

Acoustic Communication in Fish Behaviour and Neural Control

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Abstract

It has long been known that some fish can be acoustically active. But the assumption that the vast majority of fish spend their life without emitting sound is still widespread. A recent study has shown that the number of potentially acoustically active fish is much higher than previously assumed. Fish emit sound in a variety of contexts, most notably during agonistic encounters and during reproduction. The acoustic signal is a fundamental element of social communication, sometimes even more important than visual displays. Sounds are produced primarily by vibrations of the swimbladder or by rigid structures rubbing against each other, termed stridulation. The small acoustic repertoire and simplicity of the sounds make acoustic fish excellent model organism. The neural control of acoustic communication has been studied mainly in toadfishes, which emit tonal courtship sounds, largely by a group led by Andrew H. Bass. Toadfish calls are structured in the vocal pattern generating circuit of the hindbrain. Call characteristics, such as duration, appear to be regulated by vocal centres in the mid- and forebrain, as well as by certain neuropeptides.

In this review, I will outline behavioural and seasonal / diurnal aspects of acoustic communication in fish. Furthermore, I will elucidate the pattern generating circuit in the hindbrain and discuss aspects of call modulation controlled by the mid- and forebrain. At the end, I will present some questions that need further research, such as exploring the neural control of stridulation.

Layman Summary

It has long been known that some fish can be acoustically active. But the assumption that the vast majority of fish spend their lives without emitting sounds is still widespread. A recent study has shown that the number of potentially acoustically active fish is much higher than previously assumed. Fish emit sounds in a variety of situations, most notably during hostile encounters and during reproduction. The acoustic signal is a fundamental element of social communication, sometimes even more important than visual displays. Sounds are produced primarily by vibrations of the swimbladder – a gas-filled sac in the fish's abdomen – or by the rubbing of rigid structures against each other. The small acoustic repertoire and simplicity of sounds make acoustic fishes ideal for investigation. The neural control of acoustic communication has been studied mainly in toadfishes, largely by a group led by Andrew H. Bass. Toadfish calls are structured in the vocal pattern generating circuit of the hindbrain. Call characteristics, such as duration, appear to be regulated by vocal centres in the mid- and forebrain, as well as by the certain messenger substances.

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Introduction

Life underwater is often perceived as a place of tranquillity, populated mostly by species incapable of acoustic communication. Yet, fish are acoustically active, primarily by vibrating the swimbladder – the buoyancy organ with which fish regulate their height in the water column – or by rubbing body parts against each other, termed stridulation. The common view of fish as silent might actually be shaped by our own incapability to hear sounds well underwater (Hernandez-Miranda and Birchmeier 2018).

Furthermore, technological limitations made it difficult to research underwater soundscapes. Yet, the knowledge that some fish can produce sound, especially in distress situations is not new (Lobel, Kaatz, and Rice 2010). More so, as they do this also when caught by humans. And although the investigation of fish acoustic communication is technologically difficult, it can provide new insights into the field of animal communication and neural control of vocalisation (Lobel, Kaatz, and Rice 2010). It is partly because of their small acoustic repertoires that they make excellent model species (Maria Clara P. Amorim et al. 2011).

The present paper seeks to review the current state of research of fish acoustic communication. In order to do so, it will give an overview of the behavioural, neural and seasonal / diurnal aspects of this behaviour. Because of the wide variety of sound mechanism evolved in fishes, not all variations will be discussed. There are, however, two main categories of sound production, namely swimbladder sounds and stridulation sounds. The part of this paper on neural control will concentrate on fish that vibrate the swimbladder to produce sound. How stridulation is controlled neuronally, and if perhaps the same mechanisms and nuclei are involved here, is not established. Also, the paper will not be able to give a comprehensive review of all nuclei and mechanisms involved in vocalisation. But it will focus on the central pattern generator in the hindbrain, as this is the mechanism directly structuring natural calls and whose function is the most established. Moreover, this paper will not cover auditory perception in fish. Although this is an important topic, part of acoustic communication, auditory perception is beyond the scope of this paper. Similarly, ontogeny of acoustic communication is out of scope and will not be covered..

Behaviour

Which fish produce sounds

As stated above, fish sounds are sometimes difficult to witness. For diving human observers, many acoustic signals of fish will be superimposed by the sounds emitted by diving gear. Among the loudest fish are also the ones best studied, which are the damselfish, squirrelfish, the drums and toadfish. Only because sounds of a particular fish species cannot be easily detected, it does not necessarily mean that this species is indeed silent. Nonetheless there are fish that do not produce sounds. It is likely that one reason why fish do not make sounds is secondary loss. This

is especially true for species that occur in families where sound production is otherwise common (Lobel, Kaatz, and Rice 2010).

In a recent study Rice et al. tried to determine how many of the 34,000 valid extant ray-finned fish species might be acoustically active. For this, they mapped the volitional sound production of ray-finned fishes. They referred to this comparison as „most comprehensive“. It was done on a family level, i.e. not each single species was analysed, but the comparison focused on the soniferous ability within a family. This approach was supposed to allow for a broad investigation. In total there are 167 families of ray-finned fishes. The results show that 2/3 of all families in the clade ray-finned fishes show soniferous behaviour, which makes more than 20,000 species potentially capable of acoustic communication. This finding stands in stark contrast to the number of 800 – 1000 species of ray-finned fishes for which concrete evidence of soniferous behaviour exists. Yet, not all family members (of the 2/3) must be soniferous. The absence of the acoustic activity may also be due to secondary loss (Rice et al. 2020).

The sound producing mechanisms between fish species are not always the same (Lobel, Kaatz, and Rice 2010). Indeed, acoustic behaviour seems to have independently evolved at least 27 times in ray-finned fishes. In tetrapods acoustic communication has only evolved 6 times independently. Also, some fish even possess the ability to distinguish individuals based on sounds as do bicolor damselfish (F Ladich 1997). Moreover, in ray-finned fishes some species have evolved adaptations to optimise hearing, those hearing specialisation may have evolved 20 times within teleost fish. In fish whose nervous systems have been studied, the neural and hormonal mechanisms are similar to those of tetrapods. All this refers to an undecrypted complexity of the evolution of acoustic communication (Rice et al. 2020; Lobel, Kaatz, and Rice 2010).

General – Information Transmission

An acoustic signal can entail different types of information, transmitted by different aspects of the call. Because signals often show stereotyped features, they provide information about the species of the sender. Sometimes, the sender can be identified individually, as the signal varies slightly between conspecifics. Important for reproduction or combats is the information about condition, individual quality as well as motivation. Motivation may be conveyed by signal repetition or signal intensity. Information about individual quality and condition is included in the concept of honest signalling, a function often attributed to acoustic communication in fish. Moreover, acoustic signals can also inform about territorial ownership (Maria Clara P. Amorim et al. 2011).

General – Structural Characteristics

As a general rule, there seem to be structural differences between agonistic sounds and advertisement or courtship sounds. Aggressive calls have a harsh characteristic, i.e. a broad frequency range. They are also relatively low in frequency, whereas sounds in a nonaggressive

context, such as courtship sounds, are higher in frequency and more tonal, i.e. they show a relatively narrow frequency band. This is true for birds, mammals and fish, although the latter have a smaller repertoire. In fish call duration is another salient differential trait: aggressive calls are often broadband and brief. Calls with longer duration and sometimes with a more tonal characteristic occur in fish during appeasing or friendly behaviour. These two characteristics are shaped – for vocal sounds involving the swimbladder – by the contraction rate of the sonic muscles (Maria Clara P. Amorim et al. 2011).

Production

Teleost fish produce relatively simple sounds and are small in repertoire (Maria Clara P. Amorim et al. 2011). Although acoustic abilities have evolved at least 27 times in ray-finned fishes, according to Rice et al., there are just two main categories of methods applied (Rice et al. 2020).

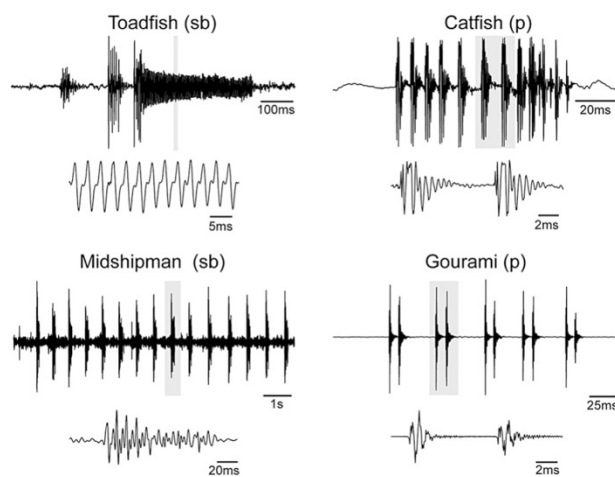


Figure 1: Vocal-acoustic signals in 4 teleost fish. Shown are representative examples of rhythmic sounds generated either with the swimbladder (sb) or pectoral stridulation (p). Signals are shown on two individual timescales. Signals are left to right, top to bottom: boatwhistle of Gulf toadfish, grunt of Raphael catfish, grunt train of the plainfin midshipman and croak of the croaking gourami. Catfish and gourami records were done by F. Ladich; Toadfish and midshipman records were done by Bass et al. (Andrew H. Bass, Chagnaud, and Feng 2015; adapted)

The first method, most reminiscent of the tetrapod vocalisation, is the production of sound with the swimbladder. The swimbladder is a gas-filled sac inside the abdominal cavity of most types of fish, which is used to control buoyancy. Sonic muscles, which are in close proximity or attached to the swimbladder (extrinsically or intrinsically), are rapidly contracted. Notably, sonic muscles are considered the fastest-contracting muscles known in vertebrates. Squirrelfish and midshipman fish show contraction rates of over 100 Hz and toadfish even over 400 Hz. Swimbladder sounds are in the range of low frequencies from 50 to 1,500 Hz (Connaughton, Fine, and Taylor 2002; Kaatz 2002; Fine and Parmentier 2015; Hernandez-Miranda and Birchmeier 2018; Hossain, Mallik, and Hossen 2019). In figure 1, on the left, two signals produced with this method can be appreciated.

The second common method is stridulation. These sounds utilise the friction of skeletal elements, like teeth and finrays. Onomatopoeically these sounds have been described as rasps or creaks. Stridulation sounds are also rapidly produced sounds, but in contrast to swimbladder sounds they show more irregular temporal parameters. Stridulation sounds are wide in frequency with higher frequencies than sounds produced with the swimbladder. For some stridulation sounds it has been suggested that the swimbladder poses as a resonating organ. However, this hypothesis seems to be disputed, because often direct evidence is missing.

Examples of stridulation mechanisms are pectoral fin beating and jaw slams (with colliding teeth; in a non-feeding activity). The best studied fish showing stridulation are catfish (Fig. 1) and damselfish (Kaatz 2002; Fine and Parmentier 2015; Hossain, Mallik, and Hossen 2019). Again, in figure 1, two signals produced by stridulating fish can be observed.

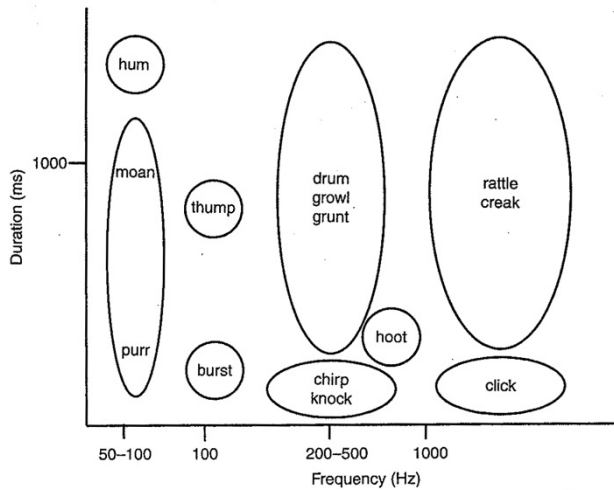


Figure 2: Descriptive terminology for sounds produced by mapped on sound duration and frequency. (Lobel, Kaatz, and Rice 2010)

The sounds fish produce ranges from 100 Hz to 8 kHz, where higher frequencies occur more often in hearing specialists. In reef fishes, similarly to other fishes, basic sound units are commonly between 10 ms and 6 s long. Generally, basic sound units can be repeated in bouts. The terms with which sounds are described in fish are exposed to subjectivity. Lobel et al. mapped the terms on the acoustic characteristics of duration and frequency, shown in figure 2. The figure might help with the appraisal of the calls described in this paper (Lobel, Kaatz, and Rice 2010).

Many fish have only two or more calls, but interestingly most of the time only one sound producing mechanism, with the exception of catfish. Both of those mechanisms – in catfish – are used in distress situations, sometimes even simultaneously. The underlying evolutionary relevance and cause are unknown (F Ladich 1997; Friedrich Ladich 1997).

Behavioural Contexts

Fish depend on sound production in a variety of contexts, most commonly during agonistic behaviour and behaviour associated with reproduction. Both contexts are important events for animals. Thereby, males are often more vocal than females, for example in species in which males hold territories and / or in which males court females. Indeed, females can often only produce agonistic sounds, or emit reproduction sounds at lower amplitude (F Ladich 1997; F Ladich and Myrberg 2006; Lobel, Kaatz, and Rice 2010; Maria Clara P. Amorim et al. 2011).

Agonistic Behaviour

Agonistic sounds are often short and compose a series of low frequency pulses. They are emitted intraspecifically or when fish are disturbed or caught. Often, our knowledge on sound production is restricted to distress calls. (Lobel, Kaatz, and Rice 2010).

Only seldom do fish use acoustic signals in other interspecific contexts, such as in the case of the mormyrid *Gnathonemus petersii* which produces click sounds against *Gymnotus*. Intraspecific aggressive sounds are said to be emitted while attacking and fighting (F Ladich 1997).

If aggressive interactions are short, mainly the aggressor emits sounds; in longer-lasting fights, both opponents are acoustically active. The acoustic behaviour begins with the visual detection of the opponent (Lobel, Kaatz, and Rice 2010).

Signal differences

Differences in signal characteristics may either influence aggressive encounters or end them before they escalate. Acoustic signals can aid the assessment of the opponent's ability and motivation to fight. Interestingly, the acoustical differences explain the outcome of those encounters better than size. Thereby, sound pressure level and repetition seem to be especially important. Pulse repetition could be indicative of the opponent's resource holding power or increasing levels of aggression. That smaller winners – in the context of intraspecific fights – emit more intense sounds, might show that amplitude encodes a motivational component. In general, modifications are often done by altered pulse repetition rate or signal duration. Thereby, it seems as if different agonistic contexts do not evoke different modifications. Ladich, 1997, reports only of two species that use different agonistic sounds: *Amphirion* which emits a loud threatening sound when opponents are far, and a quieter sound while fighting; and *Hoplosternum thoracatum* that emits territorial sounds without being directly threatened and sounds during fighting (F Ladich 1997; F Ladich and Myrberg 2006; M. C.P. Amorim et al. 2006).

Territorial

Agonistic acoustic signals are important for the long-term establishment of territories between neighbouring males. Moreover, aggression can be reduced towards familiar neighbours that are unlikely to intrude. On the other hand, if the acoustic agonistic signal is ignored by the opponent, increased aggression may follow. For example, if after the emission of sounds called 'thumbs' of *Polypterus* smaller fish do not flee, the aggressor attacks the smaller fish with bites (F Ladich 1997; F Ladich and Myrberg 2006; M. C.P. Amorim et al. 2006).

Submissive

Ladich, 1997, reports vocalisation in the context of defence or fleeing to be rare. However, Ladich does list examples of submissive vocalisations. *Polypterus*, for example, emits sounds described as 'moans' while fleeing. *Amphirion xanthurus* and *Amphirion polymnus* produce 'shaking sounds', along with a 'horizontal swimming' behaviour in reaction to attacks. Ladich emphasises that no clear distinction can be made between submissive, appeasement or distress sounds (F Ladich 1997).

Predation

Sounds in the context of predation are thought to function to startle predators. Clear evidence that these sounds have an effect on the predators or warn nearby individuals is lacking.

Nonetheless, fish engage in this specific behaviour. For example, several fish species ‚staccato‘ at predators, like moray eels (F Ladich 1997). Tropical squirrelfish even confront predators with pulsed sound bouts, which has been interpreted as mobbing behaviour, functioning as predator deterrent. On the other hand, some fish become temporarily silent in the face of a predator, like temperate Batrachoidids (toadfishes), which reduce their calling rate while confronted with playbacks of dolphin sounds (Lobel, Kaatz, and Rice 2010).

Duration

Sounds in both these contexts (submission and predation) are short, only up to 500 ms in duration. The interpose intervals are irregular, and thus each single sound can be considered simple single pulse displays (Lobel, Kaatz, and Rice 2010).

Reproduction

Volitional reproduction sounds of fishes can be categorised in two main contexts: sounds during courtship and sounds during spawning. The latter is thought to be important especially for gamete release synchronisation. Acoustic courtship signals are often very quiet, because they are directed at nearby potential mates. In this context, some of the quietest sounds of fishes occur, which are emitted by pearlfishes, gobies and also seahorses. Courtship vocalisations that are relatively well studied are often produced in species that emit loud sounds, such as toadfishes, drums, damselfish and squirrelfish. Sounds in the context of reproduction can be restricted to the breeding season (M. C.P. Amorim et al. 2006; Lobel, Kaatz, and Rice 2010).

Duration

Among sounds associated with reproduction are also the longest sounds. In toadfishes male reproductive basic sound units can last from seconds to minutes, and a call display for up to 1 to 2 hours. Moreover, these sounds have the largest number of pulses, reoccurring with a stable interpulse interval (Lobel, Kaatz, and Rice 2010; Tripp, Feng, and Bass 2021).

Honest Signalling and Female Choice

Fish vocalisation is often regarded as ‚honest signalling‘. The characteristics of a call is determined by different aspects of the fitness of fish (Connaughton, Fine, and Taylor 2002; F Ladich 1997; Lobel, Kaatz, and Rice 2010). For *Pomacentrus partitus* it was shown that female choice was based on the spectral features of male sounds (F Ladich 1997).

In male grass gobies, with territorial and so called ‚sneaker‘ males, both varieties produce courtship sounds. Thereby, the dominant frequency has a strong inverse relationship to the body size of the gobies. Although male size was found to be the most important correlate of sound properties irrespective of male morph, territorial males are often larger than the sneaking males (Malavasi et al. 2003).

A similar trend can be observed in male weakfish. The sound frequency decreases with size, whereas sound pressure level and pulse duration increase. Yet, it is proposed that the pulse duration, which determines the sonic muscle twitch duration, controls the dominant frequency. The dominant frequency is not determined by the resonant frequency of the swimbladder, which itself should be determined by the fish body size. (Connaughton, Fine, and Taylor 2002). Nonetheless, the ability to produce low frequencies sounds at high pulse duration might also be indicative of male quality.

Although friendly mannered sounds are often more tonal than agonistic sounds, pure tone frequencies are most uncommon – at least for reef fish. In the toadfishes, males of 3 species produce long tonal advertisement calls, termed boatwhistles to attract females to their nests. In another species, within ostraciids (cofferfishes), males produce a tonal spawning sound. The production of tonal sounds is physiologically demanding, and the tone is generated by specialised muscles with the fastest rates of contraction (M. C.P. Amorim et al. 2006).

Female Reproduction Rounds

As already been described above, in reproduction contexts often males emit sounds, while females are silent or emit sounds less intensely. Yet this rule does not seem to be an unbroken pattern either. *Chaetodontid* exchange sounds between paired males and females. Another interesting example is *Hypoplectrus unicolor*. This hermaphroditic fish alternates vocalisation corresponding to the current spawning role (Lobel, Kaatz, and Rice 2010).

Integration with Other Signalling Modalities

Sounds are often imbedded in more elaborated behaviour and are used alongside of visual displays. *Polypterus*, for example erects its dorsal fins while producing thumbs as agonistic sounds. Another example are damselfish that emit ‚chirps‘ along with the so-called ‚signal jumps‘, in which they rise up in the water column before they rapidly swim downwards. This behaviour is repeated and serves the purpose of courtship (Lobel, Kaatz, and Rice 2010; F Ladich 1997).

The disentanglement of the role of acoustic and visual components can be difficult. There are three experimental approaches to deal with this problem: playback of sound, muting experiments and correlative investigations. Playback experiments do not use any additional stimuli next to the playback of acoustic signal. It was found that *Holocentrus rufus* hides in caves, if confronted by ‚staccato sounds‘ and investigate the sound source later on. *Myripristis berndti* that in contrast to *H. rufus* is non-territorial, moves towards the sound. Playbacks of ‚low growling sounds‘ in acoustically, but not visually isolated *Cichlasoma centrachus* inhibited aggressive attacks. However, the directionality of those reactions might also be dependent on social status, as shown in male satinfin shiners. In dominant ‚rapid series of knocks‘ increased aggression, whereas it reduced aggression in submissive individuals. Thus, depending on species sounds could function as appeasement or signal the motivation to attack and seem to be salient on their own (F Ladich 1997).

Muting experiments can be difficult to execute, as the sound production organ has to be silenced without causing damage to the rest of the organism. This is more easily done in stridulating fish. Skunk loach that were prohibited of stridulation by fixation of the operculum with steel wire, were unable to chase off intruders, and that although their lateral displays increased. In another experiment pectoral fin tendons of male croaking gourami were cut. The stridulation movement – as it could be part of the visual display – was continually performed by the males. The experiment showed that in contests between similar sized muted and unmated males, unmuted males won more often. Both experiments indicate that visual displays are not sufficient but have to be bolstered by acoustic signals. This interpretation is backed by correlative studies, showing that if *Colis lalia* attacked while emitting sounds it would be more effective than attacking quietly, and similarly that in *Cottus gobo* contest outcome is explained better by vocalisation than by body size (F Ladich 1997).

Contact Calls

Another context in which fish produce sound, but which is not studied in great detail, is shoaling behaviour. Van Oosterom and colleagues investigated Bigeyes, *Pempheris adspersa*, a nocturnal planktivorous fish, that forms loose schools while feeding. Bigeyes actively emit 'pop' calls, which seem to act as contact calls to maintain group cohesion. Thereby, 'pop' calls have a mean peak frequency of 405 ± 12 Hz and a mean duration of 7.9 ± 0.3 ms (Van Oosterom et al. 2016).

In herring context calls are thought to be produced by releasing air from the swimbladder. Herring, which form schools, were observed to scatter at the surface in the evening and reform the schools in the morning at the bottom according to age and size of the fish. In the process of school forming a characteristic sound, described as 'sparrow chirping' can be witnessed, alongside the emergence of air bubbles (Kuznetsov 2009).

Van Oosterom et al. list in their paper on contact calls in Bigeyes several advantages of acoustic cues for group cohesion. It is probable that these benefits can also be extended to other behavioural contexts. Acoustic signals are more advantageous than visual signals where the addressee is beyond sight of the sender. Moreover, visual cues become less suitable with diminishing light. Accordingly, acoustic signals should be of high value to nocturnal species (Van Oosterom et al. 2016).

In the context of contact calls, group cohesion can also be achieved on the basis of hydrodynamic cues, next to visual and auditory. Hydrodynamic cues, however, depend on close proximity of group members. Indeed, Van Oosterom et al. showed that with higher levels of background noise, Bigeyes significantly increased group cohesion, while decreasing vocalisation, probably because the group members got within range of other contact cues, like hydrodynamic. How and why greater distance between individual Bigeyes is advantageous has not been discussed by Van Oosterom et al. (Van Oosterom et al. 2016).

Neural Control

The neural control of acoustic behaviour in fish is mostly studied in toadfish. The plainfin midshipman in particular has been established as the primary study species. Toadfish use sonic muscles along with the swimbladder to produce sounds (Andrew H. Bass, Bodnar, and Marchaterre 2000). How other acoustic behaviour in fish is controlled in the brain is not established.

Toadfish Behaviour

Toadfishes, including midshipman fish, depend on acoustic signals for social communication. The gulf toadfish for example has two main types of calls: agonistic grunts and for male additionally advertisement calls, termed boatwhistles. For these calls toadfish contract superfast muscles in high pulse repetition rates of $\sim 200 - 250$ Hz, in gulf toadfish. The muscles are attached to the swimbladder, which by vibration generates the actual sound. Toadfishes show unusually high levels of synchronous activity in vocal hindbrain sites for this behaviour (Chagnaud et al. 2012; 2021).

In male midshipman, two types of alternate male morphs exist. Whereas type I males vocally court females and show territorial behaviour, and later on parental care, type II males fertilize eggs in the nests of type I males. Type I, in contrast to type II, shows an expansive vocal motor system, with enlarged sonic muscles and vocal motor nucleus (Tripp, Feng, and Bass 2021).

Generalisability

Toadfishes might be a distinctive example of fish vocalisation. Yet, many fish vocalise as it has been set out above. Morphophysiological analyses show that there is a comparable vocal motor system in distantly related teleosts. And although fish, show relatively simple acoustic repertoires, the vocal and auditory pathways are organised similarly to those of amphibians, reptiles, birds and mammals (A. H. Bass, Gilland, and Baker 2008; Chagnaud et al. 2012).

At least for species showing acoustic behaviour that creates sounds by using sonic muscles associated with the swimbladder, the here presented findings might be extendable. Nonetheless, toadfishes show particular cases of vocalisation. The sounds, on which the here cited studies primarily focus on, are the courtship calls; long tonal calls with precise temporal patterning. The presented insights might be specific for this behaviour (A. H. Bass, Gilland, and Baker 2008; Chagnaud et al. 2012).

Synchrony and Precision

The high muscle contraction rates of the vocal behaviour are dependent on mechanisms that ensure the precise motor activation of the ‚superfast muscles‘, as highly rhythmic behaviour in

other vertebrate lineages, too. Thereby, population level synchrony is essential in motor patterning for rapid acoustic signalling, possibly driven by the analogue evolution of similar neural properties in vertebrates. Moreover, high-frequency synchronous firing is involved in various functions of the nervous system, like attention, memory, but also neurological disorders. Thus, the study of the neural control of vocalisation can also be of value to other fields of neuroscientific research. Specifically, a general understanding of how precise temporal sequencing of neural output might be achieved is promoted here by the greater simplicity of the research model (Chagnaud et al. 2012; 2021).

Increased precision can be achieved by several mechanisms in other neural circuits: feed forward inhibition in auditory circuits, recurrent inhibitory input in the cerebral cortex and neural synchrony in cortical and sensory neurons are examples. Inhibition might be the most prevalent mechanism for the synchronisation of activity (Chagnaud et al. 2021).

Central Pattern Generator

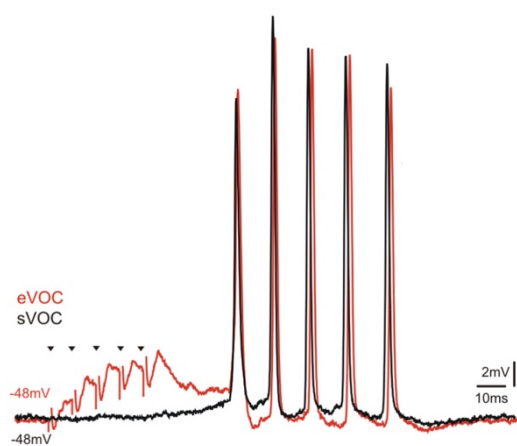


Figure 3: Recordings of VMN during spontaneous (sVOC; black) and electrically evoked vocalizations (eVOC; red; arrowheads indicate stimulus artifact) (Chagnaud, Baker, and Bass 2011)

The superfast sonic muscles of toadfish are innervated by the occipital nerve. The contraction of the sonic muscles (as has been shown in fig. 1) is controlled 1:1 by the vocal motor activity. The so called ‚fictive vocalisation‘ can be recorded from the vocal nerve and can be seen as template of the actual vocalisation. In toadfish these fictive calls are comprised of highly stereotyped repetitive series of compound nerve potentials (VOC), produced by synchronous motoneuron activity in the vocal motor nucleus (VMN) with high temporal fidelity, as can be seen in fig. 3. The action potential of motoneurons can also be mapped 1:1 to individual VOC’s. In part, individual VOC’s are determined by the central pattern generator (CPG) in the hindbrain. The CPG consists of three

topographically separate nuclei: the vocal motor nucleus (VMN), the vocal pacemaker nuclei or vocal premotor nuclei (VPN) and the vocal prepacemaker nuclei (VPP). Frequency and duration of calls are determined by the intrinsic network properties of the CPG (Chagnaud, Baker, and Bass 2011; Rosner et al. 2018; Chagnaud et al. 2021).

VPN to VMN

Motor neurons in the VMN are not spontaneously active; they fire only during coherent excitatory input provided by VPN. VMN neurons are also low excitable when no vocalisation is present. Indeed, the rhythmic ultrafast depolarisation of VPN neurons impose the network

activity in VMN and thus determine call frequency. VPN lays adjacent to and innervates VMN bilaterally, as can be seen in fig. 4 (Chagnaud, Baker, and Bass 2011; Chagnaud et al. 2012).

VPN and VMN are electrotonically coupled by gap junctions (fig. 4). The first ultrastructural evidence for these dates back to 1966. More recently, it was shown that gap junction impassable tracers injected into the VMN did only label the VMN ipsilaterally, whereas passable tracers, like biotin, labelled all three nuclei of the CPG bilaterally. This finding suggested that the complete network was coupled via gap junctions. Indeed, gap junctions between premotor neurons and motoneurons are densely distributed as shown by the co-labelling of the gap junction protein connexin 35/36 between those two neuronal populations. It is known from other neural networks that gap-junctional coupling is apt to promote neural synchrony (Chagnaud et al. 2012; Rosner et al. 2018; Chagnaud et al. 2021).

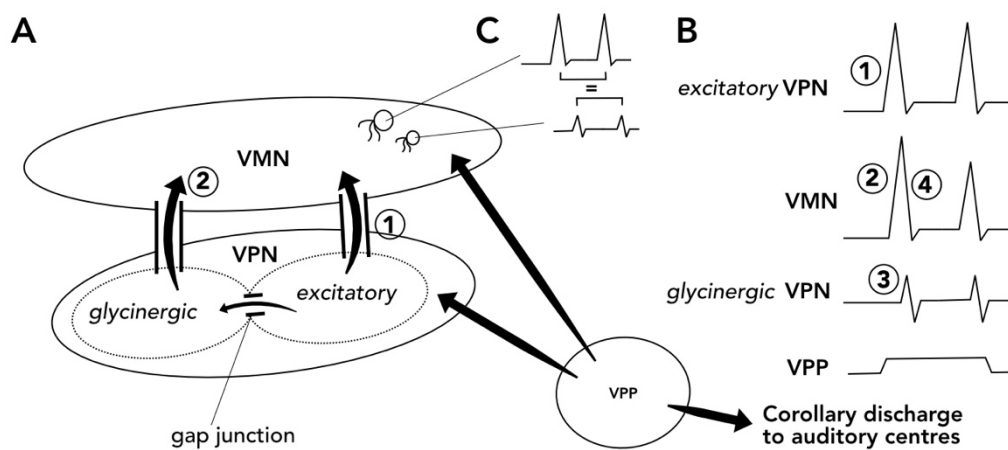


Figure 4: A: Vocal Central Pattern Generator in the hindbrain, with vocal motor nucleus (VMN), vocal pacemaker nucleus (VMN) and vocal prepacemaker nucleus (VPP). VMN and VPN, as well as the glycinergic and excitatory neurons within VPN are coupled via gap junctions. VPP projects to both VPN and VMN and sends a corollary discharge to auditory centres. B: VPP is sustained depolarised for the duration of the call. By Chagnaud et al. proposed mechanism of vocal patterning. 1) excitatory VPN neurons depolarise 2) Via gap junctions VMN becomes depolarised as well 3) At the same time VPN glycinergic neurons, also coupled via gap junctions depolarises 4) The inhibitory input from the glycinergic VPN neurons leads in VMN to rapid repolarisation. C: Differentially sized neurons encode call amplitude in VMN. (L Böger, 2021)

Inhibitory Input

The necessity of inhibitory GABAergic input for population synchrony in VMN and vocalisation was shown by local injection of GABA_A receptor antagonists. Chagnaud et al, 2012, speculated that the dense GABAergic input originated from small neurons surrounding VMN, causing synchronous population level activity and rapid motoneuron repolarisation. The repolarisation, along with intrinsic motoneural properties of low somatodendritic excitability and a slow reactivation of the repolarizing conductance, as well as the robust VPN input, was thought to prevent tonic firing. The reactivation should only be achieved at network activity and cause repetitive depolarisation at fixed intervals (Chagnaud et al. 2012).

Rosner et al., 2018, showed that in the midshipmen GABAergic and glycinergic labels are present in all CPG nuclei. The somata of the labelled cells were thereby within or immediately adjacent to the CPG (Rosner et al. 2018). Glycinergic release sites were found in a subset of VPN neurons, which contacted somata and dendrites of VMN motoneurons, illustrated in figure 4 (Chagnaud et al. 2021).

Electrotonically Coupled Circuit

Most recently, in 2021, Chagnaud et al., showed that the strong hyperpolarisation after spiking in VMN motoneurons is dependent on the activation of glycinergic VPN neurons. Probably, the glycinergic premotor neurons are activated via feedforward excitation mediated through the electrotonic coupling between the two subsets within VPN. Chagnaud et al. propose a circuit (fig. 4) in which excitatory VPN neurons input to VMN and at the same time activate the glycinergic VPN subset. The glycinergic premotor neurons in turn abruptly repolarise the VMN neurons and induce a period of decreased excitability of the motoneurons in VMN subsequently (Chagnaud et al. 2021).

Neuronal Size Encodes Call Amplitude

Chagnaud et al. found in 2012 that frequency was stable regardless of motoneuron size. This is uncommon. Normally, larger neurons fire later, because their lower input resistance makes them depolarise less than smaller neurons. Yet, the presented CPG seems to be able to ensure a constant frequency across different sized motoneurons. However, the recruitment of larger motoneurons led to higher amplitude in motoneuron activity and thus to louder natural calls (Chagnaud et al. 2012).

Summary CPG

Summarising, in the vocal CPG of the toadfish, glycinergic inhibition at gap junctions induce a window in which motoneurons show a reduced activation probability. This sets the pace for the rhythmic activation of the vocal motoneurons on a synchronised population level. The temporal precision achieved this way is in the millisecond range. Yet, the differential recruitment of variable sized motoneurons could allow for an amplitude modulation.

VPP to VPN, VMN

The prepacemaker nuclei, the most rostral of the CPG nuclei, innervates both the VPN and VMN. The VPP encodes call duration. This is done via a sustained membrane depolarisation throughout the duration of the call. The activity of VPP is independent from VPN (Chagnaud, Baker, and Bass 2011; Chagnaud et al. 2021).

The call duration is one of the most important features that characterise different calls. The VPP is also responsible for the corollary discharge to important hindbrain auditory nuclei. One of the efferent targets of the corollary discharge innervates the inner ear. Here the corollary

discharge directly reduces the peripheral auditory sensitivity to self-generated sounds (Chagnaud, Baker, and Bass 2011).

Development

Bass et al. 2008 looked at the development of the vocal network across the most caudal hindbrain and rostral spinal cord in larval batrachoidid fish. They found a similar pattern of vocal reticulo-spinal pathways, as in other vertebrates. The vocal network in these fish originates within the transitional zone of the 8th rhombomere (rh8) and the spinal cord. This zone is already at larval stages 2-3 times as large as rhombomeres 2 to 6. In all vocal vertebrates rh8 gives rise to the pattern generating circuit involved in vocalisation. Moreover, in birds and teleosts the rh8-spinal compartment can be subdivided in different nuclei. Both the vocal motoneurons and pacemaker neurons develop here. The VMN in larval fish is already present as dense midline column caudal to the reticulospinal scaffold (A. H. Bass, Gilland, and Baker 2008).

A comparison with other vertebrate groups shows that the VMN is located similarly as vocal motor neurons that target syrinx and larynx in birds and frogs, respectively. The adult phenotype additionally suggests a similar alignment with reptiles and mammals. The same is true for the comparison between prepacemaker and pacemaker nuclei in fish with premotor neurons that control the vocal-respiratory mechanisms of mammals, birds and amphibians. In all four vertebrate groups the vocal premotor neurons are innervated by midbrain vocal areas. Bass et al. suggest that the vocal muscles in fishes as well as in tetrapods are derived from the occipital somites, whereas Parmentier and Rui estimate that the sonic muscles of fish evolved from at least three different origins. In vertebrates, the sonic muscle innervation has evolved at least three times, in fish to the occipital nerve (A. H. Bass, Gilland, and Baker 2008; Parmentier and Diogo 2006).

Concluding, between fish and mammals, birds, amphibians and reptiles there is a conserved pattern of the vocal network. Circuits for vocal communication share a common ancestry (A. H. Bass, Gilland, and Baker 2008)

Seasonal and Diurnal Variation

Acoustic communication in fish, especially courtship signalling, is energetically costly. The exact timing and sender-receiver coupling is thus crucial for reproductive success. Acoustic active fish experience seasonal and diel changes, with a tendency to increase the activity during spawning. This is especially true for advertisement calls, but also agonistic sounds in territorial species is associated to the breeding season (F Ladich 1997; Ni Y. Feng and Bass 2016)

Toadfish

In some acoustically active fish sound production is most intense during night-time. Also, in the midshipman vocal activity peaks nocturnally and during the breeding season. The vocal network of male midshipmen shows higher excitability during these periods, manifesting in increased duration and decreased stimulation threshold of midbrain evoked fictive calls. It has been suggested that nocturnal melatonin action increases the vocal activity of male midshipmen during the breeding season (Ni Y. Feng and Bass 2014). Amorim 2006 reported also seasonal variation of Lusitanian toadfish vocal activity (M. C.P. Amorim et al. 2006).

Weakfish

Weakfishes are members of the drumfish family. Drums produce sound by rapid contraction of sonic muscles causing vibration of the swimbladder. In weakfish a similar seasonal pattern as in toadfish is observable. Reproductive calls are elicited at the time and location of spawning, abruptly emerging in mid-May and waning in late July. Calls of weakfish consist of 6-10 sound pulses. Accompanying the sudden emergence of reproductive calls, rising testosterone levels cause the sonic muscles in male weakfish to triple in mass. As a result of this sound pressure levels increase during spawning; beneficial, probably because more intense sound can be heard over greater distances. Also, weakfish experience a diurnal vocal cycle. In these fish, the vocal activity is reaching its maximum in the early evening (Connaughton, Fine, and Taylor 2002).

Melatonin

Melatonin is crucial for circadian rhythms, but its role has been mostly researched in the context of locomotor activity or feeding activity in fish. Yet, in songbirds, melatonin has also been found to play a role in the control of song and call behaviour. Moreover, melatonin can directly target vocal circuits and modulate vocal patterning, as it was shown to inhibit spontaneous firing of a vocal premotor nucleus in zebrafinch (Ni Y. Feng and Bass 2014).

Constant Light Conditions

Feng et al. showed 2014 in a series of experiments the effect of constant light or dark environments on the vocal behaviour of plainfin midshipman. It was observed that 5 days of constant light significantly increased stimulus thresholds for fictive calls, electrically induced at vocally active medial sites of the midbrain (midbrain tegmentum and medial periaqueductal grey (PAG)). In line with the hypothesis that vocal behaviour is controlled by melatonin, the application of a melatonin analogue (2-iodomelatonin (2-IMel)) decreased the threshold and rescued fictive calls. Interestingly, electrically induced calls at lateral midbrain sites under the application of melatonin increased call duration and latency (fig. 5) (lateral midbrain sites being: paratoral tegmentum (PTT), deep layer of torus semicircularis (TSd), ventral

paralemniscal tegmentum (PL)). Feng et al. concluded that the melatonin sensitive neuroendocrine centre might be located in the lateral midbrain (Ni Y. Feng and Bass 2014).

Conversely, 5 days of constant darkness increased vocal network excitability. This in turn could be reversed by administering a melatonin receptor agonist, that increased the induction threshold and decreased the duration of calls (Ni Y. Feng and Bass 2014).

For an overview of vocal sites in the fish brain, see figure 6.

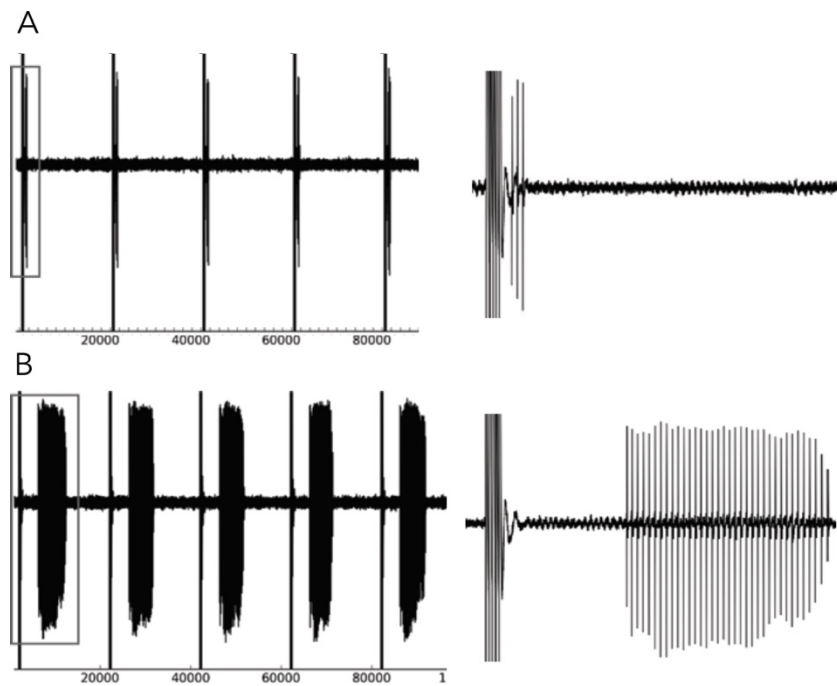


Figure 5: Longer duration and latency of evoked calls in the lateral midbrain: Fictive vocal responses evoked by medial (A left) and lateral (B left) midbrain stimulation. Fish were treated with 2-IMel. Enlarged vocal responses of outlined response on the right. Arrows indicate stimulus artefact and stimulus onset. Vocal responses between medial (A) and lateral (B) differ in duration and latency. Recordings were done by Feng and Bass. (Ni Y. Feng and Bass 2014; adapted)

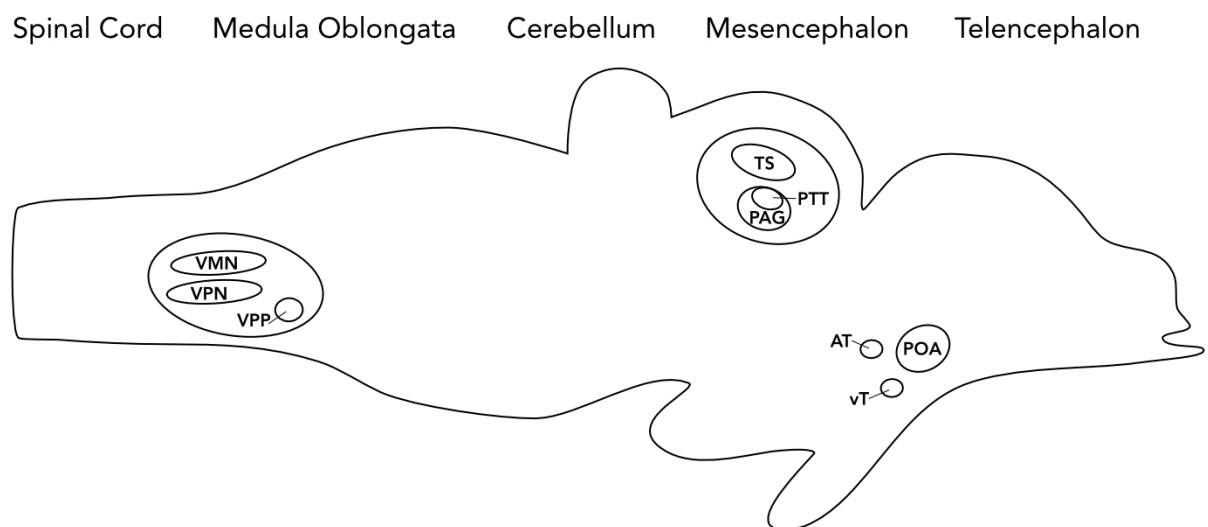


Figure 6: Brain of teleost fish with hindbrain vocal pattern generating circuit (CPG), midbrain vocal-acoustic centre (mVAC) and forebrain vocal-acoustic centre (fVAC). In detail, CPG contains vocal motor nucleus (VMN), vocal pacemaker nucleus (VPN) and vocal prepacemaker nucleus (VPP); mVAC contains among other: torus semicircularis (TS), paratoral tegmentum (PTT), periaqueductal grey (PAG) and paralemniscal tegmentum (PL); fVAC contains among other: preoptic area (POA), ventral tuberal hypothalamus (vT) and the anterior tuberal hypothalamus (AT). (L Böger, 2021, after Ni Y. Feng and Bass 2014)

Neuroendocrine Centres

Seemingly paradoxical, melatonin exerts opposing circadian effects in nocturnal and diurnal species, an overall increase in activity vs. an overall decrease, respectively. Melatonin can act via two different receptors: Melatonin receptor 1b (Mel1b) which acts excitingly and Melatonin receptor 1a (Mel1a) which has an inhibitory effect. In the nocturnal plainfin midshipman, Mel1b mRNA has been shown to be expressed in neuroendocrine, sensory and vocal motor pathways. Moreover, other genes that might control the precise and synchronous activity of VMN neurons display diurnal changes in expression. This also includes the expression of the Mel1b itself, whose abundance significantly increases in the morning, compared to the night-time in some brain areas, namely the Telencephalon and the preoptic area. Circadian control of vocal behaviour likely depends on different neural networks (Ni Ye Feng 2016; Ni Y. Feng, Marchaterre, and Bass 2019).

Irrespective of diurnal activity pattern, melatonin seems to lengthen the duration of single calls, as it has been described above, suggested by Feng et al. 2014 (Ni Y. Feng and Bass 2014). Mel1b is robustly expressed in major vocal sites in the midbrain and forebrain: preoptic area (POA), ventral tuberal hypothalamus (vT), anterior tuberal hypothalamus (AT), midbrain torus semicircularis (TS) and periaqueductal grey (PAG). In the hindbrain the VPN and VPP is labelled with mel1b, whereas VMN does not contain any mel1b label. In summary many important vocal sites in the brain are sensitive to melatonin excitation, in the nocturnally active midshipman fish (Ni Y. Feng, Marchaterre, and Bass 2019).

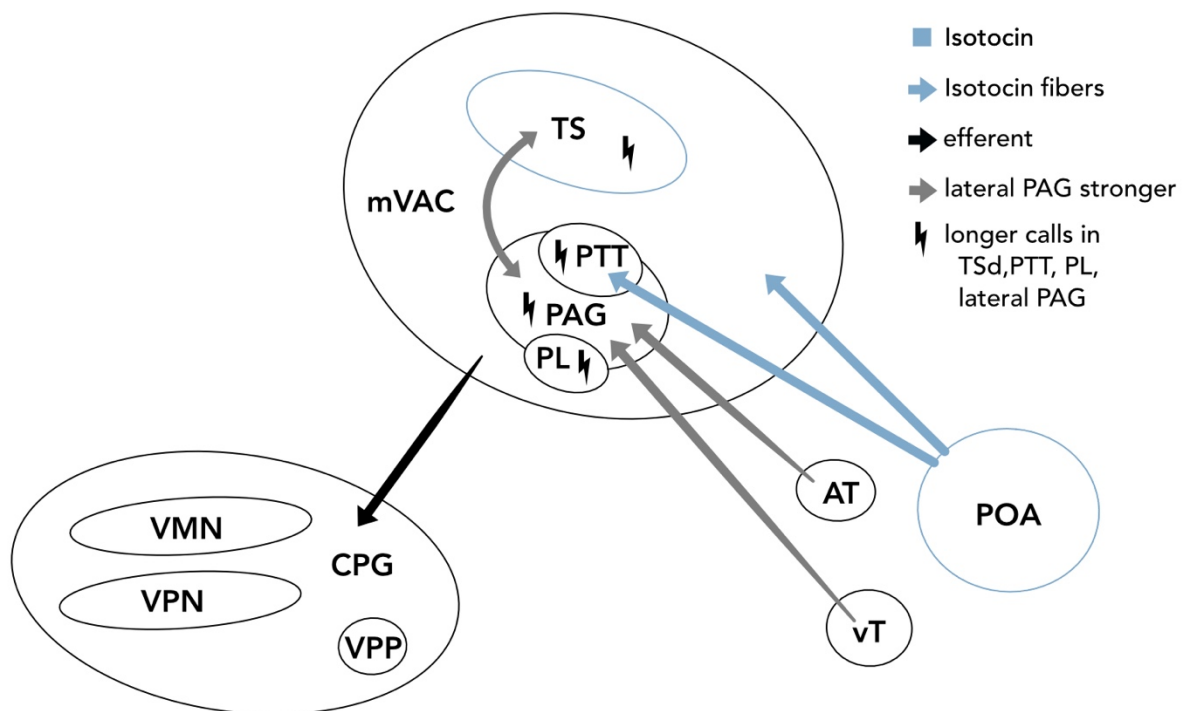


Figure 7: Functional Connections between the CPG, mVAC and fVAC. Abbreviations as in fig. 6. Blue circles and blue arrows illustrate isotocin labelled cells and fibers, respectively, Arrow heads, irrespective of colour indicate an efferent connection, grey arrows show connections that are stronger for the lateral PAG than for the medial PAG and a black bolt marks sites in which stimulation alongside the application of melatonin leads to longer calls (PAG: lateral PAG and TS: deep layer of TS (TSd)) (L. Böger 2021)

Midbrain and Forebrain Vocal Sites

In the discussed study from Feng et al. in 2014, it was observed that the stimulation of the medial and lateral midbrain vocal-acoustic network (mVAC) caused differential length of calls. For an overview of the functional connections see figure 7. At lateral sites calls were not only longer but showed also higher stimulation thresholds and longer latencies. This could either be due to a lower excitability or because of an inclusion in multi-synaptic pathways (Ni Y. Feng and Bass 2014).

The latter might be especially interesting as the lateral mVAC contains the paratoral tegmentum (PTT), which is innervated by isotocin fibres from the preoptic area (POA). The delivery of arginine-vasotocin (AVT) decreased the duration and number of fictive calls by stimulation of the POA, but mVAC stimulation did only reduced the number of calls not their duration. Bass et al. presumed that whilst mVAC, especially the periaqueductal grey (PAG), is important for call initiation, frontal vocal areas, such as POA, additionally encode call duration. The importance of PAG for call initiation is also consistent with other vertebrates (Ni Y. Feng and Bass 2014; Andrew H. Bass, Chagnaud, and Feng 2015).

Moreover, it might be possible that isotocin in general is important for call duration. The deep layer of the torus semicircularis (TSd) is sparsely labelled with isotocin and also elicits longer calls, when stimulated (Ni Y. Feng and Bass 2014).

Feng et al. described calls elicited by lateral midbrain stimulation as comparable to the hum component in grunt-hum sounds of midshipmen. The differential activation of vocal midbrain regions might modulate sound characteristics. The division between lateral and medial midbrain is in so far interesting because in vertebrates call duration is a salient feature to characterise natural calls (Ni Y. Feng and Bass 2014).

The functional segregation of lateral and medial mVAC is also supported by the differential connectivity of lateral and medial sites in mVAC. The lateral PAG shares a greater connectivity with other forebrain vocal sites, namely the ventral tuberal hypothalamus (vT) and the anterior tuberal hypothalamus (AT). Also is the lateral PAG more intensely connected with the TSd. All of these areas elicited longer calls when stimulated (Ni Y. Feng and Bass 2014; Andrew H. Bass, Chagnaud, and Feng 2015).

Perspectives

There are several topics that should be addressed in future research. Most notably, neural control of vocal behaviour in fish has predominantly been based on the midshipman fish. So far, we can only presume that findings on neural control in toadfish are generalisable across teleost fish. Rice et al. stated that acoustic communication evolved 27 times in ray finned species (Rice et al. 2020). The independent evolution is likely to imply a diversity of the neural control of acoustic behaviour. Thus, further species should be investigated in this respect.

Rice et al. also suggested that 20,000 species of ray-finned fishes are potentially acoustically active. This number probably contains species that indeed do not show acoustic behaviour, because the analysis was based on a family level and it is known that in some families, species exist that are not soniferous (Rice et al. 2020). For a better estimation it would be of value to know how large the portion of species are that are not acoustically active.

To my knowledge, the neuronal control of stridulation sounds has not been investigated. And that although, stridulation is one of the main mechanisms to produce sounds in fish. Given the highly distinctive sound production it would be intriguing to know if stridulation sounds and swimbladder sounds engage the same hindbrain nuclei or if they at least also develop in rhombomere 8 as does the vocal pattern generating circuit. Stridulation sounds are less rhythmically precise, thus it might be possible that the intrinsic neural properties of the CPG would differ. Another profitable research topic could be the identification of neuronal vocal substrates and mechanisms in catfish, that show both forms of sound production (Kaatz 2002; A. H. Bass, Gilland, and Baker 2008; Fine and Parmentier 2015; Hossain, Mallik, and Hossen 2019).

One aspect of neural control yet to be established is the coupling of VPP with the other two CPG nuclei. As has been described above, the complete CPG can be labelled with gap junction passable tracers (Chagnaud et al. 2021). Yet, it was not described if VPP shares these connections with VPN, VMN or both. The most likely scenario would be if VPP was coupled to VPN by gap junctions, because the input of VPN to VMN shapes the motoneuron activity. Nonetheless, it has been reported that VPP innervates both nuclei.

Regarding VPP which is supposed to encode duration of calls, the proposed functional segregation of medial and lateral vocal midbrain sites comes to mind, with the stimulation of lateral midbrain vocal sites causing longer calls (Ni Y. Feng and Bass 2014; Chagnaud et al. 2021). It has not been answered, whether lateral midbrain sites are more densely connected with VPP. Moreover, the investigation of morphological differences between lateral and medial vocal midbrain centres could inform on mechanisms of call modulation, e.g. by melatonin or isotocin.

The stimulation of vocal brain regions in which isotocin is present elicits longer calls. Having in mind that isotocin is an analogue of oxytocin, the question arises if isotocin modulates call characteristics in the context of reproduction behaviour. It was shown that isotocin and arginine-

vasotocin regulate parental care and that isotocin might be involved in courtship behaviour. In contrast to isotocin, arginine-vasotocin decreases call duration and call frequency, and is additionally high in males that fight in order to change their social status. In these males and males that show parental care, high levels of arginine-vasotocin could decrease call duration, possibly promote the emergence of short aggressive calls (O'Connell, Matthews, and Hofmann 2012; Kleszczyńska, Sokołowska, and Kulczykowska 2012; Ni Y. Feng and Bass 2014).

In regard to motivational components of acoustic communication, it would be interesting to understand how increasing levels of excitement during social interactions modulate sound neuronally. Specifically, are amygdala homologs in the dorsal pallium capable of modulating acoustic signals? And is estrogen, with the coexpression of the estrogen receptor α in the dorsal pallium and preoptic area involved in this modulation, as suggested for reproductive acoustic communication in the midshipman fish by Forlano et al. 2015 (F Ladich 1997; Forlano, Deitcher, and Bass 2005).

The last aspect I want to mention here is amplitude modulation by VMN. It has not been thoroughly investigated how different sized neurons are recruited for amplitude modulation of calls. Rosner et al. propose that serotonergic or cholinergic input into the CPG might be a possible cause (Chagnaud et al. 2012; Rosner et al. 2018).

Conclusion

Fish communicate acoustically in various contexts, such as agonistic encounters, reproduction and shoaling. Although not all fish engage in this behaviour, evidence exists that acoustic communication is more widespread than previously thought. The acoustic signal is thereby a fundamental element of social communication, as has been demonstrated by several playback and muting experiments as well as by correlative investigations. The neural control of acoustic communication has primarily been investigated at the hand of toadfish, that emit tonal courtship sounds. However, this might not be representative of all fishes. Indeed, a great diversity of sound producing mechanisms exist, with acoustic communication having evolved 27 times independently in ray-finned fishes. In toadfishes, the hindbrain vocal central pattern generator (CPG) and specifically the prepacemaker, the pacemaker and vocal motor nucleus determine the duration, frequency and amplitude of sound, respectively. The vocal CPG is innervated by midbrain and forebrain vocal sites, that might modify different characteristics of calls, like duration. Moreover, the soniferous behaviour of fish exhibits seasonal and diurnal fluctuations, which is regulated by melatonin. Despite the substantial advancement of knowledge about acoustic communication in fish, many unanswered questions remain. The investigation of these questions would benefit other areas of neuroscience as well.

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