1]. It was argued, however, that the extent of crossmodal transfer in this study was minimal, instead reflecting learning of a rule as the behavioral response was elicited following a cue. The opposing response, continuing down the alley, was performed in the absence of any stimulus presentation and thus animals could learn to perform correctly by the presence or absence of a cue regardless of the modality [2].

To compensate for this perceived shortcoming, Ettlinger [2] trained two groups of rhesus monkeys on a unimodal discrimination task using either visual or somatosensory cues. Objects were fixed onto box lids, and monkeys learned over repeated trials to acquire a reward by displacing one specific object from an object pair. Two months following this extensive training procedure, monkeys were again tested using the same object pair, but this time in the opposite modality. It was hypothesized that successful tactile-visual or visual-tactile transfer would be evident if monkeys in the crossmodal condition made fewer errors than animals learning the discrimination task with new objects in the comparable modality. This pattern of results was not substantiated as monkeys in the crossmodal condition required an equal, and in some cases greater, number of trials to learn the task compared to the control group [2]. However, the lack of any detectable crossmodal transfer effects may have been partially a result of the extensive two-month retention delay separating the visual and tactile discrimination tasks. Ettlinger surmised that because these same animals were able to retain the unimodal discrimination task at near perfect performance over the same interval, the extensive delay could not account for the lack of crossmodal transfer. This explanation assumes that both tasks are of equal difficulty. Recent findings, however, suggest that crossmodal tasks utilize distinct neuroanatomical and neurochemical systems beyond what is necessary for unimodal recognition [3–8]. Therefore, it remains plausible that despite intact unimodal discrimination, the extensive retention delay prevented the transfer of learning across modalities rather than an innate inability of monkeys to perform crossmodal tasks.

Emerging around this time was incidental evidence suggesting that crossmodal transfer in monkeys may require that stimuli be temporally related [9]. To explore this idea directly, Burton and Ettlinger [10] utilized a discrimination task in which rhesus monkeys had to distinguish between tones or lights. The auditory