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A review of tonic immobility as an adaptive behavior in sharks

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Abstract Tonic immobility remains one of the least understood behaviors in nature. Despite this, the behavior has been described in a diversity of species across the animal kingdom. Tonic immobility has been observed in sharks and rays both in the laboratory and field. However, actual scientific studies of tonic immobility have been completed on only a few species of elasmobranchs. The behavior is frequently induced by handling an animal in a certain way rather than utilizing chemical anesthesia in order to assess body condition and implant electronic tracking devices. This behavior functions as (1) an innate defensive passive response against a predatory attack, (2) a component of courtship and copulation, and (3) a protective mechanism limiting the effect of overwhelming sensory stimulation. We present a review of the behavioral, physiological, and neurological processes that result in tonic immobility in sharks, and compare this information to the processes of tonic immobility that are better understood in mammals.

Keywords Sharks · Behavior · Analgesia · Midbrain · Periaqueductal gray

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Introduction

There are many names for tonic immobility in animals such as the immobility reflex, freezing, death feint, thanatosis, opossum play, animal hypnosis, paralysis-like fear response, behavioral arrest, tonic immobility, and limp response. We choose the term, tonic immobility (TI), when referring to this behavior because this term is widely accepted in the fields of behavioral biology and neuroscience. This is an innate reflex. It has been described in all classes of invertebrates and vertebrates, minus the Agnatha (Whitman 1984; Henningsen 1994). Artificially elicited TI has been reported for the Osteichthyes and Chondrichthyes fishes (Whitman et al. 1986; Henningsen 1994; Brooks et al. 2011; Kessel and Hussey 2015; Yoshida

2021). It is a reversible behavioral state, which can be elicited by a wide range of external actions. The main way of eliciting TI is by physical restraint of the animal and placing it generally in an inverted body position (Monassi et al. 1999; Miranda et al. 2006, 2014, 2016; Kozlowska et al. 2015). The behavior can be induced by a diversity of stimuli but external pressure combined with physical restraint are the most common and effective stimuli (Jones 1986; Wells et al. 2005; Miranda et al. 2006, 2016). The response is exhibited by prey when caught or transported by a predator (Monassi et al. 1999; Miranda et al. 2006).

Tonic immobility is slightly different for each species, yet it is common across many taxa (Gallup 1974; Klemm 2001; Miranda et al. 2014). Reactive immobility is characterized by one feature, a neurally activated cessation of voluntary movements except rhythmic breathing (Watsky and Gruber 1990; Miranda et al. 2014) and vision (Reese et al. 1984). Because tonic immobility is commonly observed in a variety of contexts, it has generated considerable historical interest among notable scientists such as Darwin and Pavlov. They have discussed its possible significance (Ratner 1967; Gallup 1977; Reese et al. 1984; Kozlowska et al. 2015; Humphreys and Ruxton 2018).

Tonic immobility may be even more common than currently reported. At times, this behavior is simply overlooked (Humphreys and Ruxton 2018). The temporary cessation of body movement has generally been thought to be a defensive strategy (Carli et al. 1976; Gallup and Maser 1977; Monassi et al. 1999; Moskowitz 2004; Ramos et al. 2008; Miranda et al. 2014, 2016). It has been explained as being a defensive response to predation (Wilson 2004; Humphreys and Ruxton 2018). This is because immobility increases the chance of survival prior to or even after being attacked by a predator (Miyatake et al. 2009; Humphreys and Ruxton 2018). The manner in which an organism contorts its body during TI might also have a secondary benefit (Wilson 2004). For example, the more diminutive and compact posture during TI may make it a less attractive food parcel (Wilson 2004). Furthermore, it may reduce the likelihood of being seized because predators are attracted to and strike moving objects while losing interest in immobile objects (Wilson 2004).

One of the most useful physiological benefits of the tonic immobility is analgesia, or the decreased sensation of pain. This may reduce the likelihood that a predator will continue to further attack potential prey acting in this way (Wilson 2004; Miranda et al. 2006). The inhibition of pain enables the subject to use this behavior in its defense. Some originators of somatic-pain models involving mechanically, electrically, or thermally noxious stimuli argue that the perception of pain is reduced during TI (Dannemann et al. 1988; Fleischmann and Urca 1993; Morgan et al. 1998; Leite-Panissi et al. 2001; Miranda et al. 2014, 2016). Tonic immobility may also reduce visceral pain (Miranda et al. 2006) as well as prolonged noxious stimulation (Carli et al. 1976), which could be adaptive for a shark during a predatory attack or in response to the biting behavior of male sharks during with mating.

Tonic immobility in elasmobranchs

Tonic immobility has been reported for multiple species of elasmobranchs (Table 1). Little is known of the physiology behind the behavioral responses of this behavior in sharks and rays (Williamson et al. 2018; De Swaef et al. 2020). However, it has been observed in shark species during courtship (Klimley 1980; Carrier and Pratt 2004; Williamson et al. 2018; De Swaef et al. 2020). Likely, it is easier for a male to insert his clasper and eject spermatozoa into the female uterus if she remains immobile (Klimley 1980; Carrier and Pratt 2004).

Investigators have also artificially induced tonic immobility in large sharks in order to examine their health, make measurements of their length and body parts, and attach electronic tags (Watsky and Gruber 1990; Henningsen 1994; Holland et al. 1999; Bonfil et al. 2005; Wells et al. 2005; Hoyos-Padilla et al. 2016; Clayton and Seeley 2019). If a shark or a ray is captured, restrained on a surface, and turned over on its dorsum—this appears to sedate the animal (Henningsen 1994; Brooks et al. 2011). The time required to gain immobility and its duration are dependent upon the individual and species (Henningsen 1994; Brooks et al. 2011). There is great inter-individual variability in the nature of this behavior (Whitman et al. 1986; Watsky and Gruber 1990). As such, it is only possible to use this technique to sedate some species of sharks (Watsky and Gruber 1990). Tonic immobility may last from < 1 min to multiple hours (Gallup 1974; Watsky and Gruber 1990; Henningsen 1994; Klemm 2001).

Table 1 Species, for which tonic immobility, has been described in the scientific literature. Note the diversity in orders with sharks displaying this behavior, indicating the possibility that it occurs in all of the Chondrichthyes

Order	Species and genus	Common name	References
Hexanchiformes	*Notorynchus cepedianus*	Broadnose sevengill shark	Henningsen 1994
Squaliformes	*Squalus acanthias*	Spiny dogfish	Lissman 1946
	Mustelus canis	Smooth dogfish	Whitman et al. 1986
	Scyliorhinus canicula	Lesser-spotted dogfish	Kreidl 1916; Mangold 1920
Rhinopristiformes	*Rhinobatos productus*	Shovelnose guitarfish	Henningsen 1994
Orectolobiformes	*Stegostoma fasciatum*	Zebra shark	Brunnschweiler and Pratt 2008; Williamson et al. 2018
	Hemiscyllium halmahera	Halmahera walking shark	Mukharror et al. 2019
Lamniformes	*Carcharodon carcharias*	White shark	Pyle et al. 1999; De Swaef et al. 2020
Carcharhiniformes	*Cephaloscyllium ventriosum*	Swellshark	Henningsen 1994
	Triakis semifasciata	Leopard shark	Henningsen 1994
	Galeocerdo cuvier	Tiger shark	Holland et al. 1999
	Negaprion brevirostris	Lemon shark	Gruber and Keyes 1981; Watsky and Gruber 1990; Brooks et al. 2011
	Carcharhinus melanopterus	Blacktip reef shark	Davie et al. 1993; Henningsen 1994
	Carcharhinus perezi	Caribbean reef shark	Henningsen 1994
	Carcharhinus plumbeus	Sandbar shark	Whitman 1984
	Triaenodon obesus	Whitetip reef shark	Henningsen 1994
Rajiformes	*Raja eglanteria*	Clearnose skate	Henningsen 1994
	Raja clavata	Thornback skate	Schaefer 1921
Myliobatiformes	*Rhinoptera bonasus*	Atlantic cownose ray	Henningsen 1994
	Urolophus halleri	California round ray	Henningsen 1994
	Urolophus jamaicensis	Yellow stingray	Henningsen 1994

Tonic immobility has been elicited most often by manipulating the shark into a horizontally inverted position with its ventral surface facing upward (Whitman et al. 1986; Henningsen 1994). This causes stiff muscle hypertonicity in terrestrial vertebrates but relaxed muscle tone and a "limp" posture in fishes (Whitman et al. 1986; Wells et al. 2005; Brooks et al. 2011; Yoshida 2021). This is likely due to the downward force of gravity in air and upward force due to the animal's buoyancy in an aqueous environment. However, there are additional ways of eliciting TI other than rotating a shark on to its back. It can be quickly induced in the zebra shark (*Stegostoma fasciatum*) as well as other shark species by grasping the caudal fin tightly with the hands (Williamson et al. 2018).

Besides inverting the body position or applying body pressure to the caudal fin of the shark, overstimulating the ampullae of Lorenzini, with which a shark detects faint electrical or magnetic stimuli, can also induce this behavior. Located in the region of the snout and around the eyes, these organs can detect minute electric fields. Sharks are responsive to alternating current with frequencies below 8 Hz of only a few microvolts in amplitude (Bres 1993). Rubbing or even touching the shark's snout may innervate the sensors on the snout of the shark and immediately trigger an episode of tonic immobility. In the white (*Carcharodon carcharias*) sharks, touching, rubbing, or stroking the area of shark's snout has been observed to induce an episode of tonic immobility (see https://www.dailymail.co.uk/news/article-3762170/Diver-grabs-great-white-shark-nose-sedate-near-Augusta-south-Perth.html). This form of immobility resembles "freezing," e.g., the immobility of a deer when illuminated with a car headlights or in rats by applying an electric shock to their feet (Klemm 2001; Kozlowska et al. 2015).

Tonic immobility may be also elicited by applying a powerful flow of water through the branchial chambers of fish (Wells et al. 2005; Brooks et al. 2011; De Swaef et al 2020). This response has been observed in 22 species of bony and cartilaginous fishes, which occupy diverse habitats. This behavior consists of caudal muscle hypotonicity and limp posture. The shark may remain immobile for multiple hours and the activity of the subject may be revived upon the cessation of flow (Wells et al. 2005). Henningsen (1994) has recorded (1) the number of attempts required to induce immobility, (2) the necessary time that the subject must be restrained prior to immobility, (3) the percentage of individuals exhibiting TI after stimulating them for a period of time, and (4) the amount of time that each episode lasts.

Brain structure responsible for tonic immobility

The brain mass to body mass ratio (often termed the index of cephalization) of the elasmobranchs is similar to that in birds and mammals (Northcutt 1977; Bres 1993). Hence, sharks are likely exhibit complex behaviors analogous to those already identified in other large-brained vertebrates (Bres 1993). Many examples of complex behaviors such as dominance hierarchies have been observed in two shark species, the bonnethead (*Sphyrna tiburo*) and scalloped hammerhead (*Sphyrna lewini*) sharks (Myrberg and Gruber 1974; Klimley 1985).

Quantitative information on the organization and relative development of the major brain areas in Chondrichthyes is confined to a few benchmark studies (Northcutt 1977, 1978; Yopak et al. 2007). This class is divided into two subclasses, the Elasmobranchii, which is comprised of the sharks and rays, and the Holocephali, which includes the chimeras (Northcutt 1977, 1978; Compagno 1999; Yopak et al. 2007). More is known about the brain organization of teleost fishes, birds, and in particular mammals than the Chondrichthyes (Yopak et al. 2007). It is likely that the elasmobranch brain has evolved structures homologous with these other groups of vertebrates (Northcutt 1977). For example, the main midbrain structures—the periaqueductal gray (PAG) area of the brain is present in a diversity of taxa in the animal kingdom (Kittelberger et al. 2006; Vázquez et al. 2022).

Oceanic shark species from different orders generally have an enlarged midbrain that comprises on average 17% of the whole brain (Yopak et al. 2007). This is the region of the brain where the information from multiple senses is integrated, and from where instructions are sent out along motor neurons to the muscles to control the shark's movements (Tricas et al. 1997; Hofmann 1999; Yopak et al. 2007, 2019). The tectum region of the midbrain is where electrosensory and mechanosensory inputs are processed and lead to motor responses. It likely plays an important role in controlling the behavioral responses to a novel or threatening stimuli (Bodznick 1991; Bres 1993).

The periaqueductal gray region (PAG) is likely present in the brains of all vertebrate species (Kittelberger et al. 2006; Kingsbury et al. 2011). Different parts of the PAG modulate different behavioral and physiological functions, including defense and sexual responses (Bandler et al. 1991; Bandler and Shipley 1994; Bandler and Keay 1996; Kingsbury et al. 2011; Vázquez et al. 2017). In mammals, numerous studies indicate the involvement of the PAG in producing tonic immobility (Bandler et al. 1991; Morgan et al. 1998; Morgan and Clayton 2005; Miranda et al. 2016). The only neural structure, which upon direct activation elicits tonic immobility combined with analgesia, is the ventrolateral region of the PAG (Reynolds 1969; Morgan et al. 1998; Miranda et al. 2016). In general, birds have been shown to possess a midbrain anatomically different but physiologically similar to that of the mammals (Kingsbury et al. 2011).

The mesencephalon of the sharks is the most likely cerebral region, from which tonic immobility is controlled. Kittelberger and coworkers (2006) have found evidence that the PAG region in the brain of the teleost midshipman fish (*Porichthys notatus*) plays an essential role in vocalization. It is similar in both its functional and structural organization to the PAG of mammals, which emit vocalizations (Kittelberger et al. 2006). It is possible that a midbrain structure similar to the PAG may be present in their brains of many shark species, and that it produces physiological responses such as analgesia and immobility. Yet it is premature to propose that the PAG unequivocally produces tonic immobility without more studies of comparative neuroanatomy of the sharks.

Tonic immobility might elicit analgesia in sharks

There is no current information that pain is alleviated during tonic immobility in sharks (Williamson et al.

2018). Tiger sharks (*Galeocerdo cuvier*) restrained upside-down at the side of the boat became immobile, and this made it easier to remove hooks from the mouth and the attachment or implantation of electronic transmitters on or in the body (Holland et al. 1999; Yoshida 2021). This implies that there may be some degree of analgesia experienced by the sharks. Recovery from this form of tranquilization has been found to release post release stress (Holland et al. 1999; Kessel and Hussey 2015; Yoshida 2021). The tagged individuals swam away vigorously upon release, apparently free from stress (Holland et al. 1999). Kessel and Hussey (2015) prefer to immobilize sharks by moving them upside down rather than immobilizing them with a chemical anesthetic.

Suggestions for future research on tonic immobility in elasmobranchs

There is a need for further interdisciplinary research to understand the behavioral, physiological, and neurological mechanisms underlying tonic immobility (Brooks et al. 2011; Humphreys and Ruxton 2018). Future use of technology outside the laboratory and in the wild would add to this burgeoning field of study (Humphreys and Ruxton 2018). We propose studies that would provide more insight into the cause and neural control of tonic immobility. Firstly, more physiological measurements should be taken of immobile species' blood chemistry, respiratory and heart rates, blood pressure, and neurological activity of the hypothalamus–pituitary–adrenal axis. Some studies have been carried out already (Davie et al. 1993; Brooks et al. 2011; De Swaef et al. 2020; Yoshida 2021) but more are needed on a diversity of species. Thus, information is unavailable from a sufficient number of species to make generalizations about the physiology mechanisms leading to tonic immobility. Secondly, despite some important studies of brain organization (Yopak et al. 2007, 2019), there is still a paucity of neuroanatomical studies on sharks and rays. In particular, studies are lacking on several brain regions, specifically on mesencephalic structures such as the PAG because this appears to be the key neural center producing tonic immobility and analgesia in the elasmobranchs. Such studies have already been completed on species of teleosts (Kittelberger et al. 2006). Thirdly, researchers have yet to map the cyto-architecture of many regions of the shark's brain. These surgical studies could be performed on the brains of deceased sharks that are present in laboratory collections to avoid the sacrifice of living individuals. Fourthly, protocols should be developed using a pharmacological approach to understand in vivo motor control, analgesia, and tonic immobility in sharks. Fifthly, activity in specific regions of the brain, from which different behaviors are controlled, should be identified in sharks using electrophysiological techniques. This last type of study has been performed in vivo in neuroscience laboratories mainly on rodents but could be also be performed on sharks.

Summary

Tonic immobility remains one of the least studied behaviors exhibited by elasmobranchs. The rotation of the body upside down and the forceful handling of the caudal fin produces tonic immobility in sharks and rays. Periaqueductal gray matter, or its mesencephalic equivalent, is likely the brain structure that controls tonic immobility in elasmobranchs as it does in mammals. In summary, evidence indicates that tonic immobility in shark functions in the following ways: (1) it serves as an innate passive response that reduces the likelihood of a predator attack, (2) an adaptive behavioral component of courtship, and (3) a protective mechanism reducing the effect of overwhelming sensory stimulation, mainly from the facial electroreceptive receptors and branchial mechanoreceptors.

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