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Parallel and Interrelated Neural Systems Underlying Adaptive Navigation[1]

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SYNOPSIS. **The ability to process in parallel multiple forms of sensory information, and link sensory-sensory associations to behavior, presumably allows for the opportunistic use of the most reliable and predictive sensory modalities in diverse behavioral contexts. Evolutionary considerations indicate that such processing may represent a fundamental operating principle underlying complex sensory associations and sensory-motor integration. Here, we suggest that animal navigation is a particularly useful model of such opportunistic use of sensory and motor information because it is possible to study directly the effects of memory on neural system functions. First, comparative evidence for parallel processing across multiple brain structures during navigation is provided from the literatures on fish and rodent navigation. Then, based on neurophysiological evidence of coordinated, multiregional processing, we provide a neurobiological explanation of learning and memory effects on neural circuitry mediating navigation.**

INTRODUCTION

Various epistomological approaches have been used to describe the relationship between the evolution of complex anatomical systems and adaptive behavior (Lauder, 1991). Neuroecologists and neuropsychologists share the common perspective that single brain structures have evolved to support unique and specialized memory systems. There are many examples of such a view, from birdsong learning (*e.g.,* Nottebohm, 2000) to the notion that mammals necessarily have evolved multiple memory systems that are mediated by different brain regions (Sherry and Schacter, 1987). In many cases, the primary evidence is that selective brain lesions produce selective learning or memory deficits. The selectivity of a deficit following lesion to one brain area is often impressive: hippocampal lesions produce spatial learning deficits but not motor learning deficits while striatal lesions produce impairments in motor or response, but not spatial learning (*e.g.,* Kesner, 1998; McDonald and White, 1993; Packard *et al.,* 1994; Packard and McGaugh, 1996). Even though these dissociations of memory systems are clear, it has been argued that the extent to which lesion studies provide insight into the neural mechanisms of learning is limited (*e.g.,* Bolhuis and Macphail, 2001; Poucet *et al.,* 2004). Part of the problem stems from the fact that brain lesions impact functioning in not only the damaged area, but also in connected brain structures. A perhaps less obvious limitation of lesion studies is the difficulty they have in addressing the possibility that a single type of behavior (*e.g.,* memory) relies on coordinated processing across more than one brain region. By comparison, coordinated processing across brain structures is strongly implicated by neurophysiological studies of navigation and spatial learning (*e.g.,* Mizumori *et al.,* 2000*a*; Poucet *et al.,* 2004; Touretzky and Redish, 1996). Such a neural systems view of learning is consistent with the position of some evolutionary biologists who argue that complex behavioral functions necessarily involve the coadaptation of multiple structures (Lauder, 1991).

Dumont and Robertson (1986) argued that consideration of the evolutionary history of behavior could lead to the discovery or clarification of general principles regarding the organization of underlying neural circuits. If coadaptation of brain structures indeed represents a general organizing principle of complex behaviors, it should be possible to find evidence for this sort of organization across phylogeny. Here, we evaluate evidence relevant to this prediction by comparing sensory integration during navigation in fish and rodents. Experience-dependent navigation was considered a particularly fruitful model because it allows one to examine the effects of memory on neural system functions.

NEURAL SYSTEMS APPROACH TO NAVIGATION

A neural systems approach to spatial learning asserts that survival can be enhanced if multiple types of sensory information are continually analyzed in parallel. Such parallel processing should enable animals to use a vast array of environmental information in an opportunistic fashion. For example, an animal may select from the most reliable and predictive sensory modalities to guide its behavior at any point in time. Thus, if environmental conditions change (*e.g.,* visual information is no longer available or becomes unreliable as darkness falls), an animal can readily switch to other sensory modalities so that accurate behavior is minimally disrupted. In order for such switching to occur, one has to assume that during initial exposures to an environment, an animal learns specific associations between inputs from different sensory modalities, and how these associations relate to behavioral choices. The complex set of operations required to carry out such learning undoubtedly involves multiple computational operations. We hypothesized (Mizumori *et al.,* 2000*a*) that multiple brain regions, by virtue of their

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unique intrinsic pattern of neural connections, perform these diverse and specialized computations in parallel. The results of these region-specific neurocomputations must ultimately become integrated to accurately direct navigational behaviors.

ADAPTIVE NAVIGATION IN FISH

Multiple brain areas appear to have coevolved to enhance the adaptive quality of navigational behaviors of fish (*e.g.,* Demski and Beaver, 2001). This coadaptation presumably enables different sources of sensory/motor information to be processed in parallel. Furthermore, Demski and Beaver (2001) suggested that the ‘‘multiregional enhancements’’ allow for more complex, and perhaps more flexible, sensory processing.

Although much remains to be discovered about navigation behavior in fish, there are striking similarities between fish and mammalian spatial behaviors (see Braithwaite, 1998 for a review). To summarize, like mammals, different species of fish show elevated and nonrandom exploration of a new environment that declines with time (*e.g.,* Kleerekoper *et al.*, 1974). Fish learn the location of important resources such as food or shelter (*e.g.,* Aronson, 1971; Braithwaite *et al.*, 1996; Canfield and Rose, 1993; Milinski, 1994), they use distal and local landmarks to discriminate important locations (Huntingford and Wright, 1989), fish demonstrate short and long term spatial memory (Milinski, 1994), and certain fish use visual cues as compass cues (Loyacano and Chappell, 1977).

In support of the view that coadaptation of brain structures underlies the visual-based navigation skills of fish, it is interesting to note that a strong positive correlation exists between the sizes of three brain structure (telencephalon, cerebellum, and the optic tectum) and the extent to which different species of fish live in strongly photic environments (Demski and Beaver, 2001). That telencephalic enlargement is strongly correlated with the enlargement of cerebellum and tectum suggests that these structures form a functionally integrated neural circuit. Initial studies into the function of this neural circuit show that telencephalic lesions result in a selective deficit in spatial learning, whereas nonspatial learning remains intact (*e.g.,* Salas *et al.*, 1996). Also, similar to observations in rodents (described below), a single unit recording study revealed the existence of visually-dependent location-specific firing by fish telencephalic neurons (Canfield and Mizumori, 2004).

Coadaptation of different brain structures may greatly facilitate the extent to which parallel processing of sensory/motor information occurs. This is significant because such simultaneous processing is necessary for animals to use currently available sensory input in an opportunistic fashion. Indeed, goldfish and cichlids use sensory information in a parallel (yet hierarchical) fashion, preferring auditory or visual input, respectively (Canfield and Rose, 1996). When relevant and reliable inputs are available from nonpreferred senses, it has been shown that these other inputs importantly influence the effects of the preferred sensory system on behavior. Cain (1995) showed a different example of the opportunistic selection of sensory influences on behavior. In that study, when locating objects, elephantnose fish readily switched between sensory modalities as environmental conditions changed, even though the task was initially learned with only one sense. Thus fish appear to automatically process multiple types of sensory information during initial learning, then integrate this information into a single spatial referent.

ADAPTIVE NAVIGATION IN MAMMALS

Similar to the parallel processing that appears to occur in fish, the neural mechanism of mammalian adaptive navigation can also be characterized by an integration of multiple sensory and motor systems with memory systems. Much evidence to support this view comes from neurophysiological studies of rodent navigation. By extension of one of the organizing principles of sensory and motor systems (Merzenich and deCharms, 1996), navigation produces a continuous reorganization of neural representations across different levels of sensory and motor system processing (Mizumori *et al.*, 2000*a*). This reorganization results from continuously updating neural representations in experience-dependent ways. One key prediction of a neural systems view of experience-dependent navigation is that during performance of a single learning task (*e.g.,* a spatial learning task), multiple brain structures should demonstrate evidence of representational reorganization as a result of changes in the sensory context or task demands. Next, we describe the response properties of hippocampal neural representation before and after context changes. Then, we compare these hippocampal responses to those of the striatum when animals are tested under identical conditions.

SPATIAL CORRELATES OF HIPPOCAMPAL NEURON DISCHARGE

As described in many studies since the early 1970s, the primary correlate of the principal cells (pyramidal neurons) of hippocampus is location-specific discharge (O’Keefe and Dostrovsky, 1971). That is, pyramidal cells show a dramatic increase in firing when an animal occupies particular locations in its environment, referred to as the place field of a place cell (see Fig. 1C for examples). More recently, we reported the existence of another type of spatial representation in hippocampus, one that signals the momentary directional heading of the animal (Leutgeb *et al.*, 2000; Mizumori and Leutgeb, 2001). Neurons whose firing correlates with directional heading are referred to as head direction cells (Sharp, 2002; Taube, 1998). Since much more is known about the response properties of hippocampal place cells than hippocampal head direction cells, the remainder of this article will focus on place cell contributions to navigation.

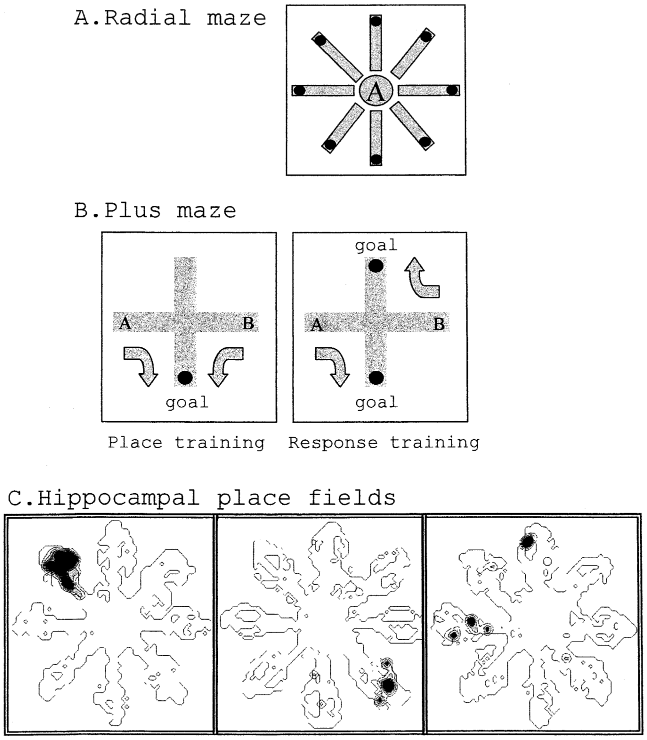

FIG. 1. A) Top-down view of an eight arm radial maze. Animals start at position A, then retrieve all rewards at the end of the maze arms (filled circles). B) Top-down view of a plus maze with two start locations (A and B) indicated on the west and east arms. Animals move along the trajectories indicated by the arrows for place and response training. C) Three examples of hippocampal place fields recorded as rats performed a spatial working memory task on a radial maze. The positions visited are outlined. Gray shading is used to indicate locations associated with elevated cell discharge. Black areas correspond to the maximum firing rate for the cell.

There are many excellent reviews of our current understanding about the sensory or motor coding properties of hippocampal place cells (McNaughton *et al.*, 1996; Muller *et al.*, 1996; O'Keefe and Burgess, 1996; Sharp, 2002). To some extent, these place fields appear to reflect the spatial arrangement of visual cues in the test room. When visual cues are rearranged, or animals are placed in novel environments, the firing patterns of place cells will change in unpredictable ways (Knierim *et al.*, 1998; Mizumori *et al.*, 1999*b*; Sharp *et al.*, 1990; Wiener *et al.*, 1995). Place fields may change locations, or stop firing altogether. It is clear that place fields are also impacted by nonvisual information, such as internally generated sensory/motor input regarding an animal's vestibular or movement state (Knierim *et al.*, 1998; Jeffery and O'Keefe, 1999; Sharp *et al.*, 1995; Wiener *et al.*, 1995). The nature of the integration between visual and nonvisual systems remains a topic of intense investigation.

Our laboratory has taken two approaches to address the issue of the understanding the hippocampal contribution to spatial learning during unrestrained navigation. First, we have tried to elucidate further the type of information that might be encoded when cells show location-specific firing. Second, we consider hippocampus place field plasticity within the context of the functions of connected brain areas. According to the first approach, many laboratories (including ours) have shown that when animals move about a familiar environment, consistent place fields are reliably displayed for days to weeks. However, as mentioned above, visual and nonvisual manipulations can result in a rapid reorganization of place fields. Furthermore, hippocampal place fields can be sustained by different sensory modalities, apparently depending upon which modality is most reliable for the animal (Jeffery and O'Keefe, 1999; Cooper and Mizumori, 2001). Thus, hippocampus may represent different visual environments with different patterns of neural activity, and a particular neural activity pattern is subject to the influence of visual and nonvisual processing.

Since the reliance on particular modalities of sensory input can vary depending upon current and past experiences, memory must have an impact. This view is consistent with the finding that when reorganization of place fields occurs, it is often only a partial change. That is, a single environmental change may cause only a subpopulation of place fields to reorganize, while place fields of other cells recorded at the same time may not change. Such partial reorganization implies that hippocampus may have at least two patterns of neural codes: place fields that do not change reflect constant, or expected, features between environments, and place fields that reorganize across changing environmental conditions code the current sensory environment (Mizumori *et al.*, 1999*b*). The frequent reports of partial reorganization was taken as evidence that memory may influence the way hippocampus represents the sensory environment. Specifically, place cells that exhibit similar place fields despite changes in a familiar environment may be driven by the memory of the expected visual spatial features. The place fields that are sensitive to even subtle changes in the environment may identify place cells that code for the current environmental conditions. The hippocampus then compares the expected and currently experienced environments, sending output messages that reflect the extent to which a match is found. If the animal perceives no change in the environment, messages may be sent to cortex to further strengthen the pattern of activated synapses that was initially established by the activated memory. If a change is perceived, then the hippocampal output message may destabilize the activated pattern, allowing for a different stable state to emerge. Presumably this new stable state reflects an updated memory. Thus, according to the hypothesis of Mizumori *et al.* (1999*b*), hippocampus contributes to adaptive navigation by providing an animal with a mechanism by which it can detect and ultimately benefit from changes in the spatial context of a behavior. By analogy to fish that continuously sample multiple sensory systems to guide their behavior, the mammalian (rodent) hippocampus continuously compares multiple memory states and the current sensorimotor environment.

Recently, different laboratories have begun to test more directly the relationship between place field properties and memory. Wood *et al.* (1999) showed that the exhibition of place fields depended upon the expected location of food reward. In this way, place cells help to distinguish different behavioral contexts, or events. We recently replicated the Wood *et al.* findings using a different behavioral task involving a plus maze (Smith *et al.*, 2002). For both the Wood *et al.* and Smith *et al.* studies, it could be argued that the place fields were conditional upon the behavioral trajectory of the animal and not memory processes per se. Therefore we sought to test more directly the impact of memory on hippocampal place fields by training rats to switch between two learned cognitive strategies (spatial and response) within the same recording session (Yeshenko *et al.*, 2001; in preparation). Importantly, the sensory and motor conditions, as well as the motivational state, were held constant during the test. Also, since recordings were made from the same cells across conditions, strategy effects on cell firing could not be attributed to sampling differences.

To test the effects of changes in cognitive strategy on place field properties, rats were subjected to either place or response training on a plus maze (Fig. 1B). For place training, rats learned to find food reward in one location on the maze (*e.g.,* south maze arm) irrespective of the rat's starting location (*i.e.*, east or west maze arms). During response training, a rat learned to make exclusively right turns (or exclusively left turns) irrespective of its starting location (*i.e.,* east or west maze arms). Importantly, the reward was found in a constant spatial location during place training, but in different locations during response learning. This training protocol is commonly used to test performance according to different cognitive strategies (*e.g.,* Colombo *et al.*, 2003; Gold, 2004; Packard, 1999; Packard and McGaugh, 1996). The unique aspect of our training regime was that the same animal performed 10 trials according to one strategy, followed by 10 trials according to the alternate strategy. A one-minute period of darkness between trials 10 and 11 provided the signal to switch strategies. After achieving asymptotic performance (*i.e.*, better than 80% choice accuracy), animals underwent surgery for the implantation of recording electrodes according to previously described methods (*e.g.,* Cooper and Mizumori, 2001; Leutgeb and Mizumori, 1999; Mizumori *et al.*, 1989, 1993, 2000*b*). Following recovery from surgery, hippocampal single unit activity was recorded as animals performed the plus-maze task.

Figure 2 shows an example of a hippocampal place cell recorded during behavioral performances that were guided by different cognitive strategies. This type of place field activity change to the switch between response and place strategies was quite typical (Yeshenko *et al.*, 2001; Yeshenko and Mizumori, in preparation). Perhaps the retrosplenial cortex plays a role in determining the appropriate strategy to be used since the retrosplenial cortex appears to serve as a critical link between hippocampus and cortical spatial memory systems (Cooper and Mizumori, 1999, 2001; Harker and Whishaw, 2002).

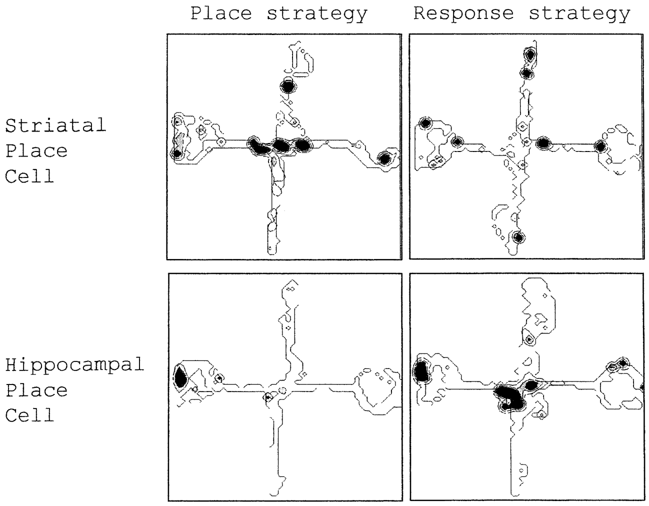

FIG. 2. Examples of location-specific firing by striatal (top row) and hippocampal neurons (bottom row) recorded during performance according to a place strategy (left column) or response strategy (right column) on a plus maze. The same cells were recorded during both strategy tests. It can be seen that the spatial distribution of firing of both striatal and hippocampal neurons changed dramatically across the two test conditions. For illustration purposes, the maximum firing rates (indicated in black) were constant across strategy conditions. Progressively lighter shades of gray correspond to firing rates below the maximum (in 25% increments). Cell firing rates do not include times when the animal was stationary.

SPATIAL CORRELATES OF DORSAL STRIATAL NEURON DISCHARGE

The neural systems approach to studying the neurobiology of spatial learning and adaptive navigation suggests that neural representations from brain structures in addition to hippocampus might undergo reorganization as contextual features change. Supporting this prediction, there is behavioral, lesion, and neurophysiological evidence that the striatum plays a role in spatial learning (*e.g.,* Annett *et al.*, 1989; Devan *et al.*, 1999; Mizumori *et al.*, 2000*a*, *b*). Neuroanatomical findings suggest that both the hippocampus and striatum might function as part of an integrated system during navigation. The most direct route for information flow between these two structures is the connection from ventral subiculum to the nucleus accumbens or ventral striatum (Groenewegen *et al.*, 1987). Also, there are polysynaptic connections from the hippocampal formation to retrosplenial and parietal cortices, and then to the dorsomedial aspect of dorsal striatum (McGeorge and Faull, 1989). Our laboratory has been studying whether striatal neural representations undergo reorganization similar to what was observed for hippocampus.

Previously, it was shown that dorsal striatal neurons code both spatial and nonspatial information, such as location, heading direction, reward, turning behavior, and forward movement (Mizumori *et al.*, 2000*b*; Ragozzino *et al.*, 2001; Wiener, 1993). The location correlates of striatal neurons were of particular interest because one could make direct comparisons to hippocampal place fields. Yeshenko *et al.* (2004) demonstrated that striatal place fields and hippocampal place fields responded similarly to cue manipulations (*e.g.,* cue removal, cue rotations) during performance of place and response maze tasks.

More recently, striatal neural activity was recorded simultaneously with the hippocampal neurons described above as rats performed the place or response task on a plus maze task described above (Yeshenko and Mizumori, 2002; in preparation). In this way, the same cells were recorded in a single recording session that included both place and response performance. Figure 2 shows that, similar to hippocampal place field responses, striatal location-selective fields showed reorganization when an animal switched to the use of a different cognitive strategy. This was the case regardless of whether rats switched from response to place or place to response training. These data show that, similar to hippocampus, striatal representations are influenced by memory systems. The hippocampal and striatal single unit results, taken together, provide evidence that changes in sensory or cognitive context result in the reorganization of neural representations in more than one neural system.

Another test of memory influences on neural representation is to determine whether changes in the expectation of a task event impact place fields. Rats were trained according to the place learning paradigm on a plus maze (Mizumori *et al.*, 2004). During the first 10 trials food reward was located on the north maze arm, while during trials 11–20, the food reward was located on the south maze arm. We found evidence that both hippocampus and striatal place fields underwent reorganization when the reward location switched in a predictable manner. Figure 3 provides clear examples that changing reward locations result in reorganization of hippocampal and striatal neuron place fields. These data strengthen the view that neural activity in both hippocampus and striatum are modulated by the memory demands of task.

Taken together, these striatal and hippocampal data support a view that both structures operate in parallel during both spatial and response learning. Such parallel operations were predicted by the neural systems view of navigation. However, the striking similar dynamic responses of hippocampal and striatal neurons, regardless of the type of memory being tested, raise an important question: what does the striatum contribute to spatial learning? Mizumori *et al.* (1999*a*, 2000*a*, *b*) extended general concepts suggested by others (*e.g.,* Houk, 1995; Schultz, 1997; Schultz *et al.*, 1995) to hypothesize that striatum may offer a *response reference system* that aids in the evaluation of the expected success of learned behavioral strategies. This is a system that compares the extent to which the context- (or memory-) based expectations of a relationship between reward and behavior is met. If response-reinforcement contingencies differ from what are expected, a striatal output message would have the effect of destabilizing the most recent pattern of cortical neural activity that supported the behavior. If the response-reinforcement contingencies occur as expected, then the outgoing message would increase the synaptic strengths within the activated neural circuit. Conceivably, such a response reference system should be useful for different forms of learning (Mizumori *et al.*, 1999*b*, 2000*a*, 2004).

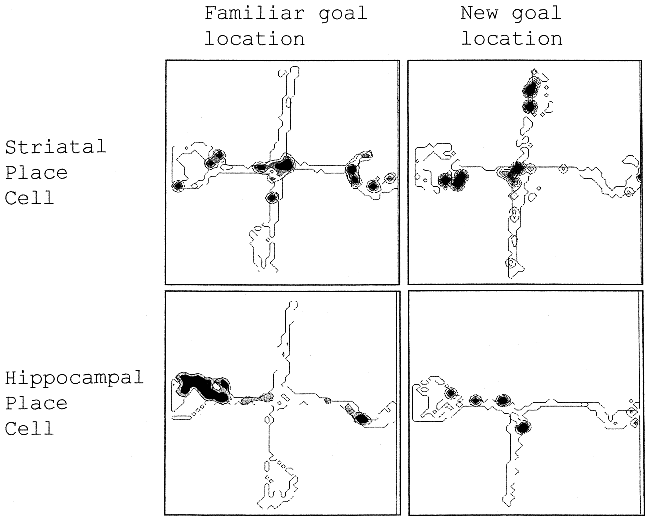

FIG. 3. Examples of location-specific firing by striatal (top row) and hippocampal neurons (bottom row) before (left column) and after (right column) animals were trained to find reward in a new location. The same cells were recorded during both test conditions. Both striatal and hippocampal neurons responded with different firing patterns in the two test conditions.

Although additional studies are needed, anatomical and physiological evidence are consistent with this interpretation of striatal function. The striatum is highly interconnected with many areas of association cortex, as well as sensory and motor cortices (McGeorge and Faull, 1989). Thus, striatum likely receives information from regions of the cortex that participates in cognitive and stimulus-response learning. The striatum also has been strongly implicated in associating reinforcement consequences with behavior via dopaminergic input from the substantia nigra and ventral tegmental area (Schultz, 1997). These anatomical data, theories of dopamine function in striatum, and the finding of greater diversity of neural correlates for striatal cells than hippocampal neurons (Kawagoe *et al.*, 1998; Mizumori *et al.*, 2000*b*; Schultz *et al.*, 1995; Wiener, 1993) suggest that the neural substrate exists in striatum that supports the type of processing required by a response reference system. The output of such a system could be used to ‘‘gate’’ behavioral selection functions in cortex (Atallah *et al.*, 2004; Mizumori *et al.*, 2004).

INTERPRETATION OF LESION AND SINGLE UNIT STUDIES: A RECONCILIATION?

Lesion studies suggest that single brain structures mediate different forms of memory. In contrast, the view that different brain structures continually carry out their specialized neurocomputations regardless of the memory requirements of a task emerges from neurophysiological data. How does one reconcile these seemingly different conclusions from lesion and single unit experiments? Behavioral effects of lesions could be attributed to multiple factors, including the loss of the target structure and/or a disruption of processing in afferent and efferent structures. The finding of no behavioral effects following a lesion could be due to the fact that the target structure plays no role in task performance, or it may be that other intact structures support alternative strategies for completing the task. Thus, we suggest the following explanation regarding the apparently different conclusions of lesion and neurophysiological studies about the neural basis of place and response learning. Response learning requires the formation of an association between a well defined motor act, or current external stimulus, and its immediate consequence. Such learning could be mediated by the direct connections of lateral striatum with motor and somatosensory cortices rather than hippocampus, which does not have such direct connections. As such, hippocampal lesions are without effect on response learning not because its processing is not important, but rather because it is not as directly connected to motor and somatosensory cortex as is the striatum. Spatial context analysis by hippocampus could very well be important for context-dependent response learning.

During navigation, we expect that both hippocampus and striatum are normally involved. To account for the finding that hippocampal, but not striatal, lesions induce spatial learning deficits we make the following argument. Hippocampus is unique in that it functions as a spatial context comparator, a function that is essential for normal spatial learning. There are, however, at least two routes whereby hippocampal information could impact ongoing behavior. One route includes the striatum, and a different (strictly cortical) route does not. Thus striatal lesions may not result in spatial learning deficits not because the evaluation of responses and their consequences is not important for spatial learning, but because a different neural system can compensate for the loss of striatal processing. Importantly, the absence of a lesion effect does not necessarily mean that the striatum does not normally play a role in spatial learning.

By observing intact neural processing during learning, the neurophysiological findings support the perspective that spatial performance normally relies on parallel processing across diverse brain regions. Intrinsic factors (*e.g.*, memory, motivation, hormone status, etc.) could impact the relative strengths of hippocampal and striatal output to behavioral expression systems. In that way, intrinsic factors could ultimately determine which region-specific neurocomputation impacts ongoing behaviors (Mizumori *et al.*, 2004). Such modulation of the impact of different neural systems on behavioral control systems presumably is a dynamic process that can be continually updated according to the outcome of the behavior itself. If the desired outcome is achieved, then the differential weighting of the outputs of different neural systems may go unchanged. If, however, the desired outcome is not realized, then the weights may shift to allow preferred access to behavioral control systems by a different form of information processing. In this way, animals can readily shift between modes of processing according to changing task and environmental demands. This form of neural systems interaction may represent an evolutionarily conserved process that allows vertebrate animals in general to behave flexibly.

CONCLUSION

It has been proposed that multiple brain regions have co-evolved and that they interact to facilitate adaptive navigation (Demski and Beaver, 2001). The study of complex sensory systems interactions has provided a model with which to explore this proposal. Specifically, the case of experience-dependent navigation appears to rely on the continuous, memory-guided active integration of external sensory context information and internally generated sensory/motor information within multiple neural systems of the brain. Different brain regions may then incorporate similar sensory/motor information into region-specific neurocomputations. The strength of each region's output to behavioral control systems of the brain may be dynamically regulated by intrinsic factors (*e.g.*, attention, the evaluation of the reinforcement outcome of behaviors, motivation, etc.). In this way, animals are able to readily and successfully adapt to ever changing environmental conditions.

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