Preface

The aim of this book is to analyze the behavioral characteristics and the physiological correlates of defense responses in animals within an evolutionary framework, focusing on tonic immobility (TI). Defensive processes, activated in response to threatening stimuli, are phylogenetically extremely old, take precedence over all other ongoing activities, and have both short- and long-term effects on animal fitness.

According to the principles of behavioral neuroscience, an integrative view of ethology and neurophysiology can contribute to revealing the underlying mechanisms of behaviors, shedding light on their function. This approach is of particular interest in the study of TI and allows to distinguish TI from other immobility-related defense responses, such as freezing and restraint-sustained immobility, occurring in natural and laboratory conditions.

Tonic immobility, originally described by Schwenter (1636) and later by Kircher (1646), is a postcontact, innate, immobility response, of an all-or-none character. Among the defensive strategies, TI represents the last antipredator resource occurring in various species, both invertebrates and vertebrates, characterized by a transient motor block.

For TI, we evaluate the response variability according to age, sex, personality, previous experience and species, the critical role of the context and of the releasing stimuli, and the mechanisms underlying its development and maintenance. In particular, the study of TI in mammals has shown that, in guinea pigs, the experience of TI releases analgesic and antiinflammatory mechanisms that persist after TI termination, improving the fitness of lesioned animals.

Experimental findings are presented starting from lower invertebrates to higher vertebrates and, in each chapter, in a chronological order to provide an evolutionary and historical perspective. The initial experimental studies mainly relied on behavioral and comparative approaches, which have later been associated with electrophysiological measures, i.e., EMG, EEG, multiunit neural activity, electrical stimulation and brain lesions, and systemic/local drug administration. More recently, ontogenetic, ecological, ethological, and evolutionary approaches have provided information useful to understand the complexity of the TI response and its relevance to survival with respect to other animal antipredator defense responses. Therefore, the description of the results of different experimental models, when necessary, is preceded by a short presentation of the morphological and functional information essential to critically evaluate the reliability, originality, and relevance of the described findings. In case of contradictory results, we provide a likely interpretation according to the experimental setting and the methods of TI induction.

We owe a great debt of gratitude to the early investigators who studied TI in different animal species and advanced various hypotheses that have later been rigorously tested. The formulation of the original hypothesis was frequently associated with the indication of TI by different labels according to the presumed involved mechanisms. The term "animal hypnosis," for instance, was used by Preyer

(1873, 1878) who advanced the hypothesis that this immobility response represented a fear-innate defense response, a theory that led to the concept that the response involves a fear-related paralysis mechanism (Amstrong, 1942; Gilman and Marcuse, 1949; McGonigal, 1942; Ratner and Thompson, 1960) and the inhibition of protective reflexes (Danilewsky, 1890). This label was later rejected, as TI does not imply mechanisms such as human hypnosis (Amstrong, 1942; Marcuse, 1955; Volberg, 1948; Weitzenhoffer, 1953). In contrast, the hypothesis of a fear-potentiated reaction serving as a defense against predation associated with motor block has been proved (Carli, 1968; Gallup, 1977). Darwin (1884) suggested that tonic immobility is due to the effects of fright and the related state of helplessness and that it represents an adaptive response of death simulation in response to a predator attack (Darwin, 1900). The latter hypothesis led to the introduction of labels such as death feigning, playing dead, playing possum, totstellung, and thanatosis, which were rejected for the underlying anthropomorphic interpretation (Gilman and Marcuse, 1949; Weitzenhoffer, 1953). Steiniger (1936) explained tonic immobility as an instinctive form of reflex inhibition. Heubel (1877) originally suggested a sleep mechanism that was further elaborated by Pavlov (1955), who postulated a cortical inhibitory mechanism released by both intense stimuli elicited by the predator and repeated, monotonous stimuli (Hoagland, 1927; Holmes, 1906). Finally, Mangold (1914) concluded that an insensitivity anesthetic/analgesic mechanism occurred during TI, as various surgical interventions in different animal species could be performed without any pain sign. This hypothesis has been proved in rabbits (Carli, 1975) and in guinea pigs (Bassi et al., 2018; Leite-Panissi et al., 2001). The labels "death feigning" and "thanatosis" are still used, but in this book, we adopt the label "tonic immobility" supported by Hoagland (1928) and not referring to the underlying mechanisms.

Among the books dealing with TI, *Hypnosis of Man and Animals* (1966)—written by the Hungarian neurologist Ferenc Andras Volgyesi who is known for the hypnosis theory of reversible vasomotor decerebration—discusses most of the fundamental papers published at that time. A more recent book titled *The Impossible Escape: Studies on the Tonic Immobility in Animals from a Comparative Psychology Perspective* (2012) by Carlo Alfredo Clerici and Laura Veneroni has presented a short review of the old and recent papers on TI in animals and of the analogy between the TI mechanisms in animals and the traumatic and dissociative mechanisms in humans. The most influential reviews in the field of tonic immobility were published by Ratner (1967) and by the contributors of the special issue of *The Psychological Record*, "Animal hypnosis: research and theory" (Crawford and Prestrude, 1977). In recent years, two highly stimulating reviews have been published: "Thanatosis" by Rogers and Simpson (2014) and "A review of thanatosis (death feigning) as an anti-predator behaviour" by Humphreys and Ruxton (2018). Finally, Sakay has recently published a monograph titled *Death-Feigning in Insects* (Springer Nature Singapore Pte Ltd. 2021), describing the most recent findings on TI in insects.

This book should attract the interest of young scientists at PhD or postdoctoral levels and tutors and teachers in the field of behavioral neuroscience, as it provides

an updated and comprehensive view on tonic immobility and its mechanisms within the evolutionary framework of animals' defensive system.

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