12 Cheng, K. and Newcombe, N.S. (2005) Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychon. Bull. Rev.* 12, 1–23

13 Hermer-Vazquez, L. *et al.* (1999) Sources of flexibility in human cognition: Dual task studies of space and language. *Cognit. Psychol.* 39, 3–36

14 Newcombe, N.S. (2005) Evidence for and against a geometric module: The roles of language and action. In *Action as an Organizer of Learning and Development. Minnesota Symposia on Child Psychology* (Vol. 33)

(Rieser, J. *et al.*, eds), Action as an Organizer of Learning and Development. Minnesota Symposia on Child Psychologypp. 221–241, Erlbaum

15 Levine, S.C. *et al.* (2005) Socioeconomic status modifies the sex difference in spatial skill. *Psychol. Sci.* 16, 841–845

Letters

The missing whole in perceptual models of perirhinal cortex

Anthony D. Cate and Stefan Köhler

Department of Psychology and CIHR Group for Action and Perception, University of Western Ontario, London, Ontario, N6A 5C2, Canada

The possibility that perirhinal cortex (PRh) plays a role in perceptual processing of objects, in addition to its well-established memory functions, has produced a growing body of research that was recently summarized by Buckley and Gaffan and integrated in their 'levels of representation' (LR) thesis [1]. The most important new experiments reviewed probed the ability of PRh-lesioned primates (human and non-human) to make perceptual discriminations in the presence of minimal memory demands. They were conducted to counter the criticism that the impairments previously observed in concurrent discrimination learning (CDL) might reflect mnemonic rather than perceptual difficulties (e.g. [2]). The new evidence discussed in support of a perceptual role for PRh was obtained with oddity tasks, morph tasks, and a re-analysis of the first trials of a CDL task involving viewpoint generalization. These tasks differ from the original CDL tasks, however, not only with respect to memory but also perceptual demands. First, they require judgements of graded similarity instead of exact matching. Second, successful performance hinges upon perceiving holistic gestalt properties of objects. These perceptual demands raise concerns whether the involvement of PRh in perceptual discriminations can be accounted for by the mechanism described in Buckley and Gaffan's LR thesis.

The LR thesis holds that PRh is recruited in tasks, perceptual or mnemonic, that require discriminations of similar objects. PRh overcomes the 'feature ambiguity' [3] that is inherent in anterior inferotemporal (TE) inputs by representing conjunctions of features that are individually insufficient to allow for unambiguous object identification. Put another way, PRh performs pattern separation on overly similar object representations in TE. In the perceptual/mnemonic feature conjunction (PMFC) model that Buckley and Gaffan cite to elaborate on the computational implementation, PRh units are narrowly tuned to prefer a close match with a unique collection of features that

represent a specific object [4]; avoiding generalization among similar inputs is the key to how the model resolves feature ambiguity. With such an architecture, however, it is difficult to explain why the integrity of PRh is crucial on tasks that entail stimulus generalization and judgments of graded similarity. Successful performance in many of the studies reviewed required subjects to generalize across changes in viewpoint of objects or across changes introduced by morphing. Such changes transform an image in nonlinear ways and can occlude salient object parts from view; the only features that persist unchanged and that observers can reliably use to recognize the same object after it has been transformed are higher-order gestalt characteristics. In the PMFC model, however, PRh does not represent the gestalt of stimuli. What is represented, instead, is a linear combination of the features, that is, a literal sum of the parts. In general, a representation that is simply a list of which features combine to define an object is not a gestalt [5].

The LR thesis also appears to be at odds with evidence on the neural coding scheme in PRh. The general idea of feature conjunctions and the specific architecture of the PMFC model imply a sparse local system in which a neural unit responds to only one or a few input patterns, while being unresponsive to other similar patterns. This principle contrasts with the notion of coarse distributed coding, in which an object is represented by the joint activity of many units, and in which each unit responds robustly to many different patterns. Recent evidence obtained with single-cell recordings suggests that primate PRh neurons do indeed use coarse coding [6]. Visually selective PRh neurons were found to be broadly tuned and were *more* coarse (i.e. less selective) than TE neurons [7]. This evidence is difficult to reconcile with the LR thesis.

Coarse coding would in fact make for an efficient scheme for the representation of objects in PRh. Responses of coarse-coding neurons as a population can distinguish between similar inputs, and unlike responses in sparse-coding systems, they are graded: the similarity of the responses reflects the similarity of the input patterns.

Corresponding author: Köhler, S. (stefank@uwo.ca)
Available online 8 August 2006.

Coarse coding can also support the assessment of item familiarity, one of the main memory functions ascribed to PRh [8]. In a recent connectionist model of recognition memory [9], the extrahippocampal component that includes PRh supplies a familiarity signal based on extensively overlapping distributions, and yet supports fine discriminations between similar objects in forced-choice recognition memory tasks successfully. A model of PRh that incorporates coarse coding thus would not only offer a promising account of its perceptual functions, but would also be in line with computational accounts of its memory functions.

Acknowledgments

References

1 Buckley, M.J. and Gaffan, D. (2006) Perirhinal cortical contributions to object perception. *Trends Cogn. Sci.* 10, 100–107

2 Hampton, R.R. (2005) Monkey perirhinal cortex is critical for visual memory, but not for visual perception: reexamination of the behavioural evidence from monkeys. *Q. J. Exp. Psychol. B* 58, 283–299

3 Bussey, T.J. et al. (2005) The perceptual-mnemonic/feature conjunction model of perirhinal cortex function. *Q. J. Exp. Psychol. B* 58, 269–282

4 Bussey, T.J. and Saksida, L.M. (2002) The organization of visual object representations: a connectionist model of effects of lesions in perirhinal cortex. *Eur. J. Neurosci.* 15, 355–364

5 Pomerantz, J.R. and Kubovy, M. (1986) Theoretical approaches to perceptual organization. In *Handbook of Perception and Human Performance* (Boff, K.R. et al., eds), pp. 36.1–36.46, Wiley

6 Hőlscher, C. et al. (2003) Perirhinal cortex neuronal activity related to long-term familiarity memory in the macaque. *Eur. J. Neurosci.* 18, 2037–2046

7 Rolls, E.T. (2000) Functions of the primate temporal lobe cortical visual areas in invariant visual object and face recognition. *Neuron* 27, 205–218

8 Brown, M.W. and Aggleton, J.P. (2001) Recognition memory: what are the roles of the perirhinal cortex and hippocampus? *Nat. Rev. Neurosci.* 2, 51–61

9 Norman, K.A. and O'Reilly, R.C. (2003) Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning–systems approach. *Psychol. Rev.* 110, 611–646

Genes and domain specificity

Gary F. Marcus and Hugh Rabagliati

New York University, 6 Washington Place, New York, NY 10012, USA

Kovas and Plomin's recent article on 'generalist genes' [1] purports to pose a strong challenge to the possibility of modular neural or cognitive structure. Pointing to the fact that 'there is substantial genetic overlap between such broad areas of cognition as language, reading, mathematics and general cognitive ability', Kovas and Plomin [1] argue that 'genetic input into brain structure and function is general not modular'.

The observation of genetic overlap in itself is not new. Our group made it recently in a more nativist account [2], while Karmiloff-Smith made it previously in the context of a less nativist proposal [3]. Given the extensive literature on a general factor (g) of intelligence, and the well-known correlation between verbal and nonverbal IQ, the overlap observation itself is unsurprising.

Kovas and Plomin's anti-modularity interpretation, however, goes far beyond the scope of these data. As researchers in other areas of biology recognize [4], modularity certainly does not require that all genes or even most of the genes involved in a given process be domain-specific; only that some genes (or even some portions thereof) be differentially expressed. Modularity can arise from the actions of a handful of 'upstream' regulatory genes, even if many or all downstream genes are broadly shared across domains.

Genes are in essence instructions for fabricating biological structure. In the construction of a house, one finds both some repeated motifs and some specializations for particular rooms. Every room has doors, electrical wiring, insulation and walls built upon a frame of wooden studs. However, the washroom and kitchen vary in the particulars of how they use plumbing array fixtures, and only a garage is likely to be equipped with electric doors (using a novel combination of electrical wiring and 'doorness'). Constructing a home requires both domain-general and domain-specific techniques. The specialization of a given room principally derives from the ways in which high-level directives guide the precise implementation of low-level domain-general techniques.

When it comes to neural function, the real question is how 'generalist genes' fit into the larger picture. Continuing the analogy, one might ask whether different 'rooms' of the brain are all built according to exactly the same plan, or whether they differ in important ways, while depending on common infrastructure. Kovas and Plomin [1] presume that the sheer preponderance of domain-general genes implies a single common blueprint for the mind, but it is possible that the generalist genes are responsible only for infrastructure (e.g. the construction of receptors, neurotransmitters, dendritic spines, synaptic vesicles and axonal filaments), with a smaller number of specialist genes supervising in a way that still yields a substantial amount of modular structure. Kovas and Plomin [1] offer no data to indicate otherwise.

Corresponding author: Marcus, G.F. (gary.marcus@nyu.edu)