COMMENTARY

Connections Between the Retrosplenial Cortex and the Hippocampal Formation in the Rat: A Review

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ABSTRACT

The retrosplenial cortex is situated at the crossroads between the hippocampal formation and many areas of the neocortex, but few studies have examined the connections between the hippocampal formation and the retrosplenial cortex in detail. Each subdivision of the retrosplenial cortex projects to a discrete terminal field in the hippocampal formation. The retrosplenial dysgranular cortex (Rdg) projects to the postsubiculum, caudal parts of parasubiculum, caudal and lateral parts of the entorhinal cortex, and the perirhinal cortex. The retrosplenial granular b cortex (Rgb) projects only to the postsubiculum, but the retrosplenial granular a cortex (Rga) projects to the postsubiculum, rostral presubiculum, parasubiculum, and caudal medial entorhinal cortex. Reciprocating projections from the hippocampal formation to Rdg originate in septal parts of CA1, postsubiculum, and caudal parts of the entorhinal cortex, but these are only sparse projections. In contrast, Rgb and Rga receive dense projections from the hippocampal formation. The hippocampal projection to Rgb originates in area CA1, dorsal (septal) subiculum, and postsubiculum. Conversely, Rga is innervated by ventral (temporal) subiculum and postsubiculum. Further, the connections between the retrosplenial cortex and the hippocampal formation are topographically organized. Rostral retrosplenial cortex is connected primarily to the septal (rostrocaudal) hippocampal formation, while caudal parts of the retrosplenial cortex are connected with temporal (caudalventral) areas of the hippocampal formation. Together, the elaborate connections between the retrosplenial cortex and the hippocampal formation suggest that this projection provides an important pathway by which the hippocampus affects learning, memory, and emotional behavior.

Key words: cingulate cortex, hippocampus, limbic system, Papez circuit

The retrosplenial cortex is a nodal point for the transfer of information between the hippocampal formation, many neocortical regions, and the thalamus. Early studies demonstrated that the cingulate (including the retrosplenial) cortex was innervated by the anterior thalamic nuclei and the neocortex and that it had a significant projection both to the hippocampal formation and via the hippocampal formation to the hypothalamus. This led Papez (1937) to suggest that this circuit subserved the elaboration of emotional “experience.”

In addition to the elaboration of “emotional experience,” the retrosplenial cortex also appears to contribute significantly to the processes of learning and memory (Gabriel and Sparrenborg, 1986; 1987; Valenstein et al., 1987; Sutherland et al., 1988; Matsunami et al., 1989; Sif et al., 1989). Further, the hippocampal formation has long been recognized as having an important role in these functions (e.g., O'Keefe and Nadel, 1978; Olton, 1983; McNaughton and Morris, 1987). In light of this evidence, the elucidation of the interconnections between the retrosplenial cortex and hippocampal formation take on an added importance.

While anatomical data documenting the cortical connections of the retrosplenial cortex have been limited, recent studies have indicated that the retrosplenial cortex has extensive connections (e.g., Domesick, 1969; Vogt and Miller, 1983; Van Groen and Wyss, 1990c; 1991a). For instance, several studies have shown that reciprocal connections exist between the retrosplenial cortex and the anterior nuclei of the thalamus (Domesick, 1969; Robertson and Kaitz, 1981) and that the retrosplenial and subicular cortices are interconnected (Sørensen, 1980; Vogt and Miller, 1983; Vogt et al., 1986). Our recent studies have elucidated the cortical and thalamic connections of the retrosplenial granular b cortex...
The results demonstrate that these interconnections provide (Rgb) and a cortex (Rga) (Wyss and Sripanidkulchai, 1984; Sripanidkulchai and Wyss, 1986b; 1987; Wyss et al., 1990; Van Groen and Wyss, 1990c), and recent studies document the cortical and subcortical connections of the retrosplenial dysgranular (Rdg) cortex (Sripanidkulchai and Wyss, 1986b; Van Groen and Wyss, 1991a).

Whereas several recent studies document connections between individual regions of the retrosplenial cortex and hippocampal formation, the present commentary takes a broader focus by considering the interconnections between the entire retrosplenial cortex and hippocampal formation in the rat. The results demonstrate that these interconnections provide the anatomical basis for the retrosplenial cortex’s role in processing and integrating information related to memory, learning, and emotional functions.

Our recent data are based on studies using two anterograde tracers and two retrograde tracers in over 100 male Sprague-Dawley rats. The anterograde tracing experiments have relied primarily on the very sensitive anterograde transport of Phaseolus vulgaris leucoagglutinin (PHA-L; Gerfen and Sawchenko, 1984) to study the pattern of axonal terminals. For retrograde transport experiments, small amounts of a fluorescent dye (fast blue [FB] or fluorogold [FG]) have been injected by pressure into a defined region of the brain (Schmued and Fallon, 1986; Sripanidkulchai and Wyss, 1986a).

NOMENCLATURE

The retrosplenial cortex is divided into two parts, granular and dysgranular, and the retrosplenial granular cortex is further subdivided into granular a (Rga) and granular b (Rgb) regions according to the mapping of Wyss and Sripanidkulchai (1984) following the classification suggested by Rose (1927a; 1927b; Figures 1 and 2). Retrosplenial granular a cortex corresponds to areas 29a and 29b, and Rgb corresponds to area 29c of Vogt and Peters (1981). The retrosplenial dysgranular cortex (Rose 1927a; 1927b) is designated area 29d by Brodmann (1909) and Vogt and Peters (1981) and 29c by Krieg (1946).

Retrosplenial dysgranular cortex has a staining pattern in Nissl preparations that distinguishes it from the adjacent cortical areas (Fig. 1). Laterally and rostrally Rdg is bordered by lateral agranular (motor) cortex (Donoghue and Wise, 1982) and caudally and laterally Rdg is bounded by area 18b (Fig. 1); the border between Rdg and area 18b is characterized by a change in Nissl staining. While layer IV of Rdg is occupied by few granule cells, this layer in 18b contains many granular cells. The border between the Rdg and the more ventral Rgb is characterized by two changes in Nissl staining. First, in Rdg compared to Rgb, layers II and III are wider, and in Rgb layer II cells are more darkly stained and form prominent clumps. Second, in Rdg compared to Rgb, layer IV is wider, and in Rdg the layer V neuronal cell bodies tend to be larger. The border between Rgb and the more ventral Rga is characterized by two changes in Nissl staining. First, in Rgb compared to Rga, layer II is wider and contains smaller and more darkly staining cells, and in Rgb these cells form more prominent clumps. Second, in Rgb compared to Rga, layer III is thin and the pyramidal cell bodies are randomly spaced; in Rga the layer III neuronal cell bodies tend to be arranged in bands parallel to the pial surface. Ventrally and caudally Rga is bounded by the postsubiculum (the dorsal part of the subicular cortex [Van Groen and Wyss, 1990b]; Fig. 1); the border between Rga and postsubiculum is characterized by a change in Nissl staining. While layer IV of Rga is occupied by granule cells, this layer in postsubiculum contains the lamina dissecans superficially and small pyramidal cells in its deeper half.

This study employs the subdivision of the hippocampal formation suggested by Lorente de Nó (1934). The hippocampal formation consists of the hippocampus proper (Ammon’s horn, i.e., cornu Ammonis fields CA1–CA3), the area dentata, and the subiculum complex (Fig. 1). For our study, CA1 consists of all of regio inferior as defined by Ramón y Cajal (1911), including CA2 of Lorente de Nó (1934) and Swanson and Cowan (1977). CA1 corresponds to the area that Ramón y Cajal (1911) termed regio superior. The subiculum complex is subdivided into subiculum proper, presubiculum, parasubiculum, and postsubiculum (Van Groen and Wyss, 1990a; 1990b; Figs. 1, 2).

Hippocampal Connections of Retrosplenial Cortex

Rdg, Efferent projections

Rostral Rdg sends out a group of axons that turn caudally in the cingulum bundle to terminate in the postsubiculum, parasubiculum, entorhinal, and perirhinal cortices (Fig. 3). At the splenium of the corpus callosum a number of these axons extend ventrally to rostral postsubiculum, where they form a dense terminal plexus in layers I–II and V–VI, with less dense terminations in layers III–IV (Fig. 4A) and a very sparse terminal field in the dorsocaudal subiculum. A small number of axons extends further ventrally to form a terminal plexus in layer I of caudal parts of parasubiculum and in the deep layers (IV–VI) of the caudal lateral entorhinal and perirhinal cortices. Contralaterally, a few axons and terminals project to layer V of postsubiculum.

Caudal Rdg gives rise to a group of axons that runs caudally in the cingulum bundle to terminate in the postsubiculum, parasubiculum, and perirhinal cortices (Fig. 3). At the splenium of the corpus callosum these axons extend ventrally to form a dense terminal plexus in layers I–II and V–VI of the caudal, ventral part of postsubiculum. A small number of axons extends ventrally to end in the superficial layer (I) of the caudal part of parasubiculum, and the deep layers (IV–VI) of the caudal perirhinal cortex. Contralaterally, a few axons and terminals project to layer V of postsubiculum.

Rdg, Afferent connections

Rostral Rdg receives hippocampal formation projections from subiculum, postsubiculum, and entorhinal cortex (Fig. 5). The Rdg receives a limited input from the septal (dorsal) part of the subiculum. Most neuronal cell bodies that project to Rdg are in the deep layers (V–VI) of the rostral part of the postsubiculum cortex and the caudal part of the entorhinal cortex.

Caudal parts of Rdg also receive a small projection from the dorsal part of subiculum. A larger number of projections arise from the deep layers (V–VI) of the caudal part of post-
Fig. 1. Four low-power photomicrographs of Nissl stained coronal sections of the hippocampal and retrosplenial cortices (A to D, rostral to caudal) to demonstrate the cytoarchitectonic divisions. Scale bar, 500 μm. CA, cornu Ammonis; Para, parasubiculum; Post, postsubiculum; Pre, presubiculum; Rdg, retrosplenial dysgranular cortex; Rga, retrosplenial granular a cortex; Rgb, retrosplenial granular b cortex; SUB, subiculum.
Fig. 2. Unfolded, schematic maps to demonstrate the position of the retrosplenial (inset, Wyss and Sripanidkulchai, 1984) and hippocampal cortices (Swanson et al., 1978). Scale bars, 1,000 μm. CA, cornu Ammonis; IEA, intermediate entorhinal cortex; LEA, lateral entorhinal cortex; MEA, medial entorhinal cortex; Pre, presubiculum; Post, postsubiculum; Para, parasubiculum; Rdg, retrosplenial dysgranular cortex; Rgb, retrosplenial granular b cortex; SUB, subiculum.

subiculum (Fig. 6B) and the deep layers (V–VI) of the caudal part of the entorhinal cortex. The termination of these projections in Rdg has been documented using the PHA-L method (Van Groen and Wyss, 1991a).

Rgd, efferent connections

Retrosplenial granular b cortex axons terminate in the postsubiculum, where they form a dense terminal plexus in superficial layer I, layer III–IV, and VI (Fig. 4B). Rostral parts of Rgd predominantly project to more ventral parts of the dorsal subiculum and more caudal parts of the postsubiculum (Fig. 7).

Rgd, afferent connections

Retrosplenial granular b cortex is innervated by a small number of pyramidal neurons in the dorsal, medial part of area CA1, and a small number of nonpyramidal neurons at the border of stratum radiatum and stratum moleculare, predominantly in area CA1 (Fig. 6D). A dense cluster of neurons in the dorsal (septal) one-third of the subiculum (Fig. 6A) also projects to Rgd, as does a band of neurons in the deep layers (i.e., layers V and VI) of postsubiculum. Contralateral neurons in the deep layers (i.e., layers V and VI) of postsubiculum also project to Rgd. Rostral parts of Rgd receive a projection predominantly from area CA1, the dorsalmost part of subiculum, and rostral parts of postsubiculum. In contrast, caudal parts of Rgd receive input predominantly from more ventral parts of the dorsal subiculum and more caudal parts of the postsubiculum (Fig. 8). These connections have been verified by anterograde tracing experiments (Fig. 4F).

Rga, efferent connections

Rostral Rga gives rise to two groups of axons that course ventrally into the caudal postsubiculum, presubiculum, parasubiculum, and entorhinal cortex. One group of axons terminates in the deep (i.e., IV–VI) layers of the postsubiculum (Fig. 4C), presubiculum, and parasubiculum (Fig. 4D). The second group of axons courses through layer I of the postsubiculum to the presubiculum, where the majority of these axons appear to terminate in layer I, but a small number of terminals also extend to postsubiculum and parasubiculum. Retrosplenial granular a cortex also projects to the contralateral postsubiculum and presubiculum in layers V and VI. Caudal Rga gives rise to terminals in the same general areas as the rostral Rga, but the terminal field in postsubiculum is considerably more caudal (Fig. 9).

Rga, afferent connections

Retrosplenial granular a cortex receives a small input from a small number of pyramidal and nonpyramidal neurons in field CA1 of the dorsal hippocampus; the nonpyramidal neurons mainly are at the border of stratum radiatum and stratum moleculare. Rostral (compared to caudal) Rga receives projections from slightly different areas of the hippocampal formation (Fig. 10). Cell bodies in the ventral part of the temporal third of the subiculum (Fig. 6C) project to rostral Rga, in contrast to the dorsal part of the temporal third of the subiculum, which projects primarily to more caudal parts of Rga. The terminations of these projections in Rga have been documented using the PHA-L method (Van Groen and Wyss, 1990c; Fig. 4E).

Laminar termination of hippocampal projections

Neurons in the septal (dorsal) third of CA1 project a few axons and terminals to Rgd, predominantly in layer II. Ventral subiculum projects to layers I, II, and III of Rga, with the greater part of the axons and terminals in layer II (Fig. 4E). Dorsal subiculum projects mainly to Rgd, with small
Fig. 4. High-power photomicrographs of coronal sections to demonstrate PHA-L labeling. (A–C) Labeled axons and terminals in postsubiculum following an injection into (A) Rdg, (B) Rgb, and (C) Rga. (D) Labeled axons and terminals in the deep layers of parasubiculum and presubiculum following an injection into Rga. (E) Labeled axons and terminals in the superficial layers of Rga following an injection into ventral subiculum. (F) Labeled axons and terminals in Rgb following an injection into dorsal subiculum. Scale bars, 100 μm.
numbers of fibers going to Rga and Rdg. In Rgb most of the axons and terminals are in deep layer II and layer III (Fig. 4F), with smaller numbers of axons in layers I and III. Both in Rgb and in Rga most of the axons in layer I are fibers of passage. Postsubiculum projects to Rga and Rgb, with a small number of fibers in Rdg. These projections end in layers I (predominantly in Ib and Ic) and III–IV. Both in Rga and in Rgb a large number of these axons in layer I are fibers of passage.

NONHIPPOCAMPAL CONNECTIONS OF RETROSPLENIAL CORTEX

In addition to the output of the retrosplenic cortex to the hippocampal formation, this region also projects to widespread areas of the brain (Domesick, 1969; Vogt and Miller, 1983; Wyss and Sripanidkulchai, 1984; Vogt et al., 1986; Sripanidkulchai and Wyss, 1987; Van Groen and Wyss, 1990c; 1991a). Retrosplenic dysgranular cortex projects to orbital, IR, retrosplenial, 18b, 17, postsubicular, parasubicular, entorhinal, and perirhinal cortices. Subcortically, Rdg projects to caudate/putamen, anterior (anteromedial, AM), lateral (laterodorsal, LD; lateroposterior, LP), reticular, and reuniens nuclei of the thalamus, zona incerta, superior colliculus, periaqueductal gray, and ventral pontine nuclei. Retrosplenic dysgranular cortex has contralateral projections to Rdg, Rgb, Rga, IR, and postsubicular cortices. Retrosplenic granular b cortex projects to IR, Rdg, Rga, and postsubicular cortices. Subcortically, Rgb projects to claustrum, anterodorsal (AD), LD, and reticular nuclei of the thalamus, superior colliculus, periaqueductal gray, and the ventral pontine nuclei. Most of the contralateral projections of Rgb are to Rgb, Rdg, Rga, and postsubicular cortices. Retrosplenic granular a cortex projects to IR, Rdg, Rgb, entorhinal, postsubicular, presubicular, and parasubicular cortices. Subcortical projections from Rga are to anteroventral (AV), LD, reticular and reuniens nuclei of the thalamus, the superior colliculus, and the ventral pontine nuclei. Most of the contralateral projections of Rga are to Rga, Rdg, Rgb, subicular, and entorhinal cortices, and to AV.

The retrosplenic cortex is innervated by axons from a wide variety of brain regions (Rose and Woolsey, 1948; Melbich and Siegel, 1977a; 1977b; Niimi, 1978; Robertson and Kaitz, 1981; Finch et al., 1984a; Sripanidkulchai and Wyss, 1986b; Vogt et al., 1986; Thompson and Robertson, 1987; Van Groen and Wyss, 1990c; 1991a). Retrosplenic dysgranular cortex receives projections from orbital, IR, retrosplenic, 18b, 17, postsubicular, and entorhinal cortices. Contralateral projections originate in Rdg, Rgb, and Rga cortices, and subcortical projections originate in claustrum, diagonal band of Broca, medial septal nucleus, anterior (AM), lateral (LD and LP), and reuniens nuclei of the thalamus, the raphe nuclei, and the locus ceruleus. Retrosplenic granular b cortex is innervated by axons from IR, Rdg, and Rga cortices, area CA1, the subiculum, and postsubiculum. Subcortical, neuronal cell bodies project to Rgb from claustrum, diagonal band of Broca, medial septal nucleus, AD, AV, LD, and reuniens nuclei of the thalamus, raphe nuclei and locus ceruleus. Contralateral projections to Rgb arise from neurons in Rgb, Rdg, and postsubiculum. Retrosplenic granular a cortex receives ipsilateral projections from Rga and Rgb, area 18b, area infraradiata, postsubiculum, hippocampus, rostroventral subiculum, presubiculum, and contralateral Rga. Subcortical projections to Rga arise from the claustrum, diagonal band of Broca, (both vertical and horizontal limbs), the reuniens, AD, AV, and LD nuclei of the thalamus, the midbrain raphe nuclei, and the locus ceruleus.

DIFFERENTIAL PROJECTIONS TO EACH REGION OF RETROSPLENIAL CORTEX

One element in the circuitry of the medial limbic structures proposed by Papez (1937) was a cortical connection between the retrosplenic and hippocampal cortices. Although direct connections with the hippocampus proper (i.e., area CA1–CA4) were not observed in subsequent studies (however, see Van Groen and Wyss, 1990c), pathways between the retrosplenic and the subicular cortices have been documented (Adel, 1951; Swanson and Cowan, 1977; Melbich and Siegel, 1977a; 1977b; Sorensen, 1980; Van Groen and Wyss, 1990a; 1990b; Witter et al., 1990; Van Groen and Wyss, 1991a). Our studies demonstrate that ventral subiculum and presubicular project to the Rga cortex, the dorsal part of the subiculum projects to the Rgb cortex, and the postsubiculum projects to Rga, Rgb, and Rdg cortices (Fig. 11). The retrosplenic cortex also receives widespread cortical innervation from infraradiata, visual, and motor cortices (Vogt and Miller, 1983; Van Groen and Wyss, 1990c; 1991a). Our experiments (Sripanidkulchai and Wyss, 1986b; Van Groen and Wyss, 1990c; 1991a) have demonstrated that Rdg is innervated by infraradiata, Rga, 18b, 17, and contralateral Rdg cortices, Rgb is innervated by infraradiata, Rdg, and contralateral Rgb cortices, and Rga is innervated by infraradiata, Rgb, Rdg, and contralateral Rga cortices. Thus, each part of the retrosplenic cortex receives a somewhat different neocortical and limbic cortex projection (Fig. 11).

The thalamic nuclei also project distinctly to each retrosplenic region (Rose and Woolsey, 1948; Niimi, 1978; Niimi...
Fig. 6. Four photomicrographs of coronal sections of the hippocampal formation following injections of retrogradely transported fluorescent tracers. (A) Labeled neurons in the dorsal subiculum following an injection into Rgb. (B) Labeled neurons in the deep layers of postsubiculum following an injection into Rdg. (C) Labeled neurons in ventral subiculum following an injection of Rga. (D) A labeled nonpyramidal neuron in area CA1 following an injection of Rgb. Scale bars (A–C), 50 μm; scale bar (D), 20 μm.

Each region of the retrosplenial cortex has distinct terminal fields within the cortex (Fig. 11). Retrosplenial dysgranular cortex projects to IR, Rga, 18b, postsubiculum, and parasubiculum, while projections from Rgb terminate predominantly in infraradiata, Rdg, Rgb, and postsubiculum. The major efferent projections of Rga are to the caudal Rdg, and the postsubiculum. Further, contralateral projections of each region are predominantly homotypic, i.e., Rdg to Rdg, Rgb to Rgb, and Rga to Rga. These connections confirm that the retrosplenial cortex plays an intimate role in the transfer of neocortical and limbic cortex information, and the differences in connections between Rga, Rgb, and Rdg suggest that each area contributes uniquely.

The connections documented in this commentary further clarify the role of the retrosplenial cortex in the so-called "Papez circuit" (Papez, 1937); most prominent inputs and outputs of the retrosplenial cortex are to areas in the limbic

Fig. 7. Schematic maps to demonstrate the labeling pattern in the hippocampal formation following injections of PHA-L into rostral (vertical hatching) and caudal (horizontal hatching) Rgb.

Fig. 8. Schematic maps to demonstrate the pattern of retrograde labeling in the hippocampal formation following injections of PHA-L into rostral (filled circles) and caudal (diamonds) Rgb.

Fig. 9. Schematic maps to demonstrate the labeling pattern in the hippocampal formation following injections of PHA-L into rostral (vertical hatching) and caudal (horizontal hatching) Rga.

Fig. 10. Schematic maps to demonstrate the pattern of retrograde labeling in the hippocampal formation following injections into rostral (filled circles) and caudal (diamonds) Rga.
the areas of the retrosplenial granular cortex to which subicular inputs end predominantly in layer Ia, the subicular input ends primarily in layer II, and the postsubicular input terminates predominantly in layers Ib, Ic, and II–III. Such an anatomical organization is ideally suited for integration of these three inputs by the retrosplenial, layer V, pyramidal neurons. The electrophysiological study of Finch and colleagues indicates that such a thalamocortical integration occurs in these layer V pyramidal cells of the retrosplenial granular cortex (Finch et al., 1984b).

FUNCTIONAL IMPORTANCE OF THE RETROSPLENIAL-HIPPOCAMPAL INTERCONNECTIONS

Functional studies demonstrate that lesions of the retrosplenial cortex impair learning of rats in a water maze; however the animals are not impaired in learning (including visual tasks) per se. Thus “posterior cingulate areas are essential to the ability to move accurately to points in space using the relationships among distal cues” (Sutherland et al., 1988). Other recent studies demonstrate that Rdg contains “head direction cells,” i.e., neurons that discharge as a function of the rat’s head direction in the horizontal plane (Chen et al., 1990), while the hippocampus proper contains “place cells” (i.e., neurons that fire when a rat is in a specific place; O’Keefe and Nadel, 1978). It should be noted that the postsubiculum, which receives a dense projection from Rdg, also contains “head direction cells” (Taube et al., 1990a; 1990b). Further, studies by Sikes et al. (1985; 1988) indicate that Rdg may be involved in the processing of visual information in relation to eye movements. Thus, in addition to the anatomical evidence (Van Groen and Wyss, 1991a), there is functional evidence that Rdg plays a role in visual-spatial behavior.

Together with the studies of others, these data suggest that the retrosplenial cortex contributes to the role of the hippocampus in memory and learning (Matsunami et al., 1989; Sif et al., 1989). Gabriel and colleagues (Gabriel et al., 1980; 1989; Gabriel and Sparenborg, 1986; 1987) have demonstrated that the response of retrosplenial cortex neurons in a learning paradigm is in part dependent on intact connections from the hippocampal formation to the retrosplenic cortex. Sutherland et al. (1988; 1989) have demonstrated that an intact retrosplenic cortex is for the to move accurately to points in space using distal cues, i.e., place navigation. Bilateral lesions of the retrosplenic cortex impair rabbits in their ability to reverse discrimination in a nictitating membrane response paradigm (Berger et al., 1986). Further, Markowska et al. (1989) have demonstrated that retrosplenic cortex lesions induce spatial memory impairments in cats, and using an identical experimental design, Murray et al. (1989) have demonstrated a similar defect in monkeys. Finally, Valentstein et al. (1987) have demonstrated the development of amnesia in a patient after lesions in the retrosplenic cortex. Thus, the retrosplenic cortex appears to be important for learning and memory in a broad spectrum of mammalian species. In light of these findings, the elucidation of the anatomy and physiology of the interconnections between the hippo-
campal formation and the retrosplenial cortex takes on an added importance.

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