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Thinking about Networks in the Control of Male Hamster Sexual Behavior

Ruth I. Wood[1]

Department of Obstetrics and Gynecology and Department of Biology, Yale University School of Medicine, 333 Cedar Street, Box 208063, New Haven, Connecticut 06520-8063

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Motivated social behaviors such as mating are controlled by a complex network of limbic nuclei. Concepts of network organization derived from computational neuroscience may aid our understanding of the links between the neuroanatomical circuitry and what is represented by the anatomy. Research in my laboratory uses mating behavior in the male Syrian hamster as a model to elucidate how chemosensory and steroid cues are integrated in the brain. An interaction of odors and hormones is required for mating in this species. These two essential stimuli are transmitted through separate parallel pathways in the limbic system. The functional organization of the hamster mating behavior circuit is characterized by distributed representation, divergent and convergent neural pathways, and recurrent feedback. Odors and hormones have different modes of action on this neural network. While chemosensory cues stimulate the input units of the network, steroids facilitate behavior through the hidden units. In this manner, steroids appear to create a permissive environment for subsequent activation by odor cues. © 1997 Academic Press

In 1986 Cottingham and Pfaff reviewed the neuroanatomical evidence for interconnections between steroid-responsive brain regions and proposed that there is a hormone-sensitive neural network within the limbic system (Cottingham and Pfaff, 1986). Based on this network structure, they proposed several hypotheses about how hormones act in the brain to control aspects of steroid-dependent behavior and neuroendocrine function. Their postulates of redundancy, amplification, stability, and selective filtering have been tested in different animal models, including the male hamster (Wood, 1996). In doing so, we not only validate these hypotheses, we further our understanding of structure–function relationships that underlie steroid-dependent sexual behavior.

The limbic system is replete with functional networks, and there is tremendous potential to expand our application of network principles to understand the generation of complex behaviors, such as mating, aggression, and parental behavior. Computational neuroscientists have avoided studying networks in the limbic system in favor of studying more highly ordered cortical circuits, such as those subserving vision and somatosensory processes. The structure of cortex facilitates network analysis because there is geometric organization in cortical information processing (Churchland and Sejnowski, 1992). Sensory input to primary visual, auditory, and somatosensory cortex is arranged topographically, and afferent and efferent connections are ordered in vertical columns. In contrast, neurons in the limbic system are clustered in nuclei (Gilman and Newman, 1992), and there is no equivalent three-dimensional organization of connections within and between individual nuclei for the processing of limbic information. While the limbic system may not be an ideal model with which to test concepts of neural computation, applying principles of network organization to limbic networks may help us understand the links between the anatomy of these circuits and what is represented by the anatomy.

My research uses sexual behavior in the male Syrian hamster as a model to investigate neural integration of chemosensory and hormonal cues. The male hamster requires both odors and hormones to mate (Wood and Newman, 1995a). Moreover, copulation is dependent upon an interaction of chemosensory and steroidal

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[1] To whom correspondence should be addressed at Departments of Obstetrics & Gynecology and Biology, Yale University School of Medicine, 333 Cedar St., Box 208063, New Haven, CT 06520-8063. Fax: (203) 785-5294. E-mail: ruth_wood@qm.yale.edu.

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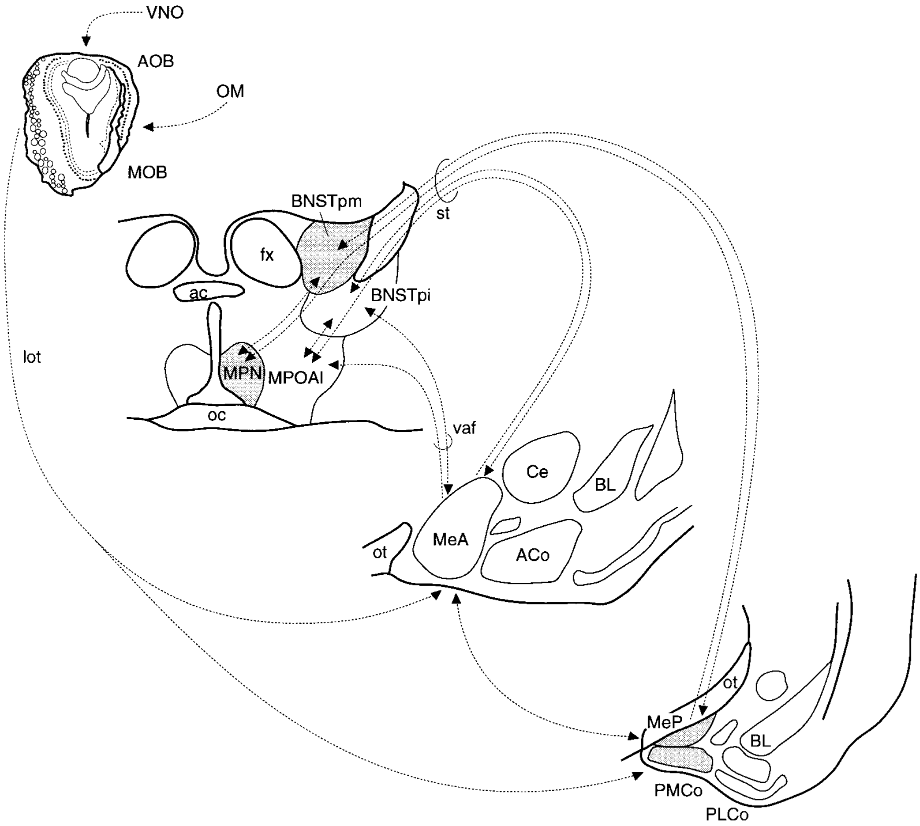

FIG. 1. Schematic diagram of principle limbic nuclei and connections in hamster brain that transmit chemosensory and hormonal cues to control male sexual behavior. Shading indicates areas with abundant steroid receptor-containing neurons. ac, anterior commissure; ACo, anterior cortical amygdaloid nucleus; AOB, accessory olfactory bulb; BL, basolateral amygdaloid nucleus; BNST, bed nucleus of the stria terminalis, BNSTpi, posterointermediate subdivision, BNSTpm, posteromedial subdivision; Ce, central amygdaloid nucleus; fx, fornix; lot, lateral olfactory tract; Me, medial amygdaloid nucleus; MeA, anterior subdivision; MeP, posterior subdivision; MOB, main olfactory bulb; MPN, medial preoptic nucleus; MPOAl, lateral subdivision of the medial preoptic area; oc, optic chiasm; OM, olfactory mucosa; ot, optic tract; PLCo, posterolateral cortical amygdaloid nucleus; PMCo, posteromedial cortical amygdaloid nucleus; st, stria terminalis; vaf, ventral amygdalofugal pathway; VNO, vomeronasal organ.

stimuli in the brain (Wood and Newman, 1995b). Thus, the challenge is to understand the neural mechanisms and pathways through which an external sensory signal and an internal blood-borne cue are weighed, prioritized, and integrated. Understanding the mechanisms of chemosensory and hormonal integration is a complex multidimensional question, which can be addressed at many different levels. My particular interest is at the neural systems level. Figure 1 depicts the principal limbic nuclei and connections that underlie facilitation of male hamster sexual behavior by gonadal steroid hormones and chemosensory cues from the olfactory mucosa and vomeronasal organ. Clearly, the hamster mating behavior circuit is a neural network. What are the unique and overlapping functions of the different subnuclei? How do the neural connections coordinate activity among different brain regions? Given the complexity of the underlying neural circuitry, we cannot rely upon a one-dimensional model to explain odor and hormonal control of mating.

LEVELS OF ORGANIZATION/LEVELS OF PROCESSING

Information processing in the brain takes place simultaneously at multiple different levels or scales (Shepherd, 1990). Examples of such organizational scales include behavioral systems, interregional circuits, local circuits, neurons, dendritic trees, microcircuits, synapses, and molecules. Each organizational scale contributes unique aspects of information processing which are not necessarily represented at the