

Acoustic communication in insects

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RESUMEN

La investigación de comunicación acústica y audición en insectos ha sido extensamente estudiada desde hace 70 años. Estudios de comportamiento de insectos han demostrado la importancia de la audición para la atracción de pareja, cortejo, rivalidad y comportamiento territorial, así como para detección de presas, evasión de depredadores y localización de huésped parasitario. Esta revisión exhaustiva describe la asociación entre el sonido de insectos y su correspondiente comportamiento, así como, comprende y ejemplifica cinco categorías de mecanismos de producción de sonido en insectos: vibración (tremulación), percusión, estridulación, mecanismos de clicks y expulsión aérea. Adicionalmente, se describen los órganos auditivos en insectos (sensilas, sensila cordotonal, órgano de Johnston, órgano timpánico y órgano sub-genual) indicando su posición en el cuerpo del insecto, el Orden que lo presenta, y su principal fuente de estimulación. Finalmente, se menciona el caso de estudio del Grillo de Campo Mediterraneo (*Gryllus bimaculatus*) explicando la fonotaxis, el cual es el proceso donde la hembra es atraída hacia el macho por su llamado.

Palabras clave: Audición, comunicación; estridulación; insecto; percusión; sonido; tremulación; vibración

1. Insect acoustic communication

Insects, representing approximately 70 percent of the world's species, are by far the most successful, and variable group of living specimens which have evolved on our planet. These arthropods are among the oldest terrestrial animals, and have existed for more than 400 million years (Straub & Lakes-Harlan, 2014). Insects present various lifestyles (aquatic, terrestrial, epizoic, among others), but perhaps one of their most interesting features is its acoustic communication. This manuscript compiles a comprehensive review on the acoustic communication behaviour in insects, including the behaviours associated with the insect sound of communication within the same species, prey detection, predator avoidance, and parasitic host localization. A compilation and exemplification of the five categories of sound production mechanisms in insects is shown. Additionally, there is a description of

ABSTRACT

Research on acoustic communication and hearing in insects has been extensively studied in the past 70 years. Behavioural studies have pointed out the relevance of insect hearing for intraspecific acoustic communication (mate attraction, courtship, rivalry and territorial behaviour), prey detection, predator avoidance, and parasitic host localization. This review describes the association between insect sound and behavioural responses, as well as compile and exemplify the five categories of sound-producing mechanisms in insects: vibration (tremulation), percussion, stridulation, click mechanisms and air expulsion. Additionally, the insects hearing organs are described (hair sensillae, chordotonal sensillae, Johnston's organ, tympanal organs, and sub-genual organ), indicating its position in the insect body, the Order that present it, and the preferred stimulus. Finally, I mention the case study of the Mediterranean Field Cricket (*Gryllus bimaculatus*) explaining the phonotactic process, where the female is attracted towards the male by its species-specific calling song.

Keywords: Communication; hearing; insect; percussion; sound; stridulation; tremulation; vibration

the insect hearing organs, indicating its body position, the Order that present it, and the triggering stimulus. Finally, a case study of the Mediterranean Field Cricket (*G. bimaculatus*) phonotactic behaviour is mentioned.

During the early 1900's, detailed anatomical descriptions of hearing organs of distinct groups of insects were carried out (Eggers, 1911; Schwabe, 1906). But only after 1940, two comprehensive reviews on "Hearing in Insects" (Pumphrey 1940) and "Insect sounds" (Haskell 1961) were performed, where insect sound was defined as "any mechanical disturbance whatever which is potentially referable by the insect to an external and localized source. Since those early studies in the field, the development of new techniques and suitable equipment for the recording and analysis of sounds have allowed the field to progress rapidly (Claridge, 2005; Hedwig, 2014; Huber, 1960; Roeder & Treat, 1957; Roeder, 1969; Suga & Katsuki, 1961).

2. Behaviours associated with insect sound

Acoustic signals (sounds) can be associated with several insect behaviours, mainly mate attraction, courtship and territorial behaviour. For instance, the mature unmated female cricket *Gryllus campestris* and long-horn grasshopper *Thamnotrizon apterus*, are attracted by the singing (chirping) of the males (Regen, 1913). Even flight noises in mosquitos are used for mate attraction (Kahn & Offenhauser, 1949). However, insect sounds can also be used in other behaviours, as mentioned below.

A. Intraspecific communication: rivalry and territorial behaviour

Some grasshoppers have developed one of the most highly intricate song behaviour amongst insects, called the “rival duet” behaviour. If a male grasshopper, singing his courtship song to a female, is interrupted by the appearance of a second male who also tries to court the female; the first male leaves the female, faces the intruder, and sings the “rivalry song”. This behaviour produces an abrupt and similar response from the interloper, and the two males sing against one another. The contest may be brief, when one or other leaves the field and the remaining male returns to his courtship, or so long that the female abandons the scene herself (Haskell, 1961).

Busnel (1953) described the territorial behaviour of the cricket *Oecanthus pellucens*; the male lives in bushes, about 50 cm above the ground and stays for the great majority of its life restrained to a small area approximately 50 sq cm. The male moves around this territory, patrolling, singing its normal song, if it encounters another interfering male, it sings a type of song called the “warning song”. This interesting behaviour appears analogous to the territory marking of certain song-birds, which is established by the male by singing at the territorial boundaries prior to the commencement of the mating season (Haskell, 1961).

B. Detection and avoidance of predators

Numerous predators utilize a combination of sensors to hunt insects: vision, olfaction, and hearing are the main ones; with a bias toward vision in diurnal animals and toward hearing

and olfaction in the nocturnal predators. Nocturnal acoustic hunters include felids, canids, owls, rodents, which are all passive listeners. Bats are also passive listeners, but also active echolocators. According to Conner (2014), all traits including visual, chemical tactile, electric, and acoustic cues, that minimize the probability of a prey being detected when potentially detectable to an observer, can be called Crypsis. For example, certain moths interrupt their sexual acoustic calls in the presence of acoustic predators, to avoid detection by the predator (Greenfield, 2014; Spangler, 1984). Similar adaptive silence behaviour have been reported in crickets and katydids (Bailey & Haythornthwaite, 1998; Belwood & Morris, 1987; Conner, 2014; Faure & Hoy, 2000; Spangler, 1984).

The cricket *Teleogryllus oceanicus* depicts one of the most remarkable examples of adaptive silence (Hedwig & Robert, 2014; Zuk, Rotenberry, & Tinghitella, 2006). The male field cricket stridulates by scissoring the wings; females are attracted to the males’ songs. Interestingly, an Australian and Pacific Island species of *T. oceanicus*, have been forced to alter that strategy because of an acoustically orienting parasitoid fly *Ormia ochracea*. Like the female cricket, this fly is attracted to the male cricket’s calling song. After locating the male cricket, the fly deposits her offspring on or near the male. The larvae burrow into the male, killing him as they develop. Within approximately 20 generations of intense selection has resulted in a morphological change in the wings of the male crickets on Kauai. Mute males, called flatwing males, have wings similar in appearance to those of females. Mute males have lost their file and scraper and are thereby silenced. Flatwing males produce no calling song and do not attract the parasitoid. However, it is not clear how the silent flatwing males now attract mates, although Cade (1980) suggested that they function as satellite males, waiting close to calling males, and intercepting females as they move toward them.

“Whispering” moths exemplify another antidetection strategy (Nakano et al., 2008). *Ostrinia furnicalis*, male Asian corn borer moths, use specialized very low intensity courts-

hip songs (46 dB sound pressure level at 1 cm) produced by sex-specific scales on the forewings and mesothorax. In order to protect the pair from conspecific competitors and predators, this male moth produces the sounds in the immediate vicinity of the female's ear, which provide a private communication channel between the male singer and the female listener (Conner, 2014).

C. Host localization by parasitoid insects

Animal acoustic signalling uncommonly constitutes a confidential communication channel. Sound tends to propagate in all directions, broadcasting towards hardly predictable destinations and, sometimes, is unintentionally received by predators and parasitoids. The Dipteran parasitic family Tachinidae and the flesh flies family Sarcophagidae take advantage of acoustic signalling in Orthoptera (crickets) and Hemiptera (cicadas), enabling the parasitic exploitation. Guided by acoustic communication signals, these flies identify and localize their singing target, depositing their larvae on or close the host. Larvae then develop as endoparasites, eventually killing the host (W. Cade, 1975; Fowler, 1987; Hedwig & Robert, 2014; Leonide, 1969; Soper, Shewell, & Tyrrell, 1976).

3. Sound-producing mechanisms in insects

Insects, as small living species in a large ecosystem, require specific methods of communication to overcome the relatively large distances separating individuals from potential mates. Their small size poses the intrinsic problem of separation of the sexes by relatively enormous distances. To overcome this problem, insects have evolved behavioural strategies and communication systems, largely visual, chemical, or acoustical, to insure effective mate finding (Capinera, 2008).

Insects have evolved special features that allow them to be acoustical animals. Many groups have specialized mechanisms of sound production and hearing organs, which are used in intraspecific acoustic communication (Claridge, 2005). Researchers have classified sound producing mechanisms in insects. Ewing

(1989) described a most recognised classification compiling five categories of sound producing mechanisms (Claridge, 2005) (Table 1).

A. Vibration (including Tremulation) –

Sound emissions that result from vibrations of relatively unspecialized body parts of the insect, generally oscillations of the abdomen, either dorso-ventrally or laterally. The oscillatory movement of the wings of an insect sets up regions of compression and rarefaction and a vibrational sound is produced. Tremulation sound is transmitted through the legs to the substrate on which the insect is walking or standing.

The flight sound, made by the wings, in swarming mosquitoes is considered to be used for species-specific recognition (e.g. Gibson, Warren, & Russell, 2010; Pennetier, Warren, Dabiré, Russell, & Gibson, 2010; Roth, 1948). Wing vibration is also used in the courtship dances of *Drosophila* species (Von Schilcher, 1976).

B. Percussion –

Striking one part of the body against another as a communication system for pair formation, as known for example, the Australian moth (Lepidoptera); males produce ultrasonic acoustical long distance signals to attract sexually receptive females and to establish territorial residency in competition with other males (Alcock & Bailey, 1995).

Striking the substrate with the tip of the abdomen is also considerate as a “*percussion*” signal. An example of an insect that uses percussion as a sound-producing mechanism is a species of the suborder Arctoperlaria (Plecoptera), which produce drumming signals on the substrate as a mating system. The male emits a species-specific call searching for the female, once the female answer a duet is established with vibrational signals then she became stationary; the male starts localizing the stationary female until location and mating are accomplished (Stewart & Sandberg, 2005).

C. Stridulation –

In general the term stridulation is inaccurately used to name any mechanism of sound production in insects (Haskell, 1961), however that denies the utility of the term. Stridulation consists of sounds

produced by frictional mechanisms, involving the movements of two specialized body parts against each other in a systematic patterned manner (Claridge, 2005).

Stridulation has been associated to three phases of mating behaviour in certain Orthoptera. The first phase comprises of the response stridulation from the receptive female orientation towards and locomotion to the male. The female arrived near the male, stridulating in response to mate song; the male, once noticing the female, sings the courtship song, engages the genitalia and copulation occurs (Haskell, 1958).

D. Click mechanisms – These sounds depend on the deformation of a modified area of cuticle, generally by contraction and relaxation specialized musculature within the insect body. This movement results in a succession of clicks which may be repeated quickly in distinctive patterns. Tymbal is the name of the specialized area of cuticle, as exemplified in the loud singing cicadas (Hemiptera). For example, the males of *Tibicina* (Hemiptera) cicada species produce a sustained and monotonous calling song by tymbal activity. This acoustic signal constitutes the first step in pair formation, attracting females at long distances, and is involved in male-male interactions (Sueur & Aubin, 2003).

E. Air expulsion – This is an unusual sound-producing mechanism within insects. This sound is described as an exhalatory sound, frequently expelled via the tracheal spiracles, however little is known about its function (Ewing, 1989). The Madagascar hissing cockroach *Gromphadorhina portentosa*, is able to produce audible hisses from a pair of modified spiracles. Adult males hiss in three social contexts: during courtship, during copulation, and during aggressive encounter. Adults and nymphs of both sexes also hiss when disturbed (Nelson & Fraser, 1980).

The above-mentioned categories are not completely exclusive and some insects may use combinations of them. There are a great variety of sound-producing mechanisms evolved by insects; this should suggest the importan-

ce that sound plays in their biology. Different mechanisms have evolved in the same orders of insects; this suggests that sound-producing mechanisms may have evolved many times over the phylogeny of a group (Haskell, 1961).

4. Insect hearing

Insects are adapted to produce and receive acoustic signals (sounds), which they use in different behavioural contexts, primarily intraspecific communication (e.g. mate attraction, courtship and rivalry behaviour), detection and avoidance of predators and host localization by parasitoid insects (Straub & Lakes-Harlan, 2014). All sounds derive from vibrations transmitted through solid substrates or fluid media, such as air and water. Insects have specialised receptors that detect external vibrations as airborne and substrate transmitted emissions (Claridge, 2005).

There are five main types of hearing organs in insects (Table 2). These are:

A. Hair sensillae of various types – Insects have numerous sensory organs scattered over and within their body. Many of the sensory structures are mechanical sensors that bend, indicating contact with a surface or wind and air movement over the structure. The simplest of mechanoreceptors may consist of a single hair or seta that projects from the cuticle surface. Sensillum is called at the simple receptor, generally with only one sensory neuron connecting it to the central nervous system (Capinera, 2008).

B. Scattered chordotonal sensillae – More complex sensory organs are composed of many sensillae, that is, they have many sensory neurons connecting to the central nervous system. Whether one or many, each sensory neuron is enclosed in one to several sheath cells, and connected by a relatively long axon to the central nervous system. The scolopale, sclerotized cap cell, is in contact with the site where stimulation will occur, usually some internal structure or the cuticular surface. Any stretching or movement of the structure to which the scolopale is attached will stimulate the dendrites of the sensory neuron and may

Table 1. Insect vibrational communication categories

Sound-producing mechanisms in insects				
Five categories (Ewing, 1989)	Description (Claridge, 2005)	Representative Orders (Capinera, 2008; Klots, 1977)		Major function(s) (Capinera, 2008)
A. Vibration (Tremulation)	Sound emissions which result from vibrations, most usually oscillations of the abdomen, either dorso-ventrally or laterally, and/or by the wings. Tremulation - sound production transmitted through the legs to the substrate on which the insect is walking or standing.	-Diptera -Hemiptera -Heteroptera	-Neuroptera -Plecoptera -Trichoptera	-Mate finding -Species-specific recognition -Mating inducement (Neuroptera)
B. Percussion	Striking of one body part against another or striking of the substrate with the tip of the abdomen.	-Blattodea -Coleoptera -Hemiptera -Heteroptera -Hymenoptera -Isoptera	-Lepidoptera -Orthoptera -Plecoptera -Psocoptera -Trichoptera	-Mate finding -Species-specific recognition -Mating inducement (Blattodea) -Queen stimulation (Hymenoptera) -Colony alarm (Hymenoptera, Isoptera)
C. Stridulation	Sounds produced by frictional mechanisms, involving the movements of two specialized insect body parts against each other in a regular patterned manner.	-Blattodea -Hemiptera -Heteroptera	-Orthoptera -Plecoptera	-Mate finding -Mating inducement (Blattodea) -Species-specific recognition -Defensive and territorial behaviour
D. Click Mechanisms	These sounds rely on the deformation of a modified area of cuticle, generally by contraction and relaxation of special musculature within the insect body. This movement results in a succession of clicks which may be repeated quickly in distinctive patterns. Tymbal is the name of the specialized area of cuticle.		-Hemiptera -Heteroptera	-Mate finding
E. Air Expulsion	Unusual exhalatory sounds, often expelled via the tracheal spiracles.		-Blattodea -Lepidoptera	-Mate finding -Defensive and territorial behaviour

set up a series of nerve impulses transmitted to the central nervous system. If only one sensory neuron and scolopale is present, the single unit is called a scolopodium, or chordotonal sensillum (Capinera, 2008).

C. Johnston’s organ – Johnston’s organ is a large complex chordotonal organ (collection of sensory cells) that usually consists of many scolopidia. This organ is located between the second (the pedicel) and third joints of each antenna of most adult insects; some hexapods (Collembola and Diplura) do not have a Johnston’s organ. This organ responds to several kinds of stimuli in different insects, including acting as a proprioceptor to indicate movement of the antennae; serving as a gravity indicator; monitoring wing-beat frequency in relation to flight speed in some Diptera; indicating ripples at the water surface in gyrenid beetles; and functioning as a sound reception in mosquitoes and perhaps other insects (Capinera, 2008).

D. Tympanal organs – Paired structures are characterized by the presence of a thin

cuticular tympanum stretched across a frame backed by an air sac or other tracheal structure behind the tympanum, and sensory neurons organized in scolopidia attached to the tympanal membrane. Air-borne sound waves cause the tympanum to oscillate, and activate sensory neurons enclosed by sending nerve signals to the central nervous system. The air cavity or tracheal sac plays an important role as a resonating chamber and for directional processing (Capinera, 2008).

E. Sub-genual organ – This hearing organ is a complex chordotonal organ composed of numerous scolopidia. The name “subgenual” means below the knee (from Latin for knee, *genu*). This complex chordotonal organ usually is located near the joint between the femur and tibia. It acts as a proprioceptor (a receptor of internal stimuli) and detects vibrations of the substrate on which the insect rests. The subgenual organ is especially well developed in crickets (Gryllidae) and katydids (Tettigonidae) and is closely associated with a tym-

panal organ, with both organs located on the tibia (Capinera, 2008).

Straub & Lakes-Harlan (2014) mentioned that tympanal organs have evolved at least 18 times independently in diverse taxa of seven insect orders as: Lepidoptera (butterflies and moths), Orthoptera (locusts, crickets, bush crickets, and katyids), Diptera (flies), Hemiptera (cicadas and water striders), Coleoptera (beetles), Mantodea (mantids) and Neuroptera (lacewings). However, according to Straub & Lakes-Harlan (2014) further studies on the evolution of hearing are required to solve some central evolutionary questions, mainly (1) where in a given lineage did tympanal ears

appear, (2) from which sensory precursor organ did an ear evolve, (3) under which selection pressure(s) did the ear originate, (4) how did the hearing organ diversify further, and (5) which physiological and behavioural adaptations occurred with a hearing sense?

5. Case of study-Cricket acoustic communication

Crickets use acoustic signals for communication; their melodic songs can be appreciated on a warm summer evening. Male crickets produce a calling, courtship and rivalry song by rhythmically rubbing their wings against each other (Hedwig, 2014). The calling song of the Mediterranean Field Cricket (*Gryllus bimaculatus*)

Table 2. Insect hearing organs

Insect hearing organs			
Receptor (Haskell, 1961)	Order	Position	Preferred Stimulus
A. Hair sensillae of various types	-All orders	Almost anywhere. Found predominantly on thorax and abdomen of Orthoptera and Lepidoptera and on anal cerci of Orthoptera	Usually tactile sensillae, but respond to fairly high intensity air-borne sound
B. Scattered chordotonal sensillae	-All orders	Almost anywhere in the body	Air-borne sound Water-borne sound Vibration of the substrate
C. Johnston's organ	-All orders	2nd segment of antenna	Air-borne sound Water-borne sound Vibration of the substrate
D. Tympanal organs	-Orthoptera: <i>Acridoidea</i> <i>Tettigonioidea</i> <i>Grylloidea</i>	1st segment abdomen Tibia of fore leg Tibia of fore leg	Air-borne sound Detection of high frequency sound waves in the air
	-Homoptera: <i>Cicadidae</i> <i>Diptera</i>	Metathorax and base of abdomen	Air-borne sound
	-Lepidoptera: <i>Noctuoidea</i> <i>Pyralidina</i> <i>Geometroidea</i> except <i>Axiidae</i>	Metathorax Abdomen 1st or 2nd segment abdomen 7th segment abdomen	Air-borne sound
	-Heteroptera: <i>Corixidae</i> <i>Notonectidae</i> <i>Pleidae</i> <i>Nepidae</i> <i>Naucoridae</i>	Metathorax Metathorax Metathorax Metathorax Metathorax	Water-borne sound, perhaps air-borne as well
E. Sub-genaal organ	-Orthoptera -Plecoptera -Lepidoptera -Hymenoptera -Hemiptera	Commonly the proximal region of the tibia of all legs	Vibration of the substrate

consists of chirps of four to five sound pulses (Figure 1A) that are repeated at 2-3 times per second. Female crickets are attracted by this calling song and walk or fly towards singing males (Figure 1B). This acoustic orientation is called phonotaxis (Doherty, 1985; Hedwig, 2006; Popov & Shuvalov, 1977).

Phonotactic behaviour can be studied by playing computer generated artificial calling songs to a female cricket walking on a trackball. This method allows a highly precise measure of the female walking speed and direction towards a sound pattern (Doherty, 1991; Hedwig & Poulet, 2004, 2005). Song pattern, frequency, and intensity are parameters that can be tested in order to identify the species-specific female preferences for a calling song.

CONCLUSIONS

Insects are highly acoustic animals that have fascinated nature scientists since many centuries.

Insects, as small living species in large ecosystems, require specific methods of communication to overcome the relatively large distances separating individuals from potential mates. To overcome this problem, insects have evolved behavioural strategies and communication systems, largely visual, chemical or acoustical, to insure effective mate finding. Many groups of insects have specialised mechanisms of sound production and hearing organs, which are used in acoustic communication within the same species.

The acoustic signals that the insects produce can be associated with insect behaviours, such as mate attraction, courtship, and territorial behaviour. Interestingly, sound can be used not only for communication within the same species, but also between different species. This interspecific behaviour is present in flesh flies who take advantage of acoustic signalling in crickets and cicadas. Guided by acoustic communication signals, these flies identify and localise their singing target, de-

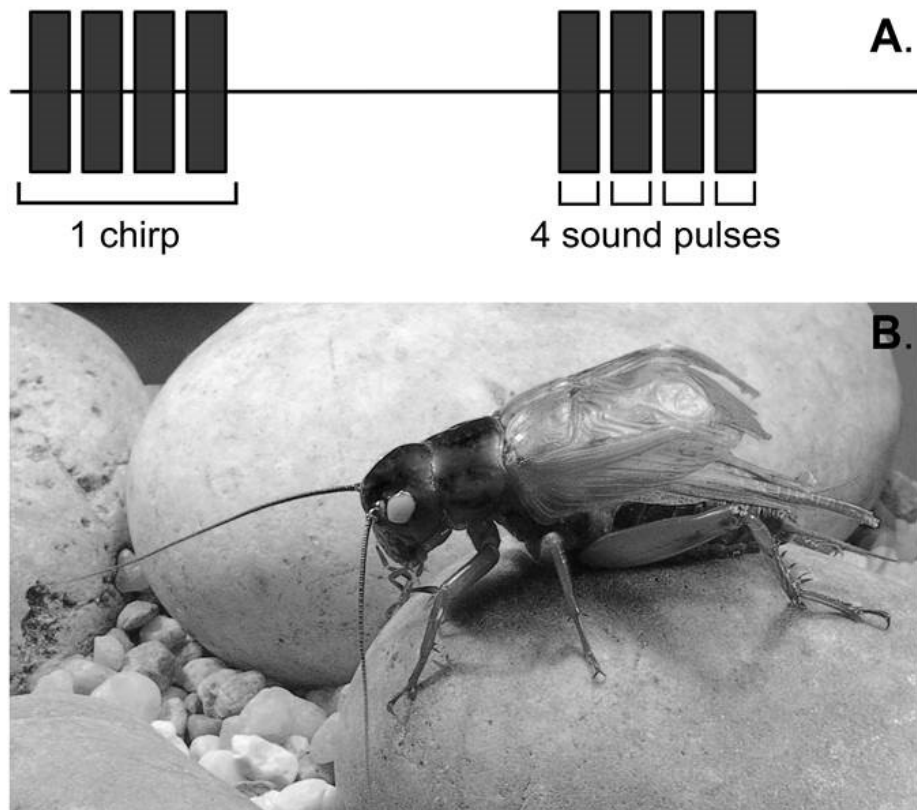


Figure 1. A. Natural calling song of the Mediterranean Field Cricket (*Gryllus bimaculatus*) consisting of chirps of four sound pulses. B. Male Mediterranean Field Cricket singing rubbing his wings against each other. In addition, the ear of the cricket can be visualized as a white spot in his front leg.

positing their larvae on or close the host; larvae then develop as endoparasites, eventually killing the host.

The study of animal communication is a very interesting discipline that not only enlightens us with pure biological knowledge, but also can be useful as a strategy to control insect pests, which affect every year and causes losses of millions of pounds in farming. The communication of animals still has unrevealed mysteries, which future research will help to discover.

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