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The vertebrate social behavior network: Evolutionary themes and variations☆

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Abstract

Based on a wide variety of data, it is now clear that birds and teleost (bony) fish possess a core "social behavior network" within the basal forebrain and midbrain that is homologous to the social behavior network of mammals. The nodes of this network are reciprocally connected, contain receptors for sex steroid hormones, and are involved in multiple forms of social behavior. Other hodological features and neuropeptide distributions are likewise very similar across taxa. This evolutionary conservation represents a boon for experiments on phenotypic behavioral variation, as the extraordinary social diversity of teleost fish and songbirds can now be used to generate broadly relevant insights into issues of brain function that are not particularly tractable in other vertebrate groups. Two such lines of research are presented here, each of which addresses functional variation within the network as it relates to divergent patterns of social behavior. In the first set of experiments, we have used a sexually polymorphic fish to demonstrate that natural selection can operate independently on hypothalamic neuroendocrine functions that are relevant for (1) gonadal regulation and (2) sex-typical behavioral modulation. In the second set of experiments, we have exploited the diversity of avian social organizations and ecologies to isolate species-typical group size as a quasi-independent variable. These experiments have shown that specific areas and peptidergic components of the social behavior network possess functional properties that evolve in parallel with divergence and convergence in sociality.

Keywords: Sociality; Aggression; Sexual behavior; Communication; Vocalization; Arginine vasopressin; Arginine vasotocin; Isotocin; Mesotocin; Oxytocin; Fish; Bird; Bed nucleus of the stria terminalis; Amygdala; Lateral septum; Anterior hypothalamus; Ventromedial hypothalamus; Preoptic area; Periaqueductal gray; Nucleus intercollicularis; c-*fos*; egr-1; Zenk

The research program described below is designed to address two major goals. The first of these goals is to elucidate evolutionary themes in the neuroendocrine, functional, and connectional organization of brain circuits that regulate social behavior. This will provide a phylogenetically broad framework for examining the neural and neuroendocrine mechanisms of behavior and will allow detailed and meaningful comparisons to be made across the major vertebrate classes. Building upon this foundation, the second primary goal is to capitalize on the extraordinary behavioral diversity of birds and teleost (bony) fish to elucidate the ways that neural and neuroendocrine mechanisms are adjusted over evolutionary time to produce intraspecific and interspecific variation in behavior. If conducted within a well-characterized, comparative framework, these findings obtained in birds and fish should yield solid predictions for other vertebrates as well. Thus, our work addresses evolutionary *themes*, as described in the first section below, and *variations* on those themes, as presented in the second section.

Evolutionary themes and the concept of a vertebrate social behavior network

As originally suggested for mammals (Newman, 1999), the brain's social behavior network is comprised of six nodes—the extended medial amygdala (i.e., the medial

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amygdala and the medial bed nucleus of stria terminalis, BSTm), the lateral septum (LS), the preoptic area (POA), the anterior hypothalamus (AH), the ventromedial hypothalamus (VMH), and the midbrain (Fig. 1 and Table 1). The relevant midbrain areas include the periaqueductal gray (PAG) and various areas of the tegmentum that link forebrain regions with motoneuron pools of the hindbrain. The other five nodes lie within the basal ("limbic") forebrain. Newman (1999) proposed that these areas comprise a social behavior network based upon a few important criteria. First, each of the nodes has been implicated in the control of multiple forms of social behavior. These include aggression, appetitive and consummatory sexual behavior, various forms of communication, social recognition, affiliation, bonding, parental behavior, and responses to social stressors (Bamshad and Albers, 1996; Coolen et al., 1997; Cushing et al., 2003; Delville et al., 2000; Ferguson et al., 2002; Gammie and Nelson, 2001; Heeb and Yahr, 2001; Kalinichev et al., 2000; Kirkpatrick et al., 1994; Kollack-Walker and Newman, 1995; Kollack-Walker et al., 1997; Lim and Young, 2004; Lonstein et al., 1998; Morgan et al., 1999; Sheehan et al., 2001; Wang et al., 1997). The nodes are also bidirectionally connected (Coolen and Wood, 1998; Coolen et al., 1998; Dong and Swanson, 2004; Risold and Swanson, 1997b), and each area contains sex steroid receptors that are essential for the sexual differentiation and temporal coordination of social behavior (Commins and Yahr, 1985; Morrell and Pfaff, 1978; Simerly et al., 1990; Wood and Newman, 1995). The mammalian brain obviously contains a large number of other areas that are relevant for social behavior (e.g., other basal forebrain areas that regulate stress and reward processes, and cortical areas that serve executive functions); thus Newman's network should be regarded as the "core" of the social brain, not the social brain in toto.

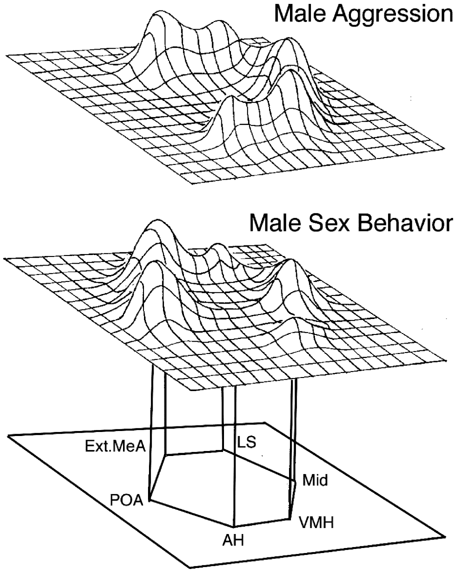

Fig. 1. The social behavior network as originally suggested for mammals (schematics modified from Newman, 1999). The network is comprised of six nodes—the extended medial amygdala (i.e., the medial amygdala and the medial bed nucleus of stria terminalis), the lateral septum (LS), the preoptic area (POA), the anterior hypothalamus (AH), the ventromedial hypothalamus (VMH), and various areas of the midbrain, including the periaqueductal gray. Each of the nodes binds sex steroid hormones and has been implicated in the control of multiple forms of social behavior. Newman (1999) proposes that this network does not contain segregated, linear systems for each kind of behavior. Rather, as shown in these schematic representations of immediate early gene data, each behavioral context is associated with a distinct pattern of activation across the nodes.

Newman (1999) proposes that this network of brain areas does not contain segregated, linear systems for the regulation of each kind of social behavior. Rather, each node of the network responds to a variety of stimuli, with each social context and behavioral response being associated with a distinct *pattern* of response across the nodes. For instance, some of the same areas show increases in immediate early gene (IEG) activity during male sexual behavior, female sexual behavior, and male aggression, but the overall pattern is distinct for each behavioral context (Fig. 1). Although this model is in some ways very simplified (e.g., each area may have distinct neuronal populations with different response profiles), the idea is nonetheless compelling and supported by a good body of data (see references above).

Increasing evidence suggests that this network is present in all vertebrates. While most relevant findings have come from birds, consistent data are also available for amphibians, fish, and reptiles (see Table 1 and the following two sections), and Newman's model has been explicitly applied as a conceptual framework for data in geckos (*Eublepharis macularius*) (Crews, 2003). Interestingly, data from geckos demonstrate that behavioral variations are correlated with distinct patterns of functional connectivity within the network (Sakata and Crews, 2004; Sakata et al., 2000), a finding that lends good empirical support to Newman's (1999) ideas about the significance of distributed activation patterns.

Our own research expands upon these studies in two important respects: First, our work on the vocal circuitry of the plainfin midshipman fish (*Porichthys notatus*) provides the first comprehensive mapping of the network's connections in a non-mammal and has yielded strong evidence that the social behavior network arose in the earliest vertebrates (Goodson and Bass, 2002). As detailed below, the vocal system of the midshipman offers opportunities for systems-level experiments on the network that are not possible in most other animals (i.e., the whole brain can be exposed during analyses of social behavior patterning), thus understanding the comparative organization of the relevant circuitry in fish is particularly valuable. Secondly, our anatomical and behavioral experiments in both fish and birds demonstrate that many functional, structural, and neuroendocrine features are exceptionally similar to those in mammals, thereby rendering detailed comparisons across classes much more feasible than we initially anticipated.