Chapter 2
Historical Review on Thanatosis with Special Reference to the Work of Fritz Steiniger

Hans-Joachim Pflüger, Ansgar Büschges, and Ulrich Bässler

Abstract Fritz Hermann Steiniger (1908–1985) was among the first to study in detail thanatosis and catalepsy in insects, in particular stick insects and water striders. He looked at these phenomena from a behavioral point of view and tried to unravel underlying neuronal mechanisms. In particular, he examined which kind of sensory stimuli are required to induce such an akinetic condition in insects. His studies also led him to explain and define many of the different terms of akinetic and immobile states which existed at that time and ranged from death feigning, tonic immobility to reaction inhibition, and even animal hypnosis.

Keywords Catalepsy · Flexibilitas cerea · Thanatosis · Tonic immobility · Reflex activation · Central nervous system · Protective reflex

H.-J. Pflüger (✉)
Department Biology, Chemistry, Pharmacy, Institute of Biology, Neurobiology, Freie Universität, Berlin, Germany
e-mail: pflueger@neurobiologie.fu-berlin.de

A. Büschges
Institute of Zoology, University of Cologne (Köln), Köln, Germany
e-mail: ansgar.bueschges@uni-koeln.de

U. Bässler
Stuttgart, Germany

M. Sakai (ed.), *Death-Feigning in Insects*, Entomology Monographs,
https://doi.org/10.1007/978-981-33-6598-8_2

2.1 Introduction

Fritz Steiniger[1] was one of the first authors, who dealt with catalepsy in stick insects[2] in detail. His doctoral thesis was concerned with the phenomenon of catalepsy in stick insects and water striders. He published his main results in *Zeitschrift für Morphologie und Ökologie der Tiere* (*Journal of Morphology and Ecology of Animals*; Steiniger 1932/1933). The phenomenon of "catalepsy," particularly known from stick insects and water striders, is generated by a mechanical stimulus leading to akinesis and "Flexibilitas cerea" ("waxous motility") and according to earlier studies was also believed relating to the protective stick posture (Schleip 1911; Schmidt 1913). Explanations ranged from cataleptic state being the outcome of an "inner motivation" (Schmidt 1913) to being induced by light resulting in a cataleptic posture ("akinesis") whereas movements of these nocturnal animals only occur in darkness. Steiniger gives the following definitions: Akinesis (immobility); Catalepsy, where muscles are still with a tone; Animal Hypnosis (immobility), increasing sensory thresholds, painless state, no correction of postural displacement. After Heymons and v. Lengerken (1926) the opposite to hypnosis is thanatosis, the latter being an active reaction of the animal to avoid predation. What is a cataleptic state in the stick insect? A passively displaced leg stays apparently motionless in this new posture but in fact returns very slowly to the previous set point. The return motion is so slow that animals and humans alike will not notice it. Bässler vividly compared cataleptic movements of the stick insect with the velocity of the hour hand of a watch (Bässler 1983).

[1] Fritz Steiniger (1908 to 1985) was a scientist during politically difficult times in Germany. He did his doctoral studies at the University of Greifswald with Prof. Günther Just. He remained there as a private docent and later, in 1945, was promoted to apl-Professor (extraordinary professor). He seemed to have been very close to his supervisor as Steiniger and Just made similar career decisions and took similar career paths. Steiniger was a member of the NSDAP (National Sozialistische Deutsche Arbeiter Partei, National Socialist German Workers' Party, commonly known as the Nazi-party) and chose to become a civil servant like his former supervisor Just. During this period, he served in various functions in the Reichskommissariat Ostland (Administration of Eastern provinces) that comprised tasks like "pest control and racial policy." In fact, Steiniger and Just worked in the field of hereditary science and anthropology in the most prominent institute in Berlin. The work of this institute was devoted to the scientific justification of the racial policies of the Nazi-regime. Judged from today's perspective this was a task that certainly would have resulted in such a person not being allowed to continue with his career after the outcome of the second world war and the atrocities of the Nazi-regime. It should, however, also be noted here that reports exist, that Steiniger had rescued individual Jews. This may have aided him in continuing with his career after the war as a civil servant. Finally, he lectured at the Tierärztliche Hochschule Hannover (University of Veterinary Science). For his former supervisor Just, this clearance took longer, but in the end, he became a professor at the University of Tübingen after the war.

[2] Many of the experiments cited in the following article have been performed in the stick insect *Carausius morosus*. This species may be called a laboratory animal, because today it only lives in laboratories. All cultured *Carausius morosus* are descendants of a few animals that were found 1897 in India (Leuzinger et al. 1926). Since *Carausius morosus* has obligatory parthenogenesis, all animals are females which exclusively propagate by parthenogenesis. This was perhaps the reason, why it was kept in private houses hundred years ago, because children would not ask "how descendants are made.".

2.2 Which Kind of Stimuli Induce or Abolish the Cataleptic State?

Light influences a cataleptic state and the stick posture and, therefore, a circadian rhythm is thought to underlie these states. It is also noted that stick insects have two periods of feeding activity: one after sunset and the other before sunrise. Interestingly, approx. 10% of tested animals also reveal catalepsy during a quiescent resting period around midnight. A behavioral condition abolishing a cataleptic state is hunger and corresponding to this, the presentation of food odors yields the same result. Strong mechanosensory stimuli, for example, to antennae or abdomen, also abolish the cataleptic state and induce escape movements. However, animals show great variability in their responses to mechanical stimuli and in as much as they induce or abolish a cataleptic state. However, Steiniger dismisses suggestions by Rabaud (1919) who made a difference between induced and spontaneous catalepsy and described the latter as related to sleep. The cataleptic state is also influenced by the age of the animals with young animals moving much more than old animals. This may suggest that the cataleptic state is "not yet fully" developed. However, Steiniger notes that nymphs are sensitive to light like adults and that they also have a protective stick posture. Steiniger also mentions that the cataleptic state is accompanied by analgesic conditions as in deep catalepsy a very high threshold to nociception seems to exist.

2.3 Localization of "Center of Cataleptic State"

The cataleptic state is associated with the central nervous system as destruction of the cerebral ganglion ("brain") completely abolishes the cataleptic state. Similar observations were already made by previous authors like Schmidt (1913) and Reisinger (1928). Schmidt (1913) cut both connectives between the first and second thoracic segment and could induce catalepsy only in the prothoracic leg which still had a connection to the cerebral ganglion. Reisinger (1928) however found that the severed posterior part had still the ability to show catalepsy which was not observed in Steiniger's experiments and therefore, he agrees to the findings of Schmidt. Without a cerebral ganglion (decerebrated animals), the gnathal ganglia (former suboesophageal ganglion) are not capable to induce a cataleptic state (Reisinger 1928). Within the cerebral ganglion the most important area is the Central Complex (CC), as an intact CC is necessary for the cataleptic state (Steiniger 1932/1933). Steiniger suggests that the state of catalepsy may vary in its intensity with the deepest cataleptic state being the stick posture and the weakest cataleptic state being "full" movement capability. In this view all transitional states are possible, and the actual degree of catalepsy depends on how all external and internal influences (stimuli) contribute to it. Thus, catalepsy is the net result of "catalepsy-promoting and catalepsy-inhibiting" influences. Very similar conclusions were found for the other

insects, water striders, which show similar behavioral conditions of catalepsy with the deepest cataleptic state corresponding to the animals taking a protective posture spontaneously. As most water striders touch the underground with their ventral side this was also considered as Thigmotaxis. In the cataleptic state water striders do not react to optical stimuli which they usually do. In addition, cold temperatures seem to favor the cataleptic state in water striders.

2.4 The Ecological Importance of the Cataleptic State

The stick posture was considered as a mimesis and protective against attacks by birds and lizards as was supposed for the conspicuous rocking movements of stick insects (Rupprecht 1971; Pflüger 1977). Both catalepsy and rocking movements serve the task of hiding the insect in its environment from predators.

2.5 Evolutionary Considerations

In comparing stick insects and water striders, Steiniger asks whether catalepsy is an inherent trait of more ancient insects, for example, the common ancestors of stick insects and water striders, or whether it has evolved as a kind of "stick mimicry"? Steiniger mentions that there may have been an increased likelihood of similar mutations in the Orthopterans and Hemipterans due to their common origin and, perhaps, a stick posture was formed under similar selection constraints in Mantids, Phasmids, Acridids, and Hemipterans. He argues that a stick-like body-morphology will favor catalepsy and, dependent on the length of the body, the cataleptic state will increase in intensity as will be a tendency for a mimetic stick posture. This is supported by studies on Proscopiids, an insect group, which has evolved twig mimesis independently of phasmids (Wolf et al. 2001; see below).

2.6 Definitions of Various Animal Immobilities by Steiniger

In his large article on "animal hypnosis," Steiniger (1936, Fig. 2.1) gives the definitions for various aspects discussed at the time. Those are (with some modifications by the authors of this article): "Animal hypnosis" (*Tierische Hypnose*), in analogy to human hypnosis not a valuable term according to Steiniger; Akinesis (*Bewegungslosigkeit*), no movements, motionless; Reflex immobility, immobilization (*Reflektorische Bewegungslosigkeit*), only inducible by an external stimulus to which no reaction (movement) follows; Thanatosis, death feigning (*sich totstellen*), protective posture to avoid predation (Steiniger does not like this explanation and completely dismisses it); "Mechanohypnosis," a special case of hypnosis, following

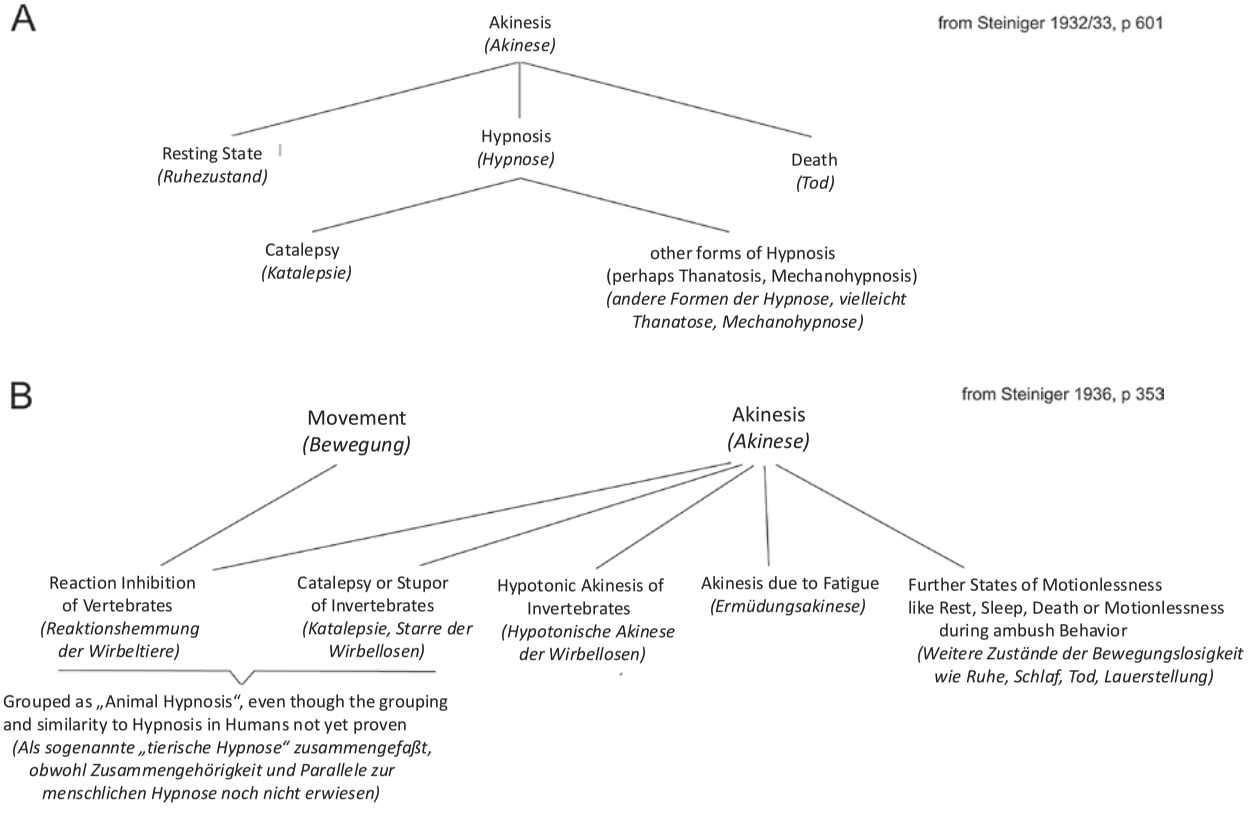

Fig. 2.1 (**a**) Steiniger's attempt to put catalepsy into a context of other forms of motionlessness in his 1932/1933 article in "Zeitschrift für Morphologie und Ökologie der Tiere (*Journal of morphology and ecology of animals*)". His understanding of catalepsy is: akinesis with increased muscle tone and flexibilitas cerea, and additional observation of decreased reflex excitability, analgesy and lacking ability for correcting position in space. (**b**) Extended version of the relationship of terms (and behaviors) discussed in his 1936 article in" Ergebnisse der Biologie (*Results in Biology*)"

a mechanical stimulus a movement reaction is lacking; Reaction-inhibition of vertebrates (*Reaktionshemmung*), exertion of movement is prevented (this is what Steiniger favors to the term hypnosis); Cataplexy (*Schreckstarre*; Preyer 1878, cited in Steiniger 1936): equivalent to stupor (daze) (as a result of fear, "Angst"), Catalepsy (*Katalepsie*); here defined as a particular state of the musculature leading to *flexibilitas cerea (wächserne Biegsamkeit)*, Analgesia (*Analgesie*); absent feeling of pain during normally painful actions (in the state of "hypnosis" also reduced pain sensation); Hypnotic akinesis (*Hypnotische Akinese*), muscle tone more relaxed than during catalepsy (but rather weak definition as differences between vertebrates and invertebrates are not well explained); Stupor (*Starre*), a result of many different conditions such as tetanus, toxins, death (rigor mortis), or cataleptic conditions (?); Akinesis due to fatigue (*Ermüdungsakinse*), a particular muscular condition. Tonic reflexes (*Tonische Reflexe*), long lasting (tonic) contractional state of vertebrate musculature.

2.7 Conditions for Inducing Immobility in an Animal

The initiation of the "hypnotic state" is very similar in many different phyla: after the animal is quickly turned on its back it often remains motionless in this posture (but not necessarily). A good example is when a chicken is pushed to the ground and its head stretched and pushed to the ground as well and held for some time, it may remain in this motionless posture for a while. Steiniger mentions that some sensory and motor reactions persist, including picking and vocalization. As some animals close their eyes during this period, some authors have described the inhibition of reaction as related to sleep, and corresponding to this, a black head cover renders many birds motionless. Some authors described the cause of such absence of motion as an instinct released by fear, particularly in squirrels and opossums. In mice and rats immobile postures induced by fear, mainly by the sight of a predator, were named "freezing."

2.8 Problems with the Term "Animal Hypnosis"

Steiniger is very critical as far as the word "hypnosis" is concerned and takes a very cautious approach to the claims of previous authors who suggested to have hypnotized vertebrate animals by fixing their eyes and holding them tightly or forcing them to gaze on a light spot or object. He also reports on horses that apparently were "hypnotized" by special hand movements and eye contact. The best correspondence to human hypnosis should occur in primates and indeed there are corresponding reports. Steiniger concludes, however, that the experiments do not allow to distinguish true hypnosis, in the human sense, from sleep or inhibition of reaction (*Reaktionshemmung*). The latter term is preferred by him. Particularly enlightening

is Steiniger's response to the book of F. Völgyesi on Human and Animal Hypnosis (Völgyesi 1938). In his reply (Steiniger 1940), he clearly makes a difference between people like Völgyesi who look at hypnosis not from a scientific and physiological point of view but rather regard it as unveiling some more mysterious and psychic forces unexplained by natural sciences, and those relying more on science-based explanations. Accordingly, Völgyesi misinterpreted all examples where animals where immobilized by some hypnotic action, often with added ingredients of *charlatanry*, as true hypnosis, although explanations such as reaction inhibition or training of animals could not be excluded and, according to Steiniger, would have been more appropriate. Correctly, Steiniger pointed out that Völgyesi completely misinterpreted the work of Pavlov who looked at nervous systems and behavior from a physiological and exclusively scientific point of view (Pavlov 1926).

References

Bässler U (1983) Neural basis of elementary behavior in stick insects. Springer, Berlin, p 169

Heymons R, Lengerken H (1926) Studien über die Lebenserscheinungen der *Silphini*. Z Morph u Ökol Tiere 6:287–332

Leuzinger H, Wiesmann R, Lehmann FE (1926) Zur Kenntnis der Anatomie und Entwicklungsgeschichte der Stabheuschrecke Carausius morosus Br. G Fischer, Jena

Pawlow (Pavlov) JP (1926) Die höchste Nerventätigkeit (das Verhalten) von Tieren. JF Bergmann, München

Pflüger H-J (1977) The control of the rocking movements of the phasmid Carausius morosus Br. J Comp Physiol A 120:181–202

Preyer W (1878) Die Kataplexie und der thierische Hypnotismus, Slg physiol Abh 2, Reihe H1

Rabaud E (1919) L'immobilisation réflexe et l'activité normale des Arthropodes. Bull biol France et Belg 53:1–149

Reisinger L (1928) Katalepsie der indischen Stabheuschrecke. Biol Zbl 48:162–167

Rupprecht R (1971) Bewegungsmimikry bei Carausius morosus (Phasmida). Experientia 27:1437

Schleip W (1911) Über den Einfluß des Lichtes auf die Färbung von Dixippus und die Frage der Erblichkeit des erworbenen Farbkleides. Biol Zbl 52:151

Schmidt P (1913) Katalepsie bei Phasmiden. Biol Zbl 33:193–207

Steiniger F (1932/1933) Die Erscheinungen der Catalepsie bei Stabheuschrecken und Wasserläufern *(The phenomena of catalepsy in stick insects and water striders)*. Z Morph Ökol Tiere 26:591–708

Steiniger F (1936) Die Biologie der sog. "Tierischen Hypnose" (Biology of the so-called "animal hypnosis"). Ergeb Biol 13:348–451

Steiniger F (1940) Eine Erwiderung auf das Buch von Franz Völgyesi, Menschen- und Tierhypnose (A reply to the book of Franz Völgyesi, human and animal hypnosis). Z für Tierpsychol 4(2):272–280

Völgyesi F (1938) Menschen und Tierhypnose. Orell Füßli, Zürich und Leipzig, p 230

Wolf H, Bässler U, Spiess R, Kittmann R (2001) The femur-tibia control system in a proscopiid (Caelifera, Orthoptera): a test for assumptions on the functional basis and evolution of twig mimesis in stick insects. J Exp Biol 204:3815