



Arginine vasotocin neuronal phenotypes, telencephalic fiber varicosities, and social behavior in butterflyfishes (Chaetodontidae): Potential similarities to birds and mammals

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ABSTRACT

The neuropeptide arginine vasopressin (AVP) influences many social behaviors through its action in the forebrain of mammals. However, the function of the homologous arginine vasotocin (AVT) in the forebrain of fishes, specifically the telencephalon remains unresolved. We tested whether the density of AVT-immunoreactive (-ir) fiber varicosities, somata size or number of AVT-ir neuronal phenotypes within the forebrain were predictive of social behavior in reproductive males of seven species of butterflyfishes (family Chaetodontidae) in four phylogenetic clades. Similar to other fishes, the aggressive (often territorial) species in most cases had larger AVT-ir cells within the gigantocellular preoptic cell group. Linear discriminant function analyses demonstrated that the density of AVT-ir varicosities within homologous telencephalic nuclei to those important for social behavior in mammals and birds were predictive of aggressive behavior, social affiliations, and mating system. Of note, the density of AVT-ir varicosities within the ventral nucleus of the ventral telencephalon, thought to be homologous to the septum of other vertebrates, was the strongest predictor of aggressive behavior, social affiliation, and mating system. These results are consistent with the postulate that AVT within the telencephalon of fishes plays an important role in social behavior and may function in a similar manner to that of AVT / AVP in birds and mammals despite having cell populations solely within the preoptic area.

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Arginine vasopressin (AVP) and its non-mammalian homolog arginine vasotocin (AVT) are neuropeptides that modulate vertebrate social behavior (Goodson and Bass, 2001). The relationship between the organization of the AVP system and social behavior in microtine rodents provided functional information for this neuropeptide and a foundation for research on affiliative behavior and social disorders (Hammock and Young, 2006). In non-mammalian AVT systems, comparisons of closely

related species are limited to birds (e.g. Goodson et al., 2006) and virtually unstudied in the highly speciose and behaviorally diverse fishes (Dewan et al., 2008; Lema and Nevitt, 2004a). Thus, comparative studies in closely related species are needed to test whether the neuroanatomical organization and density of the AVT system are correlated and potentially influence fish social behavior. This is also necessary in order to ultimately determine whether these relationships in fishes are similar to those in other vertebrates.

The neural organization and function of the mammalian AVP system are well studied and provide a basis for predictions of AVT function in other vertebrates. Comparative studies in mammals show correlations with the density of AVP production, release sites or receptor properties and different social behaviors. Although sometimes based on relatively few species, these studies indicate that the density of AVP features within the bed nucleus of the stria terminalis or lateral septum were related to parental behavior (Bamshad et al., 1994; Bester-Meredith and Marler, 2003), aggression (Bester-Meredith et al., 1999), affiliation (Ho et al., 2010), and mating system (Insel et al., 1991). Additional studies provided for support for these hypotheses with either injection manipulations (parental behavior: Parker and Lee, 2001; Wang et al., 1994; and aggression, Ferris, 2005), or measures of AVP production (parental behavior: Wang et al., 2000 and aggression: Veenema et al.,

Abbreviations: BA, basal amygdala; BNST, bed nucleus of stria terminalis; Dc2, central part of the dorsal telencephalon, subdivision 2; Dd, dorsal part of the dorsal telencephalon; Dld, dorsal division of lateral part of the dorsal telencephalon; Div, ventral division of the lateral part of the dorsal telencephalon; Dm1, medial part of the dorsal telencephalon, subdivision 1; Dm2, medial part of the dorsal telencephalon, subdivision 2; Dp, posterior part of the dorsal telencephalon; gPOA, gigantocellular group of preoptic area; mPOA, magnocellular group of preoptic area; pPOA, parvocellular group of preoptic area; Vc, central nucleus of the ventral telencephalon; Vd, dorsal nucleus of the ventral telencephalon; Vi, intermediate nucleus of the ventral telencephalon; Vl, lateral nucleus of the ventral telencephalon; Vp, postcommissural nucleus of the ventral telencephalon; Vs, supracommissural nucleus of the ventral telencephalon; Vu, cuneate nucleus of the ventral telencephalon; Vv, ventral nucleus of the ventral telencephalon.

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Table 1

Proposed homologies for teleost brain regions.

Butterflyfish brain region	Presumed mammalian homolog
Dc	Dorsal pallium ⁶ (Neocortex)
Dd	Dorsal pallium ¹ (Neocortex)
Did	Dorsal pallium ^{1,6} (Neocortex)
	Hippocampus ² (Archicortex)
	Medial pallium ⁴ (Archicortex)
Dlv	Medial pallium ^{1,3,4,6} (Archicortex)
	Hippocampus ² (Archicortex)
Dm	Dorsal pallium ⁶ (Neocortex)
	Pallial amygdala ^{1,2,3,4} (Paleocortex)
Dp	Lateral pallium ³ (Paleocortex)
Vc	Striatum ^{4,5}
Vd	Striatum ^{4,5,7,8}
Vi	Unknown
VI	Septum ^{4,5,7}
	Olfactory tubercle ⁷
Vp	Basal amygdala ⁷
Vs	Basal amygdala ⁷ , bed nucleus of stria terminalis ⁷
Vu	Unknown
Vv	Septum ^{4,5} , lateral septum ⁷

1—Rodríguez et al., 2002; 2—Portavella et al., 2002; 3—Wullimann and Rink, 2002; 4—Northcutt, 2006; 5—Wullimann and Mueller, 2004; 6—Yamamoto et al., 2007; 7—Northcutt, 1995; 8—Braford, 1995.

2010). Alternatively, larger data sets with multiple species can also provide further information regarding these hypotheses (Turner et al., 2010). Thus if function is conserved, non-mammalian vertebrate social behavior should also covary with AVT features in the lateral septum and bed nucleus of the stria terminalis. In fact, intraseptal injections of AVT modulate aggressive behavior in birds (Goodson, 1998) while a comparison of five finch species yielded a relationship between the density of V1a binding sites in the septum and social group sizes (Goodson et al., 2006). In addition, AVT neurons within the bed nucleus of the stria terminalis of multiple species of finches increased their Fos expression upon exposure to a positive social stimuli (Goodson et al., 2009a). While AVT within the lateral septum and bed nucleus of the stria terminalis of birds may have some conserved function, no study to date has attempted to address whether AVT within homologous regions such as the ventral, supra commissural or lateral nuclei of the ventral telencephalon (Table 1) of fishes may also function in aggression, sociality or other relevant social behavior.

Butterflyfishes (family Chaetodontidae) are a good system to examine these relationships among wild populations. Species within this family exhibit diverse social behaviors (Hourigan, 1989) that can be mapped on a robust morphological and molecular phylogeny (Fessler and Westneat, 2007; Smith et al. 2003). In addition, descriptions of the aggressive behaviors, social affiliations, and mating systems, as well as the timing of their protracted spawning season, are well characterized and temporally stable (Hourigan, 1989; Ludwig, 1984; Ralston, 1981; Tricas and Hiramoto, 1989; Walsh 1987). The AVT system of butterflyfishes (and perciform fishes in general) consists of three main cells groups within the preoptic area (gigantocellular (gPOA), magnocellular (mPOA), or parvocellular (pPOA) preoptic groups) and one small cell

group within the ventral hypothalamus (Dewan et al., 2008). The innervation pattern of each of these four cell groups has not been analyzed in butterflyfishes and is unclear in fishes in general; however, intracellular label of single mPOA AVT cells determined that this cell group projects towards the telencephalon, thalamus, and pituitary (Saito et al., 2004). While AVT-ir cells within gPOA and some within mPOA appear to project to the thalamus, periventricular prefrontal nuclei, and optic tectum (Holmqvist and Ekström, 1995). In addition, rostral AVT cells presumably from the gPOA cell group have extensive connections with the telencephalon (Holmqvist and Ekström, 1995). The pPOA AVT cell group of butterflyfishes has only a single projection that appears to join the preoptico-hypophyseal tract towards the pituitary but this has not been analyzed in detail (Dewan et al., 2008). The gPOA and mPOA of fishes are thought to be homologous to the supraoptic nucleus while the pPOA is thought to be homologous to the paraventricular nucleus of mammals (Moore and Lowry, 1998). Recent work shows distinct differences in the size of the AVT-ir gPOA and mPOA groups and qualitative differences in telencephalic AVT-ir fiber projections among the paired, aggressive, monogamous multiband butterflyfish (*Chaetodon multicinctus*), and a non-aggressive, shoaling, polygamous milletseed butterflyfish (*Chaetodon miliaris*) (Dewan et al., 2008). While there is a clear association with AVT and social behavior in these two closely related species, further work is needed to test the broader prediction that this correlation applies to a range of species. In addition, the site-specific role of AVT in the fish telencephalon remains untested as well as the potential for functional similarities with the AVP system of mammals.

This study investigates the AVT system in reproductive males of seven Hawaiian butterflyfishes (Table 2): three monogamous paired aggressive species; multiband butterflyfish (*Chaetodon multicinctus*), oval butterflyfish (*Chaetodon lunulatus*), threadfin butterflyfish (*Chaetodon auriga*) in different clades, two polygamous shoaling non-aggressive species; milletseed butterflyfish (*Chaetodon miliaris*) and pennant butterflyfish (*Hemiochus diphreutes*) in different clades, one aggressive harem species; forceps fish (*Forcipiger flavissimus*), and one monogamous species; teardrop butterflyfish (*Chaetodon unimaculatus*) that occurs as solitary individuals, pairs or large groups and whose extent of aggression is not yet reported (Fessler and Westneat, 2007; Hourigan, 1989; Roberts and Ormond, 1992). Females were not used in this study for several reasons. First, species differences in social behavior are likely more robust in males, as monogamous males are more aggressive than females and defend territories that contain mates rather than food resources (Hourigan 1989; Tricas, 1989). Second, females of at least two of the species analyzed in the current study exhibit vast differences in gonad condition during the spawning season (Ralston, 1981; Tricas and Hiramoto, 1989) whereas all males used for this study had mature sperm and enlarged testes. Third, AVT research in male butterflyfishes provides a better comparison to mammalian AVP research, most frequently performed in male rodents. The results show strong correlative evidence for the involvement of AVT in the regulation of fish social behavior and preliminary evidence for a functional role potentially similar to that of AVT in birds and AVP in mammals.

Table 2

Taxonomic and behavioral comparisons of seven species of butterflyfish.

Species	BW (g)	Clade	Aggressive	Social grouping	Mating system
Pennant butterflyfish (<i>Hemiochus diphreutes</i>)	41.8 ± 28.6	B	Non-aggressive ²	Shoal ¹	Polygamous ⁵
Forcepsfish (<i>Forcipiger flavissimus</i>)	54.5 ± 19.1	B	Aggressive ³	Trio ³	Harem ³
Pebbled butterflyfish (<i>Chaetodon multicinctus</i>)	25.2 ± 3.7	C2	Aggressive ²	Pair ¹	Monogamous ¹
Milletseed butterflyfish (<i>Chaetodon miliaris</i>)	56.6 ± 10.9	C2	Non-aggressive ²	Shoal ¹	Polygamous ¹
Teardrop butterflyfish (<i>Chaetodon unimaculatus</i>)	67.3 ± 14.2	C2	Unknown	Mixed ¹	Monogamous ⁶
Oval butterflyfish (<i>Chaetodon lunulatus</i>)	54.3 ± 10.6	C3*	Aggressive ⁴	Pair ⁴	Monogamous ⁴
Threadfin butterflyfish (<i>Chaetodon auriga</i>)	69.7 ± 6.8	C4	Aggressive ²	Pair ¹	Monogamous ⁵

Phylogenetic clades are from Fessler and Westneat, 2007. * *C. lunulatus* was not analyzed in Fessler and Westneat but *C. trafascilis*, a closely related species was placed within this clade. 1—Hourigan, 1989; 2—Roberts and Ormond, 1992; 3—Boyle and Tricas in prep; 4—Yabuta, 1999; 5—Whiteman and Cote, 2004; 6—Sancho et al., 2000;

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