Hormones and Behavior 64 (2013) 103–112

Contents lists available at SciVerse ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Review

# What's in a name? Considerations of homologies and nomenclature for vertebrate social behavior networks

James L. Goodson *, Marcy A. Kingsbury

*Department of Biology, Indiana University, Bloomington, IN 47405, USA*

ARTICLE INFO

*Article history:*
Received 22 March 2013
Revised 15 May 2013
Accepted 18 May 2013
Available online 27 May 2013

*Keywords:*
Social behavior
Social decision-making
Homology
Evolution

ABSTRACT

Behavioral neuroendocrinology is an integrative discipline that spans a wide range of taxa and neural systems, and thus the appropriate designation of homology (sameness) across taxa is critical for clear communication and extrapolation of findings from one taxon to another. In the present review we address issues of homology that relate to neural circuits of social behavior and associated systems that mediate reward and aversion. We first address a variety of issues related to the so-called "social behavior network" (SBN), including homologies that are only partial (e.g., whereas the preoptic area of fish and amphibians contains the major vasopressin–oxytocin cell groups, these populations lie in the hypothalamus of other vertebrates). We also discuss recent evidence that clarifies anterior hypothalamus and periaqueductal gray homologies in birds. Finally, we discuss an expanded network model, the "social decision-making network" (SDM) which includes the mesolimbic dopamine system and other structures that provide an interface between the mesolimbic system and the SBN. This expanded model is strongly supported in mammals, based on a wide variety of evidence. However, it is not yet clear how readily the SDM can be applied as a pan-vertebrate model, given insufficient data on numerous proposed homologies and a lack of social behavior data for SDM components (beyond the SBN nodes) for amphibians, reptiles or fish. Functions of SDM components are also poorly known for birds. Nonetheless, we contend that the SDM model provides a very sound and important framework for the testing of many hypotheses in nonmammalian vertebrates.



**Contents**



## Introduction

One of the great strengths of the behavioral neuroendocrinology literature is its taxonomic diversity, which provides a richer understanding of neural mechanisms than exists for most other areas of neurobiology. However, diversity comes with substantial challenges, particularly the challenge of determining "sameness" in the evolutionary sense — that is, homology. How do we decide whether brain areas in different taxa are homologous and should be called the same thing in different species? There is no rigid criterion, but rather a judgment must be made based on converging lines of evidence. These lines of evidence can be hodological (i.e., based on topographical and connectional relationships to other brain structures),

* Corresponding author.
*E-mail address:* jlgoodso@indiana.edu (J.L. Goodson).

0018-506X/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.yhbeh.2013.05.006

functional, histochemical, genomic, or embryological. A similar question arises in relation to neurochemical systems — how do we determine whether neuropeptides or receptors are homologous across vertebrate groups? Again, there is no set formula, but overall sequence identity, tissue localization and function are useful markers (Butler and Hodos, 2005).

Over the years, many errors have been made in the determination of homology, but as science progresses, the errors are generally corrected (albeit sometimes slowly, as for much of the avian brain; see Reiner et al., 2004). In the present commentary we critically review, and suggest modifications to, assignments of homology in neural systems that are of major importance in the field of behavioral neuroendocrinology. These are the so-called "social behavior network" (SBN), the associated mesolimbic dopamine system, and structures that link the mesolimbic dopamine system to the SBN. This latter circuitry has been included in a recently expanded model of the SBN under the name of the "social decision-making network" (SDM) (O'Connell and Hofmann, 2011).

In the case of the SBN, we here make a case for some revisions to the definition of specific nodes, based largely on recent findings in birds, and also suggest a more conservative approach to homologies in teleost fish. Based on both neurochemical anatomy and function, we also argue that the paraventricular nucleus of the hypothalamus (PVN) of amniotes should be added to the SBN, effectively incorporating neuronal elements that are homologous to those found in the preoptic area (POA) of anamniotes, which is already considered an SBN component. With regards to the mesolimbic dopamine system, relevant afferents, and their incorporation into the proposed pan-vertebrate model for social decision-making (O'Connell and Hofmann, 2011), we discuss a variety of cases in which additional data are needed for clear designations of homology, and also suggest reconsiderations based on recent pieces of evidence. Because 1) the homologies for some of the SDM nodes remain to be clarified in nonmammalian taxa, and 2) experimental evidence for the social behavior functions of SDM network components (outside of the SBN) is lacking in most nonmammalian classes, we suggest that the SDM network model is most appropriately viewed as an important framework for generating hypotheses, rather than viewing tSDM as a validated pan-vertebrate construct.

Before proceeding, a very important point needs to be made: Determinations of homology have always tended to be controversial. Indeed, even the definition of homology has been a matter of controversy. Perhaps the most centrist description of homology is provided by Ghiselin, who states "Structures and other entities are homologous when it is true that they could, in principle, be traced back through a genealogical series to a (stipulated) common ancestral precursor" (Ghiselin, 1966). But regardless of whose definition is employed, homology is often not cut and dried. We point this out because the sections below suggest modifications to aspects of nomenclature that have been established by some of the best scientists who work, or have worked, in our field (and some of our most valued colleagues). Thus, it is certainly not our goal to suggest that the nomenclature has been established in the absence of careful thought, but rather to suggest that some more conservative approaches are appropriate with respect to homologies that are not yet completely clear, particularly with regard to function.

## The social behavior network

Based on a wide variety of functional and anatomical data, Newman (1999) first proposed a "social behavior network" (SBN) in mammals that represents the core neural machinery for the regulation of social behavior. A critical defining feature of SBN components is that, unlike many other brain areas that influence social behavior, the six nodes of the SBN are absolutely essential for basic behaviors such as maternal care, sexual behavior, communication and aggression. As proposed by Newman, those nodes are the *medial extended amygdala* (medial amygdala, MeA, and medial bed nucleus of the stria terminalis, BSTm), *POA*, *lateral septum* (LS), *ventromedial hypothalamus* (VMH), *anterior hypothalamus* (AH), and *midbrain* (periaqueductal gray, PAG, and adjacent tegmentum). These areas are all reciprocally connected and express sex steroid hormone receptors. Of course, other important areas could be included as well, such as components of the mesolimbic dopamine system and the PVN. The PVN is an important source of neuropeptide projections to the nodes just listed, and is thus a major regulator of social behavior (de Vries, 2008; Goodson and Thompson, 2010).

As early as the 1970s, general functional and anatomical similarities of SBN components were apparent across the various vertebrate classes, including similarities in the distribution of sex steroid hormone receptors (Kelley et al., 1975; Morrell and Pfaff, 1978; Morrell et al., 1975; Pfaff, 1968). As additional data accrued over the years, particularly in the 1990s, the homologies became even clearer. This was particularly the case in birds, which were the focus of relatively more investigations than other nonmammalian groups (e.g., Ball and Balthazart, 2001, 2004). The realization that fish also exhibit an SBN homologue came somewhat later, through extensive tracings of neurophysiologically identified vocal–acoustic circuitry in the plainfin midshipman fish (*Porichthys notatus*) (Goodson and Bass, 2002). Combined with a variety of other histochemical, neurophysiological and behavioral data from diverse fish species, these tracings demonstrated that social behavior in fish is controlled by a network of brain areas with sufficiently strong similarities to mammals to be considered a homologous neural network for behavioral control (Goodson, 2005; Goodson and Bass, 2002).

Drawing on these findings and the accumulating data in other vertebrate groups, an SBN model encompassing all vertebrates was proposed in 2005 (Goodson, 2005), although other researchers had already gained the same insight and adopted Newman's model for their own systems — most notably Crews, who had elegantly applied the model to reptiles (Crews, 2003). An important subsequent modification of the SBN model came with a later application of the model to songbirds by Maney et al. (2008), who explicitly modified the midbrain component to include the ventral tegmental area (VTA). The idea that mesolimbic dopamine circuitry is central to the regulation of social behavior likewise led O'Connell and Hofmann (2011) to propose an expanded SBN model, which they called the "social decision-making network" (SDM, as noted above). This expanded model further incorporates the nucleus accumbens, pallial (basolateral) amygdala, and numerous other areas as addressed in the next section.

In general, the basic structure of the vertebrate SBN as originally proposed has remained sound. That is, when comparing the various classes of vertebrates, the homologies of the individual SBN nodes are very clear, at least in most cases, based on a wide range of functional, histochemical and hodological data (Goodson, 2005; Newman, 1999). However, multiple revisions and clarifications are needed in relation to 1) the identity of the avian AH and PAG; 2) major peptidergic differences in the POA of amniotes and anamniotes; and 3) the use of mammalian nomenclature in cases of partial homology, particularly in teleost fish.

### *The avian PAG*

The first of the brain regions requiring attention in birds is the PAG. Although an avian PAG (substantia grisea centralis, or central gray) had long been recognized, it is laterally contiguous with a relatively large area known as the nucleus intercollicularis (ICo), which abuts the auditory torus. Note that because the avian tectum is hypertrophied and expands laterally, PAG subdivisions that lie dorsally in mammals (i.e., under the optic tectum, or superior colliculus) can be expected to lie laterally in birds, and thus medial to the laterally placed tectum (see topography in Fig. 1). In fact, based on a survey of known connections (e.g., Berk and Butler, 1981; Wild, 1989),