



## Reviews and perspectives

## Neural structures and mechanisms involved in scene recognition: A review and interpretation

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## ABSTRACT

Since the discovery in 1996 that a region within caudal parahippocampal cortex subserves learning and recall of topographical information, numerous studies aimed at elucidating the structures and pathways involved in scene recognition have been published. Neuroimaging studies, in particular, have revealed the locations and identities of some of the principal cortical structures that mediate these faculties. In the present study the detailed organization of the system is examined, based on a meta-analysis of neuroimaging studies of scene processing in human subjects, combined with reviews of the results of lesions on this type of processing, single neuron studies, and available hodological data in non-human primates. A cortical hierarchy of structures that mediate scene recognition is established based on these data, and an attempt is made to determine the function of the individual components of the system.

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**Abbreviations:** AI, primary auditory cortex; AIP, anterior intraparietal area; AON, accessory olfactory nucleus; CA1, hippocampal ammonic field 1; CA3, hippocampal ammonic field 3; CL, caudal lateral auditory area; CM, caudal medial auditory area; CPB, Caudal parabelt auditory area; DG, dentate gyrus; DP, dorsal prelunate area (macaque); EC, entorhinal cortex; ECcl, caudolateral division of EC; ECrm, rostromedial division of EC; FST, superior temporal fundal area (macaque); Gu, gustatory cortex; lav, ventral agranular insular cortex; Id, dysgranular insular cortex; Ig, granular insular cortex; LIP, lateral intraparietal area; LO1, lateral occipital area 1; LO2, lateral occipital area 2; M1, primary motor cortex; MST, medial superior temporal area; MT, middle temporal area; OP1, parietal operculum area 1; OP2, parietal operculum area 2; OP3, parietal operculum area 3; OP4, parietal operculum area 4; Pal, parainsular area; PaS, parasubiculum; PE, superior parietal area; PEc, caudal superior parietal area; PEci, cingulate superior parietal area; PF, inferior parietal area PF of Pandya and Seltzer (1982); PFG, inferior parietal area PFG of Pandya and Seltzer (1982); PG, inferior parietal area PG of Pandya and Seltzer (1982); PGM, medial parietal area PG (area 7 m); PGop, opercular inferior parietal area PG; Pir, piriform cortex; PMv, ventral premotor cortex; PMd, dorsal premotor cortex; POda, dorsal anterior parieto-occipital area; Ppt, posterior parietal area; PR, parieto-rostral area (macaque); PrC, perirhinal cortex; PrCO, precentral opercular cortex; PreSMA, pre-supplementary motor area; ProSt, area prostriata; PrS, prosubiculum; PV, parieto-ventral area (macaque); Ri, retroinsular area; RPB, rostral parabelt auditory area; Rsp, retrosplenial area; SMA, supplementary motor area; SOG, superior occipital gyral area; Sub, subiculum; TE, inferior temporal cortical area; TEav, anteroventral division of TE; TEad, anterodorsal division of TE; TEpv, posteroventral division of TE; TEpd, posterodorsal division of TE; TEO, caudal inferior temporal area; TF, macaque parahippocampal area TF; TFO, macaque parahippocampal area TFO; TFr, human rostral parahippocampal area; TFC, human caudal parahippocampal area; TG, temporopolar cortex; TGD, dorsal division of TG; TGSts, sulcal division of TG; TGA, agranular division of TG; TH, parahippocampal area TH; TPO, area TPO of macaque temporal cortex; TPOc, caudal division of area TPO; Tpt, temporoparietal area; VIP, ventral intraparietal area; amts, anteromedial temporal sulcus; aos, anterior occipital sulcus; casd, dorsal calcarine sulcus; casv, ventral calcarine sulcus; ces, central sulcus; cings, cingulate sulcus; colls, collateral sulcus; ifs, inferior frontal sulcus; ips, intraparietal sulcus; its, inferior temporal sulcus; lorbs, lateral orbital sulcus; olfs, olfactory sulcus; ots, occipitotemporal sulcus; pmts, posteromedial temporal sulcus; poces, postcentral sulcus; pos, parieto-occipital sulcus; rhs, rhinal sulcus; sfs, superior frontal sulcus; sps, subparietal sulcus; sts, superior temporal sulcus; tos, transverse occipital sulcus.

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## 1. Introduction

The vertebrate visual system continually processes neural information derived from retinal cells that respond to visual stimuli present in the entire visual field. Objects present in the foreground, located primarily in the central visual field, are processed separately from those in the background, which occupy the peripheral visual field. The ensemble of the latter objects constitutes a scene, and may also be considered to be the spatial context of present events involving the self. In the analysis of these events, recognition of the objects present in central vision, and of the scene or spatial context in which those objects are present are both essential, and it is not surprising that a system dedicated to scene/context recognition should exist.

Scenes could, in principle, be recognized either through holistic processing (i.e. the entire scene could be recognized as a single visual object), or as spatial configurations of independent objects, that is, as multicomponent stimuli. Obviously, the complexity of naturalistic scenes demands that they be treated as multicomponent stimuli, so that the recognition of a given scene requires the recognition of at least some of its component objects, and the encoding of the location of those objects. Complex buildings are probably also treated as multicomponent objects, the components being wall segments, doors and windows, and processed much like naturalistic scenes.

The participation of peripheral versus central visual representations in scene recognition was investigated by van Diepen and colleagues (van Diepen, De Graef, Lamote, & van Wijnendaele, 1994; van Diepen & Wampers, 1998), who examined the effects of deprivation of central or peripheral information, and demonstrated that it is possible to recognize a scene even if the central part of the visual image is missing. In a related vein, it was recently proposed that a fundamental principle that governs the layout of human visual object-related areas is that object representations in these areas are arranged according to a central versus peripheral visual field bias (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Levy, Hasson, Harel, & Malach, 2004), such that single important objects are processed in central representations, and background scenes

in peripheral representations. This proposal is in accord with the observation that cortical projections of the central and peripheral visual field representations in extrastriate areas of macaque monkeys, including areas V1, V2 and V4, to other extrastriate areas are distinct (Colby, Gattass, Olson, & Gross, 1988; Gattass, Sousa, Mishkin, & Ungerleider, 1997; Ungerleider & Desimone, 1986; Ungerleider, Galkin, Desimone, & Gattass, 2008; Zeki, 1969, 1980). Thus, for instance, the upper visual field peripheral representation of macaque area V2v projects to parahippocampal area TF (which is, in part, homologous to the human parahippocampal place area, PPA, a region involved in scene processing), but the central visual field does not (Gattass et al., 1997). Moreover, the responses of neurons in macaque area TF are maximal when stimulated at eccentricities of more than 10° (Sato & Nakamura, 2003). In a recent neuroimaging study Levy et al. (2001) reported that face-related regions in human extrastriate and temporal visual cortex are associated with central visual field representations, whereas building-related regions are associated with peripheral field representations. Thus, for example, the visual field representation in the human fusiform face area (FFA) is predominantly, if not exclusively, central, whereas the representation in the PPA is dominated by the peripheral field, so it appears that peripheral field representations in both humans and monkeys are at least partially reserved for background or contextual (scene) recognition (Bar, Aminoff, & Schacter, 2008).

The location and identity of the structures that process object location, both for centrally presented visual objects, and for the component objects in a scene, are still in debate. According to the “two streams” theory of object processing (Ungerleider & Mishkin, 1982), object location is represented in components of the primate dorsal (parietal) processing stream, primarily in structures located in and the intraparietal sulcus and/or inferior parietal lobule. However, it has been reported recently that inactivation of the human intraparietal sulcus fails to produce deficits in scene encoding or recognition (Rossi et al., 2006). In fact, the “two streams” notion that the dorsal stream is dedicated to processing object location is now in question, as it becomes increasingly evident that the principal function of areas in the intraparietal sulcus in both humans and monkeys is the allocation of attention to particular objects in complex visual object arrays (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Cowey & Irving-Bell, 2006).

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