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Review

The endocrinology of 1α-hydroxycorticosterone in elasmobranch fish: A review ☆

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ABSTRACT

The endocrine underpinnings of the stress response in fish have been the subject of intense research for well over 50 years. Much of the research has focussed on teleost fish and so the endocrine mechanisms for cortisol production, transport and action at the target site have received significant attention. However, corticosteroidogenesis in elasmobranchs is exceptional on a number of levels. Unlike teleost fish the interrenal tissue is anatomically distinct from both renal and chromaffin (catecholamine producing) tissue; further the final product, 1α-hydroxycorticosterone (1α-OH-B), is unique to chondrichthyans where the carbon atom at position 1 of corticosterone has a hydroxyl group attached in the α orientation. The homologous nature of interrenal tissue in elasmobranchs presents an obvious advantage in the study of corticosteroidogenesis, however, the unique chemical nature of 1α-OH-B has presented distinct disadvantages as it has proven to be difficult to synthesise, and therefore studies examining the mineralocorticoid and glucocorticoid actions of this steroid are limited. Over the last decade molecular techniques have provided significant insight in the involvement of corticosteroiogenic enzymes in the elasmobranch interrenal in addition to the evolution of corticosteroid receptors. Given the number of excellent reviews focussing on the role of cortisol in the stress response of teleost fish, this short review aims to synthesise the endocrine basis for the synthesis, release, and action, of the enigmatic 1α-OH-B in elasmobranch fish.

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1. Identification and measurement of 1α-hydroxycorticosterone

In the late 1950s and early 1960s corticosteroids were first isolated and identified in both teleost and elasmobranch fish (Chester-Jones et al., 1959; Chester-Jones et al., 1968). Early reports indicated that corticosterone and cortisol were measurable in the plasma of elasmobranchs and indeed were the dominant secretions from tissue analogous to mammalian adrenocortical tissue (Phillips and Chester-Jones, 1957; Phillips, 1959). However, in 1966 Idler and Truscott, in a landmark paper, isolated a novel corticosteroid 1α, 11β, 21-trihydroxypregn-4-ene-3, 20-dione from the plasma of two species of ray (Idler and Truscott, 1966). This was later to be confirmed as 1α -hydroxycorticosterone (1α-OH-B) and was found to be the dominant corticosteroid produced by the interrenal tissue in an additional 6 species of ray, 2 dogfish and 5 sharks (Idler and Truscott, 1967; Truscott and Idler, 1968; Truscott and Idler, 1972) (Table 1). It was postulated that the earlier reports of high concentrations of cortisol and corticosterone were due to the unknown 1α-OH-B interfering with the fluorimetric technique used to measure steroid concentration (Truscott and Idler, 1972).

Increased sensitivity for the measurement of 1α-OH-B was provided using the double isotope derivative method which further validated the presence of this unique steroid in elasmobranchs (Truscott and Idler, 1972). In the same year biochemical synthesis of 1α-OH-B (Kime, 1972) led to the development of a radioimmunoassay (RIA) for the

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Table 1
Measured concentrations of corticosteroids in the body fluid of elasmobranch fishes. Concentrations are in μg/100 mL. Data are presented as a mean ± sem where possible. Table adapted from (Chester-Jones et al., 1968).

Species	Sex	Source	F	1α-OH-B	B	Method of measurement	Reference
Carcharhinus plumbeus (sandbar shark)	♀	Plasma	2.6		5.9	TLC + fluorescence	(Phillips, 1959)
Carcharhinus leucas (bull shark)	♀	Plasma	2.9		1.7		(Phillips, 1959)
	♂	Plasma	0.9		1.8		
Carcharhinus obscurus (dusky shark)	♀	Plasma	3.3		2.7		(Phillips, 1959)
Carcharhinus brevipinna (spinner shark)	♂	plasma	2.9		0.8		(Phillips, 1959)
Galeocerdo cuvier (tiger shark)	♀	plasma	1.6		5.2		(Phillips, 1959)
Dasyatis Americana(American southern ray)	♀	plasma	4.3		4.0		(Phillips, 1959)
Raja eglanteria(clear nose skate)	♀	plasma	5.3				(Phillips, 1959)
Aetobatus narinari (spotted eagle ray)	♂	plasma	6.8		20.4	TLC + fluorescence	(Chester-Jones et al., 1959)
Raja clavata (thornback ray)	mixed	plasma			8.0	TLC + fluorescence	(Phillips and Chester-Jones, 1957)
Scyliorhinus canicula (European dogfish)	mixed	Whole blood	2.5				(Phillips and Chester-Jones, 1957)
Amblyraja radiata (Thorny skate)	mixed	plasma		0.5–2.0		TLC + acid fluorescence	(Idler and Truscott, 1967)
Raja ocellata (winter skate)	mixed	Plasma		0.5–2.0			
Amblyraja radiata	mixed	Plasma		0.8 ± 0.4		TLC + acid fluorescence	(Idler and Truscott, 1968)
		Perivisceral		17 ± 6.6			
		Pericardial		8 ± 1.2			
		Cranial		0.8 ± 0.4			
Raja clavata	Mixed	Plasma		4.7 ± 0.7		TLC + acid fluorescence	(Idler and Truscott, 1969)
Amblyraja radiata	Mixed	Plasma		3.8 ± 3.7		RIA	(Kime, 1977)
Scyliorhinus canicula	Mixed	Plasma		0.36 ± 0.1		RIA	
Amblyraja radiata	Mixed	Plasma		0.6 ± 0.08	0.021	DIDA	(Truscott and Idler, 1972)
Raja ocellata	Mixed	Plasma		0.43 ± 0.1	0.18		
Raja laevis	Mixed	Plasma		0.9 ± 0.02	0.16		
Torpedo marmorata (marbled electric ray)	♀	Plasma		0.082			
Squalus acanthias (spiny dogfish)	Mixed	Plasma		2.3 ± 0.5	1.5 ± 1		
Prionace glauca (blue shark)	Mixed	Plasma		0.87 ± 0.05	0.3		
Isurus oxyrinchus (shortfin mako)	Mixed	Plasma		5.3	0.052		
Scyliorhinus canicula (European dogfish)	♀	Plasma		3.97 ± 0.28		RIA	(Hazon and Henderson, 1984)
Scyliorhinus canicula (European dogfish)	Mixed	Plasma		~3.6		RIA	(Hazon and Henderson, 1985)
Scyliorhinus canicula (European dogfish)	Mixed	Plasma		~2		RIA	(Armour et al., 1993a)
Dasyatis sabina (Atlantic stingray)	♂				0.04 ± 0.008	RIA	(Snelson et al., 1997)
	♀				0.01 ± 0.001		
Hemiscyllium ocellatum (epaulette shark)	Mixed	Faeces			1.2–20.9[a]	HPLC	(Karsten and Turner, 2003)
Triaenodon obesus (whitetip reef shark)	♂	Plasma			0.03 ± 0.003	RIA	(Rasmussen and Crow, 1993)
	♀	Plasma			0.01 ± 0.002	RIA	
Negaprion brevirostris (lemon shark)	♀	Plasma			~0.04	RIA	(Rasmussen and Gruber, 1993)
	♂	Plasma			~0.1	RIA	
Sphyrna tiburo (bonnethead shark)	♂				~0.245	RIA	(Manire et al., 2007)
	♀				~0.05	RIA	

~ – value estimated from graphical representation of the data; RIA – radioimmunoassay; TLC – thin layer chromatography; HPLC – high performance liquid chromatography; DIDA – double isotope derivative assay. F – cortisol; 1α-OH-B – 1α-hydroxycorticosterone; B – corticosterone; cortisol and corticosterone are frequently referred to as Kendall's F and B compounds respectively following the original designation by E.C. Kendall (1949).
[a] Units ng/g of faecal mass.

measurement of the steroid from significantly smaller volumes of plasma (Kime, 1977). This assay relied on the conversion of 1α-OH-B to 1-dehydrocorticosterone and subsequent measurement of the derivative. However, a limited amount of 1α-OH-B was synthesised and despite repeated attempts to synthesise and purify the steroid commercially, available supplies were exhausted in the early 1990s.

Despite the lack of available homologous steroid, RIA's developed for the measurement of corticosterone have been used to measure circulating levels of corticosteroids in elasmobranch plasma (Honn and Chavin, 1978; Rasmussen and Crow, 1993; Rasmussen and Gruber, 1993; Snelson et al., 1997; Manire et al., 2007). However, as with the original attempts to isolate the steroid, the presence of 1α-OH-B significantly interfered with these assays and the resultant measurements of corticosteroids were far from accurate. Nonetheless, an indication on circulating levels in a variety of species has been provided (see Table 1). Where both corticosterone and 1α-OH-B have been measured 1α-OH-B is consistently higher, demonstrating the dominance of this steroid in the plasma of elasmobranch fish. Interestingly in those studies that employed the heterologous corticosterone RIA, males consistently have a higher circulating concentration of measured corticosteroids than females, regardless of species, which may indicate sexual dimorphism in the stress response in elasmobranchs, however, such a conclusion is speculative at this stage given the diversity of sampling procedures and the heterologous nature of measurement. Recent reports indicate that synthetic 1α-OH-B is now again available and was used in steroid receptor studies to examine the evolution of the corticosteroid receptor system (Carroll et al., 2008). The same synthetic 1α-OH-B was used to develop and validate an enzyme linked immunosorbent assay (ELISA) for the measurement of this unique corticosteroid in the Atlantic stingray, *Dasyatis sabina* (Evans et al., 2010).

With the development of this assay it is hoped that future studies will be able to accurately link the effects of stress on free swimming and captive elasmobranchs and the role of 1α-OH-B in regulating the stress response. It is important to note, however, that measurement of the final product from the interrenal tissue is not the only route by which one can examine at least the stimulation of corticosteroidogenesis in elasmobranch interrenal tissue. This complex biosynthetic pathway, simplified in Fig. 1, requires a number of key enzymes for the production of intermediates from the precursor, cholesterol, and the final synthesis of 1α-OH-B. Before we examine what is known about the stimulation of corticosteroidogensis in elasmobranch fish we will briefly discuss the steroidogenic pathway.

2. Steroidogenesis of 1α-hydroxycorticosterone

Cholesterol, synthesised from acetate as a result of fatty acid oxidation or glycolysis, acts as the precursor for the synthesis of steroids in vertebrate steroidogenic cells (Sandor et al., 1976; Norris, 2007). One key step in the conversion of cholesterol to intermediates is the

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