Tonic Immobility as an Evolved Predator Defense: Implications for Sexual Assault Survivors

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This article reviews research concerning the possible relationship between tonic immobility (TI) and human reactions to sexual assault. This review includes a description of the characteristic features of TI and a discussion of the most widely accepted theoretical explanation for TI. The possibility that humans may exhibit TI is explored and conditions that might elicit TI in humans are identified. In particular, we focus on TI in the context of sexual assault, because this form of trauma often involves elements that are necessary for the induction of TI in nonhuman animals, namely, fear and perceived physical restraint. The important similarities and differences in how TI manifests in humans and nonhuman animals are highlighted, future research directions are offered, and clinical implications are suggested.

Key words: **freezing, PTSD, rape, rape-induced paralysis, sexual assault, tonic immobility, trauma.** ***[Clin Psychol Sci Prac 15: 74–90, 2008]***

It is well documented (see Gallup, 1977) that nonhuman animals exhibit a set of unconditioned responses, such as temporary gross motor inhibition and hypertonicity, when exposed to mortal threat and/or physical restraint (i.e., capture or entrapment by a predator). Psychologists, psychiatrists, zoologists, neurologists, and even theologians have studied this reflexive response set, known collectively as tonic immobility (TI), for more than three centuries (Maser & Gallup, 1977). TI can be elicited in a wide range of vertebrates and invertebrates (Hennig, 1978; Holcombe, Sterman, Goodman, & Fairchild, 1979).

This article describes the nature and phenomenology of TI, naturalistic and experimental conditions known to induce it, and what is known about the correlates of the response. In so doing, we outline a widely accepted theoretical account of TI, known as the fear hypothesis, and show how this model integrates naturalistic and experimental findings across several levels of analysis. The remainder of the article extends this analysis to humans, with specific attention to the relation between sexual assault and TI. As will be seen, most human sexual assaults entail the necessary conditions for the induction of TI in nonhuman species. Indeed, a substantial number of sexual assault survivors report peritraumatic experiences that bear a striking resemblance to TI as observed in nonhuman species. We conclude by highlighting several distinctions between TI in humans and in nonhuman animals and suggest future directions for research in this area.

WHAT IS TONIC IMMOBILITY?

Animals progress through a series of defensive reflexes, known collectively as the defense cascade (see Figure 1), in response to increasing proximity of a predator (Ratner, 1967).

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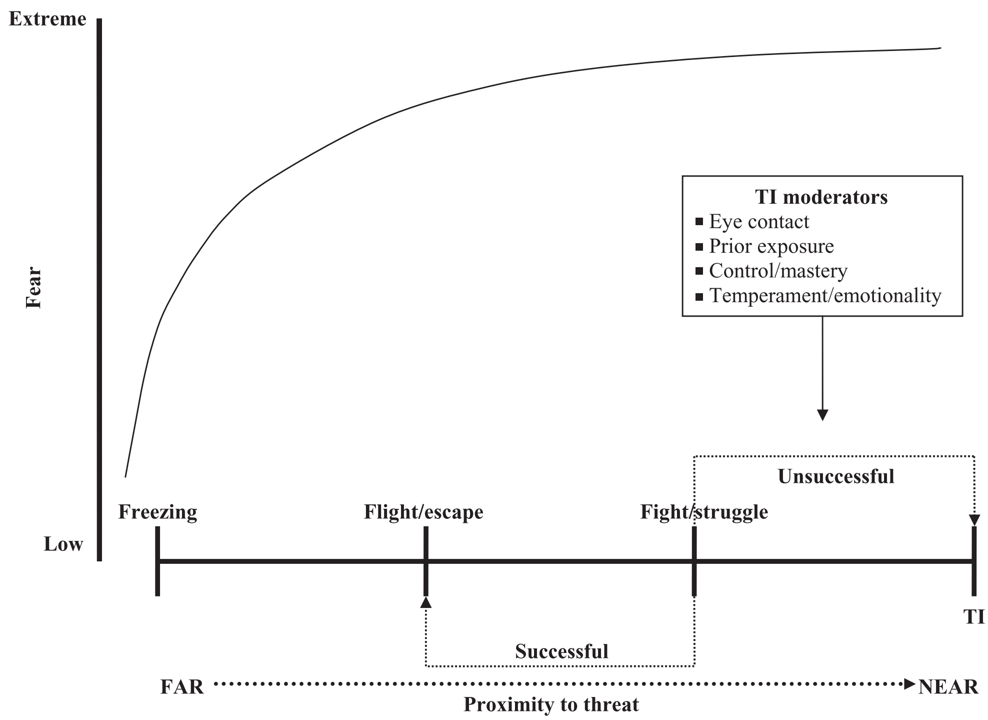

Figure 1. The defense cascade as a function of proximity to threat and fear.

In the *preencounter* stage of the defense cascade, predators have yet to be encountered. Thus, target-specific defense behavior is not yet engaged and appetitive motivation may be simultaneously present. In the *encounter* stage, a predator has been detected and the immediate response is for the prey animal to cease all movement (freeze). Additional responses during this stage include focused attention, sustained cardiac deceleration, defensive analgesia, and potentiated startle. These responses orient the animal toward potential threat and prepare it for action. Freezing also minimizes detection as many predators are highly dependent on movement for prey identification (see Gallup, 1977).

Continued approach by the predator sets in motion a sequence of active defensive postures (e.g., flight or fight) that characterize the *postencounter*, or *circa strike*, stage. Here, most prey will first attempt to escape. When escape is not possible or thwarted (as indicated by tactile contact with a predator), a prey animal will subsequently fight or resist. Clear evidence that the organism has changed to a defensive posture is first seen in the startle reflex response, a response that is often potentiated during this stage, coupled with rapid acceleration in heart rate and electrodermal activity. These behavioral action tendencies are associated with the multicomponent emotional response known as fear (LeDoux, 2000).

Unsuccessful escape or resistance typically results in the prey entering a state of TI. The most obvious feature of TI is profound but reversible physical immobility and muscular rigidity. This immobilized state includes a sustained and largely involuntary pattern of neuromuscular activity (i.e., cataleptic–catatonic) and sympathetic and parasympathetic responses. Additional characteristics of the response include intermittent periods of eye closure, fixed, unfocused gaze or stare, Parkinsonian-like tremors in the extremities, suppressed vocal behavior, analgesia, and waxy flexibility (Gallup, 1974a; Gallup & Rager, 1996).

Although sometimes confused, TI is very different from the freezing behavior seen earlier in the encounter stage of the defensive reflex (Marks, 1987; Ratner, 1967). Early encounter stage freezing is associated with increased responsivity to stimuli, an alert posture, and volitional action tendencies (Marks, 1987), whereas TI involves a catatonic-like motionless posture and unresponsiveness to painful stimulation (Gallup & Rager, 1996; Ratner, 1967). Moreover, TI is different from learned helplessness (Maier & Seligman, 1976; Overmier & Seligman, 1967). TI is an unlearned response in which animals are unable to locomote, regardless of the opportunity to do so. In contrast, learned helplessness is a learned response that usually requires several trials of inescapable aversive stimulation. In learned helplessness, there is no evidence that the animal is unable to locomote, but rather it learns that action is effective in terminating the aversive stimulus.

Tonic immobility demonstrates an abrupt onset, subsequent to fighting or struggling. Termination is also abrupt and followed by renewed struggle or attempts to escape (Ratner & Thompson, 1960). Immobility can last from a few seconds to many hours, depending on the species and circumstances (Gallup, 1977), and can be terminated in response to salient visual or auditory cues (e.g., a sudden, loud noise; Gallup & Rager, 1996; Hatton & Thompson, 1975; Ratner, 1958). In animals that are immobilized on their back or side, the righting response and supporting reflexes are absent (Klemm, 1971).

Evidence suggests that TI is not associated with disruptions in memory or consciousness. In fact, during TI, memory for the eliciting event remains intact (Woodruff, 1977) and organisms, although unable to resist or flee, are actively processing features of the event and the environment (Gallup, Rosen, & Brown, 1972; Klemm, 1971; Richardson, Schumaker, & Harvey, 1977; Sigman & Prestrude, 1981).

Studies also have shown that learning is not disrupted during TI. Animals conditioned in a state of TI perform as well as, if not better than, animals conditioned in a normal volitional state (Gallup, Boren, Suarez, Wallnau, & Gagliardi, 1980). Results from two experiments also provide evidence of both retrieval and extinction of previously learned associations during TI (Gallup et al., 1980). These findings suggest that, while the efferent pathways are inhibited during an episode of TI, the afferent pathways and central processing capabilities remain intact. In other words, although the animal may appear dead or unresponsive to exteroceptive stimuli, internally, the animal is highly alert. Several electromyogram studies have shown phasic changes in muscle hypertonicity during TI (e.g., Klemm, 1977).

For some time, TI has been conceptualized as an evolutionarily adaptive survival strategy. Not only does TI make prey less visible, but it also appears to function as a potent inhibitor of aggression in predators, often leading predators to abort attack–kill responses (e.g., Herzog & Burghardt, 1974). Moreover, freezing by prey animals may serve a signaling and decoy function, allowing conspecifics a better chance for escape. Loss of blood pressure during TI may also help prevent bleeding when injured. An immobile prey animal is, in summary, less likely to be attacked, and if attacked, it is less likely to be killed and eaten, thus increasing its chances of escape and reproduction (Ewell & Cullen, 1981; Marks, 1987; Sargeant & Eberhardt, 1975; Thompson et al., 1981).

Tonic immobility has been documented in a large number of different species from most representative taxonomic groups, such as insects, crustaceans, fish, amphibians, reptiles, birds, and rodents and other mammals. While chickens, rats, and rabbits have been widely used in laboratory studies of TI (Gallup, 1974a), there are documented instances of TI in a variety of other mammals, including pigs (Andersen, Boe, Foerevik, Janczak, & Bakken, 2000), sheep (Gelez, Archer, Chesneau, Lindsay, & Fabre-Nys, 2004), goats (Moore & Amstey, 1962), dogs (Reese, Newton, & Angel, 1982), and primates (Hennig, 1978).

Induction of the Tonic Immobility Response

In naturalistic settings, TI is elicited by extended physical restraint and intense fear (i.e., capture by a predator). Similarly, laboratory procedures that involve restraint and arouse considerable fear can elicit the TI response (Gallup, Nash, Donegan, & McClure, 1971). In experimental situations, TI is most frequently induced by suddenly inverting the animal, so that it is either on its back or side, followed by the application of restraint in that position until the animal stops struggling (e.g., Gallup, 1977; Gallup & Rager, 1996; Klemm, 1971). Continued immobility following the withdrawal of physical restraint is taken as a behavioral indicator of TI. Such procedures model physical contact and subsequent immobilization seen following predatory attack in the wild (Gallup & Rager, 1996).

It should be noted that inversion is not necessary to induce TI. Studies show that TI may be induced using restraint alone (e.g., Crawford, 1977; Ratner, 1967). Nonetheless, many researchers use inversion to induce TI, because it provides a straightforward means to assess termination of the response by the occurrence of the righting reflex (i.e., turning right side up; for example, Gallup, 1974a, 1977). Furthermore, TI can be induced in some species (e.g., opossum, hognose snake) without the application of tactile pressure, leading Ratner (1967) to suggest that it is the perception of entrapment, with or without physical restraint, which is central to the evocation of TI. Put simply, circumstances that induce extreme fear and prevent the powerful action tendency to escape may function to evoke TI (see Figure 1).

Habituation, Sensitization, and Conditioning of Tonic Immobility

Numerous studies have shown that the repeated elicitation of TI leads to habituation and the eventual loss of the response, and in most species, habituation occurs across repeated immobility trials with long intertrial intervals (e.g., Nash & Gallup, 1976). Habituation also proceeds faster when immobility is allowed to terminate naturally rather than being induced (Nash & Gallup, 1976). In contrast, massed TI induction trials, characterized by short intertrial intervals, result in sensitization of the response over time (Nash & Gallup, 1976).

One account of the habituation of TI that occurs over repeated testing is reduced fear. As the experimental situation (and the experimenter) becomes more familiar, it is increasingly difficult to induce TI despite employing adequate restraint (e.g., Crawford, 1977; Gallup, 1974a; Gallup & Rager, 1996; Gilman et al., 1950; Jones, 1993; Jones & Waddington, 1993; Nash & Gallup, 1976; Ratner, 1967). This is also the reason why TI is not typically shown by household pets. Yet, for an animal whose TI response has been habituated, application of an aversive stimulus (e.g., electric shock, loud noise, conditioned fear stimuli, and stuffed predatory birds) may produce a reinstatement of TI in response to subsequent restraint (e.g., Gallup, 1974b; Gallup et al., 1971; Gallup, Nash, & Ellison, 1971; Ratner, 1967). This further suggests that both fear and restraint are essential in the elicitation of the TI response.

Characteristics of the physical environment also may either potentiate or antagonize TI. For example, preinduction exposure to predatory contextual cues (e.g., placement in an open field) can prolong the duration of TI (Suarez & Gallup, 1981), as can exposure either to stimuli paired with other aversive stimuli (e.g., foot shock) or more intense fear-inducing conditioned stimuli (Contarino, Baca, Kennelly, & Gold, 2002; Gallup, 1973; Kiernan, Westbrook, & Cranney, 1995). In contrast, the presence of safety cues (e.g., presence of an imprinting stimulus) can shorten the duration of the TI response (Berns & Bell, 1979). Resistance to TI habituation, in turn, is greater in the context of predatory cues and situations where predation is likely (for example, at night; Rovee-Collier, Capatides, Fagen, & Negri, 1983). Similarly, prior exposure to uncontrollable events can potentiate the probability that environmental cues will yield TI under the right circumstances (Rodd, Rosellini, Stock, & Gallup, 1997). Collectively, this work suggests that TI and associated fear-related behaviors can be activated by learned signals for aversive stimulation, including the experience of aversive stimulation itself.

THEORETICAL ACCOUNTS OF TONIC IMMOBILITY

Most early theoretical accounts of TI, such as the animal hypnosis theory (Volygesi, 1966), the disruption of vestibular sensation theory (Hoagland, 1928), the sleep theory (Pavlov, 1927, 1934), and the cerebral inhibition theory (Hoagland, 1928; Pavlov, 1934) have been discredited through empirical research. Recent research regarding the basis, function, and mechanisms underlying the TI response has resulted in the widespread acceptance of a multidimensional model of TI, referred to as the fear hypothesis (FH; Gallup, 1977), which emphasizes the relation between fear and TI. The model stipulates that fear on the part of prey is an integral antecedent condition that modulates susceptibility to and duration of the response.

The FH model has received considerable empirical support, provided by studies that have examined the direct and indirect contribution of fear in relation with TI (Edson & Gallup, 1972; Gallup, 1973, 1974a; Gallup et al., 1970, 1971; Gallup, Cummings, & Nash, 1972; Gallup, Creekmore, & Hill, 1970; Leftwich & May, 1974; Maser, Gallup, & Barnhill, 1973; Nash, Gallup, & McClure, 1970). Research on age-related delays in the emergence of the TI response in avians shows that one cannot induce TI prior to the development of the capacity to respond fearfully (e.g., Ratner & Thompson, 1960; Salzen, 1963). TI habituates over repeated testing (e.g., Crawford, 1977; Gallup, 1974a; Ratner, 1967), with genetic differences in susceptibility to and duration of TI correlating with strain differences in emotionality and fear (e.g., Erhard & Mendl, 1999; Erhard et al., 1999; Gallup, Ledbetter, & Maser, 1976). Finally, studies examining the neurobiology underlying TI provide evidence for the role of fear in producing and maintaining the response, as various manipulations designed to alter the level of fear, including lesions of the limbic system, particularly septal lesions and lesions of the amygdala (e.g., Brady & Nauta, 1953; Davies et al., 2002; Woodruff & Lippincott, 1976), administration of tranquilizers (e.g., Gallup, Nash, & Brown, 1971; Maser et al., 1974), and administration of fear-potentiating chemicals such as adrenalin (e.g., Braud & Ginsberg, 1973; Thompson & Jensen, 1979; Thompson & Joseph, 1978; Thompson, Piroch, Fallen, & Hatton, 1973; Thompson, Scuderi, & Boren, 1977) alter susceptibility to and/or duration of the TI response. Collectively, this work shows that actively influencing extent of fear (either up or down) has a substantial effect on TI, either by prolonging or attenuating the response, as well as reducing or increasing the number of inductions necessary to elicit it.

To be clear, according to the FH model (see Gallup, 1974a, 1977), fear is neither the sole cause of nor a sufficient condition for the elicitation of TI. Rather, TI requires restraint or entrapment and fear. Extreme fear without restraint or entrapment is unlikely to result in TI. Likewise, restraint absent fear is unlikely to yield TI. However, in the context of restraint, the magnitude of fear is understood as perhaps the most important antecedent variable affecting the phenomenology of TI. This is why we have portrayed fear intensity as covarying in a somewhat simplified fashion with proximity to threat. As Figure 1 shows, as threat increases, so does fearful responding; as attempts to flee and fight fail, fear reaches its asymptote, thus, making TI likely, although not inevitable.

THE ROLE OF TONIC IMMOBILITY IN HUMANS

Under certain conditions, humans show the cascade of defensive responses similar to those observed among nonhuman species. For example, Barlow, Chorpita, and Turovsky (1996) applied the first three stages (freezing, fleeing, and fighting) of Ratner's (1967) defensive distance theory in conceptualizing psychopathology among persons suffering from anxiety disorders. Similarly, Fanselow (1994) proposed a model of human defensive responding to fearful situations that utilizes the first three stages of Ratner's (1967) defensive distance model. Empirical evidence from psychophysiological research has suggested that this pattern of defensive responding (specifically, the first three stages of Ratner's theory) occurs in humans as stimuli become more threatening or aversive (e.g., Bradley, Codispoti, Cuthbert, & Lang, 2001; Cuthbert, Bradley, & Lang, 1996). In short, humans and nonhuman animals appear to exhibit similar patterns of defensive behavior under certain conditions.

The idea that TI may be exhibited in humans in response to fearful situations involving some degree of perceived (or real) restraint is consistent with anecdotal reports from those who have survived intensely traumatic experiences coupled with some form of perceived restraint (e.g., attacks by wild animals, plane crashes, sexual assaults). Such reports, in turn, often contain reference to a feeling of paralysis at some point during the experience (Burton, 1931; Johnson, 1984). The notion that humans can become frightened to the point of experiencing profound efferent inhibition is so common that the phrases "scared stiff" and "frozen with fear" are widely used when describing human responses to highly fearful situations. TI is thought to be particularly relevant to survivors of rape and other sexual assault.

Tonic Immobility and Sexual Assault

Sexual assault survivors often report losing the ability to move and/or call out during the assault, a phenomenon previously referred to as "rape-induced paralysis" (Burgess & Holmstrom, 1976; Russell, 1974). Burgess and Holmstrom (1976) reported that 37% of rape survivors reported experiencing some paralysis in response to an open-ended question asking how they coped with the experience of being sexually assaulted as it happened. Statements by survivors regarding their sexual assaults, such as "I felt faint, trembling and cold . . . . I went limp" (Burgess & Holmstrom, 1976, p. 416) and "My body went absolutely stiff" (Russell, 1974, p. 233), resemble TI under laboratory and naturalistic conditions. Such statements led Suarez and Gallup (1979) to theorize that anecdotal reports of paralysis and inability to call out during sexual assault might be an expression of TI in humans.

Suarez and Gallup (1979) argued that instances of sexual assault contain some essential parallel features in common with predator–prey relationships, with the assailant being cast in the role of a predator and the victim as the prey. However, in the case of sexual assault the aggressor and victim are members of the same, rather than different, species. TI, in contrast, typically occurs in the context of predator–prey, or interspecific (between species) encounters. Thus, in order to strengthen the case for the parallel between TI and sexual assault, it would be helpful to document intraspecific instances of TI that occur as a consequence of agonistic encounters among members of the same species.

In rats, for instance, there is a well-documented defensive/submissive response to attack by a more dominant rat that shows clear parallels to TI. As an aggressive encounter between two rats becomes more violent, it is common for the victim to roll over and lie motionless on its back as a means of appeasement to reduce the probability of further attack (e.g., Blanchard, Blanchard, Takahashi, & Kelley, 1977). Similar submissive TI-like postures have been noted among dogs and wolves during particularly vicious attacks (Schenkel, 1967), and even tree shrews show such defensive behaviors (Blanchard, Ohl, van Kampen, Blanchard, & Fuchs, 2001).

Still another example that seems particularly relevant to the present model involves the sexual behavior of female rats. In response to courtship and mounting by a male, receptive female rats display what is called lordosis, a behavior that consists of elevating the hind quarters, moving the tail to the side, and assuming an immobile posture that persists for the duration of copulation. As evidence that lordosis may contain a TI component, research has shown that stimulation of the female rat's vaginal cervix facilitates TI in otherwise unsusceptible subjects (Naggar & Komisaruk, 1977). It has also been shown that hormonal treatments that potentiate lordosis enhance TI in rats (Smith, Webster, Van Hartesveldt, & Meyer, 1985).

Sexual assault is a form of trauma that appears to entail virtually all of the salient elements associated with the induction of TI in nonhuman animals, namely, fear, contact, and restraint (cf. Suarez & Gallup, 1979). Additional evidence from retrospective reports suggests that the biobehavioral sequelae to rape-induced paralysis (e.g., changes in body temperature, numbness, analgesia, uncontrollable shaking, suppressed vocal behavior, and vivid recall of details) strongly resemble characteristics known to be associated with TI (Russell, 1974; Schultz, 1975; Suarez & Gallup, 1979). It is not surprising that several researchers and professionals who work with sexual assault survivors recognize the immobility reaction, or "rape-induced paralysis," as a distinct response that frequently occurs during sexual assault (Foa & Rothbaum, 1998; Levine, 1997; Ogden & Minton, 2002; Prentky, Burgess, & Carter, 1986; Ullman & Knight, 1995).

The animal literature suggests that TI would be unlikely during the initial stages of the assault, when victims are likely to experience more general fear and panic and the powerful action tendency to flee or fight (Gallup, 1977). Accordingly, TI ought to be more likely only after several behavioral strategies (i.e., escape, screaming, and fighting back) have failed and general feelings of fear have escalated into extreme fear or panic (see Figure 1). This view leaves open the possibility that individuals may experience fear and panic, but not TI, because they are successful in terminating the assault by either fighting back or escaping from the perpetrator.

Although the adaptive significance of TI in predatory encounters is well established, it is less obvious in survivors of sexual violence. However, research has shown that rapists often react to the actions of their victims in much the same way that many animal predators respond to their prey. Specifically, some rapists require the victim to struggle in order to complete the rape (Burgess & Holmstrom, 1976). Furthermore, some rapist classification systems (e.g., the Massachusetts Treatment Center: Rapist Typology, Revision 3; MTC: R3; Marshall, Laws, & Barbaree, 1990) suggest that rapists may differ in how they respond to active resistance by a victim. For some rapists, victim resistance is likely to induce anger and results in additional physical harm, often brutal and sometimes fatal (Marshall et al., 1990), whereas other rapists are likely to flee rather than fight in response to resistance.

Such issues may help explain reports of individuals escaping rape by fighting back and, by extension, the fact that police and the legal system often search for signs of resistance in classifying an incident as a rape (e.g., Abarbanel, 1986; Rose & Randall, 1982). It is possible that in some cases of sexual assault, TI may abort an attack, and in some instances, decrease the probability of intercourse and the amount of physical injury suffered by the survivor. Here, however, it is important to not confuse adaptive significance with voluntary choice. TI is an unlearned, involuntary response to fear and predation that occurs after all volitional actions have failed. Animals and humans do not choose TI, and in fact TI could be maladaptive when faced with extreme threat. TI is more akin to a hardwired response, a response that can be quite frightening itself.

Empirical Evaluations of Tonic Immobility in Sexual Assault Survivors

To date, there have been surprisingly few empirical studies of TI in sexual assault survivors. Yet, findings gleaned from the handful of studies suggest that TI is more common than one might think, and associated with a range of negative outcomes. Here, we briefly review this work.

In one of the first studies of its type, Galliano, Noble, Travis, and Puechl (1993) examined the prevalence of TI in 35 adult female rape survivors. The women were classified into three groups (immobile, intermediate, and mobile) based on retrospective report paralysis/freezing experienced during the rape (Galliano et al., 1993). Of the sample, 37% reported experiencing complete immobility during the sexual assault, comparable to that reported by Burgess and Holmstrom (1976).

The three groups were then compared in terms of the frequency and severity of specific features of TI that are known to accompany the response in nonhuman animals (e.g., presence of tremors, eye closure, and drop in body temperature). Results demonstrated that biobehavioral accompaniments of TI (i.e., motor inhibition, tremors, eye closure, increased respiration, and reduced core body temperature, or a subjective feeling of coldness) were greater in the immobile group, compared with their mobile and intermediate counterparts. Moreover, the immobile group reported more postassault self-blame and less help-seeking behavior relative to the mobile group. This work suggests that rape-induced paralysis may be a human counterpart to animal TI.

Importantly, the authors based their conclusions on responses to the rape survivors questionnaire (RSQ; Galliano et al., 1993), a brief, 31-item forced choice survey designed to assess sexual assault attitudes and experiences. The RSQ does sample some domains thought to characterize TI, but omits others, namely, the inability to vocalize, feelings of numbness, and characteristics of TI believed to occur in humans (e.g., feelings of fear and panic, memory for the event, fear for life, and dissociative experiences, such as derealization and depersonalization). Furthermore, Galliano et al. (1993) adopted a categorical view of TI by employing arbitrary cutoffs to classify participants into groups. At this time, it remains unclear whether TI is best-represented categorically or dimensionally. Finally, this study did not investigate the possibility that TI might be associated with childhood sexual abuse (CSA). This is important given that CSA is an event in which the individual is likely to experience intense fear and physical restraint/entrapment.

In response to these issues, Heidt, Marx, & Forsyth (2005) examined the prevalence and psychological correlates of TI in clinical (psychiatric inpatients) and nonclinical (college undergraduates) participants who reported a history of CSA. TI was assessed using the Tonic Immobility Scale—Child Abuse Form (TIS-C; Forsyth, Marx, Heidt, Fusé, & Gallup, 2000), a new measure specifically developed to assess the nature and sequela of TI in victims of CSA.

Over 52% of participants reported TI in response to CSA. Furthermore, participants reporting rape and attempted rape were more likely to report TI relative to participants reporting other forms of contact CSA. This finding makes sense when considering that CSA episodes involving rape or attempted rape included greater extent of fear, risk of sustained injury, perceptions of inescapability, and restraint compared with other forms of contact CSA. These features, in turn, parallel the conditions associated with TI in basic animal research.

Additionally, the age of the perpetrator and the perpetrator–victim age difference were both positively correlated with TI severity: older perpetrators and greater age differences between perpetrator and child were both associated with more severe TI. These findings suggest that age-related variables may be a proxy for perceived perpetrator control and power, factors that may increase fear and perceived inability to escape. Finally, CSA-related TI was positively correlated with reports of psychological distress, including depression, anxiety, posttraumatic stress disorder (PTSD), and peritraumatic dissociation. These findings suggest that TI is associated with long-term psychological distress and impairment.

In another recent study of TI in a large sample of adult sexual assault survivors ($n = 88$), Fusé, Forsyth, Marx, Gallup, and Weaver (2007) found that 41.5% of respondents reported significant immobility and 12.5% reported extreme immobility (defined as a TIS score above the 90th percentile). This finding was replicated in a second independent sample of female sexual assault survivors (n = 191), with 41.7% of participants reporting significant immobility during their most recent sexual assault and 10.4% reporting extreme immobility.

Collectively, the studies to date suggest that a substantial number of women with sexual victimization histories as children and adults report experiencing characteristics of the TI response during their assaults. Although one must be mindful that this work is based largely on retrospective self-report, it is interesting that any bias in reporting did not favor culturally sanctioned behaviors (e.g., struggle and resistance) that are often deemed more appropriate responses during sexual assault.

Although rape is one circumstance that has been explicitly discussed as a potential elicitor of TI in humans, there are likely many others, including attack by predators, motor vehicle accidents, military combat, airplane crashes, physical assaults, and even thrill rides (e.g., roller coasters). For example, Johnson (1984) interviewed flight crews involved in serious crashes and documented that crew members frequently encountered otherwise uninjured passengers who appeared frozen and were unable to move from their seats. Anecdotal reports from combat veterans also suggest that high fear circumstances that preclude escape may be sufficient for the induction of TI-like responses (Gallup & Rager, 1996; Solomon & Mikulincer, 2006).

Comparative Evaluation of Nonhuman and Human Expressions of Tonic Immobility

Emerging work suggests several points of similarity between human and nonhuman animals in how they respond when exposed to conditions that involve both extreme fearfulness and restraint. More specifically, reports of feeling paralyzed among CSA and rape survivors resemble the physical immobility observed in laboratory animals following TI induction (Gallup & Rager, 1996). The same is true of survivors' self-report of trembling and shaking and the tremors seen in animals during TI. Feeling unable to call out or scream corresponds to animals' lack of vocalizations, whereas reports of feeling numb may relate to the lack of responsiveness to pain found in animals during TI. Subjective feelings of coldness reported by assault survivors correspond with findings of decreased body temperature in immobile animals. Emotional and cognitive/evaluative responses to sexual assault (e.g., feelings of extreme fear or panic, or fear for one's life) are typically assumed to occur in animals when exposed to cues related to predation (Gallup, 1977).

In cases of rape, as with TI in nonhuman animals, factors affecting the level of fear and amount of restraint experienced by the victim should be predictive of the experience and expression of TI. For example, sexual assaults that are characterized by greater levels of restraint, such as attempted rape and rape, may be associated with increased susceptibility to TI. Moreover, individuals who are sexually assaulted by a stranger and/or in an unfamiliar context may be more likely to exhibit TI or a potentiated TI reaction due to increased levels of fear. This latter proposition is consistent with previous work showing that novel experimental conditions produce greater fear and, thus, increase the likelihood of TI.

More violent sexual assaults involving extensive contact between the victim and perpetrator may also potentiate fear, resulting in increased TI susceptibility. Individuals who consume alcohol or other sedatives may be less likely to exhibit TI in response to an episode of sexual assault, (e.g. assault, perhaps) perhaps due to associated attenuation in the neurobiological mechanisms responsible for potentiated fearful responding. Alternatively, alcohol or other sedatives may not attenuate neural mechanisms responsible for potentiated fear responding, but produce a reduction in other socially instilled inhibitory behaviors. Similarly, genetic differences in emotionality and its expression, particularly the tendency to experience high levels of fear in response to salient stimuli, may be associated with differential susceptibility to TI.

Verbal–Cognitive Domains Influencing Fear and Restraint

Humans differ from nonhuman organisms in one key respect, language and verbal–cognitive relational abilities. This difference has important implications for understanding how humans experience fear as well as perceptions of restraint. For instance, although fear is a primitive emotional response, whether or not organisms experience fear—and more importantly what they do about it—may depend on the perceived meaning or significance of the situation. In other words, the representation and appraisal of circumstances and accompanying emotion is a critical element in determining the strength, expression, and regulation of emotions in humans. In contrast, nonhuman animals have no known means of representing features of their environment or cognitive world, and as a consequence can only act to regulate and respond to the cues that evoke threat and danger. They do not appear to act deliberately or intentionally to regulate their emotional responses (e.g., struggle with fear, suicide to escape pain; see Forsyth, Eifert, & Barrios, 2006).

To account for how humans respond to threat, Foa and Kozak (1986) adopted Lang's (1977) notion of fear as a cognitive structure containing representations of the feared stimuli, fear responses, and the meaning associated with these stimuli and responses. This account suggests that cognition and emotion are inextricably intertwined, that the meanings associated with fearful stimuli and responses affect what humans may perceive as frightening and the magnitude of fear experienced. According to this view, perceptions and judgments of what is frightening in future contexts are determined, in large part, by prior experiences and the perceived outcomes of those experiences (Foa & Kozak, 1986). Consequently, individuals may vary widely in terms of what they perceive as fearful, based simply on the outcome of past experience with a similar stimulus or set of stimuli. These stimuli can be actual situational elements or emotions and thoughts that are reminiscent of earlier experiences that were associated with fear.

There are numerous additional variables that may play a role in determining what humans perceive as fearful, including genetic vulnerabilities (e.g., temperament, neuroticism), coping and attributional styles, perceptions regarding particular elements of the situation (e.g., controllability and predictability), cultural and contextual variables, and family history (see Mineka & Zinbarg, 2006). There are also individual differences in the magnitude of fear experienced given a certain set of circumstances. That is, two people presented with identical situational variables may experience differing levels of fear, based on individual differences in one or more of the aforementioned variables.

Collectively, this work suggests that any conceptualization of fear as a modulating factor in the susceptibility to and duration of TI in humans (see Figure 1) must be predicated on an understanding of the numerous variables that can interact in determining what is frightening for an individual in a particular context. Acknowledging that the conceptualization of fear in humans may be somewhat more complex relative to nonverbal animals does not diminish the role of fear in TI. To date, available evidence suggests that it would be unlikely for humans to experience TI absent a strong fear response.

Perceptions of Restraint, Escape, and Control

Human cognitive–verbal–symbolic representation capabilities also make it possible for humans to construe a wide range of stimuli and contexts as suggestive of restraint or inescapability. For instance, feeling trapped in a sexual encounter may functionally generalize to circumstances that are quite dissimilar from sexual trauma, such as feeling trapped in an elevator or trapped in a relationship. Such stimuli or contextual elements include the presence of a weapon; the apparent size and strength differentials between the perpetrator and victim in cases of violence, psychological intimidation, and threats; verbally transmitted information about the likely consequences of attempts at escape; attributions made regarding predictability and controllability; and the perception of entrapment as a result of the characteristics of the physical surroundings (e.g., novel environment, no visible escape routes). In short, advanced verbal–cognitive capacities can broaden the effects of various contexts and stimuli so as to occasion and influence the perception of restraint and inescapability in humans in ways that go well beyond similarity based on formal stimulus properties of events (e.g., stimulus generalization). In fact, among humans, such perceptions may be even more important than the direct contingencies (e.g., actual physical restraint; Abramson, Seligman, & Teasdale, 1978).

Differential perceptions of predictability and controllability may be strongly influenced by preexisting memory networks, resulting in wide variability in the experience of fear among individuals, given similar situational variables (Abramson et al., 1978; Foa, Zinbarg, & Rothbaum, 1992). Research with nonhuman animals has shown that experiences with uncontrollable and unpredictable aversive events not only produce persistent arousal and increased fear, but they also result in central nervous system opioid-mediated analgesia (a hallmark symptom of TI), enhanced learning of passive avoidance (i.e., avoidance of an aversive event through nonresponding), and impaired learning of active avoidance (i.e., avoidance of an aversive event through emitting a specific response; Foa, Zinbarg, & Rothbaum, 1992; Overmier & Seligman, 1967; Rush, Mineka, & Suomi, 1982; Seligman & Maier, 1967). Additionally, enhanced learning of passive avoidance often persists even when environmental contingencies are altered, such that animals will not attempt to escape when presented with an escapable situation (Seligman & Maier, 1967). With regard to TI, Maser and Gallup (1974) found that animals exposed to uncontrollable shock exhibited TI durations four times longer than those exposed to escapable shock, suggesting that controllability may, in part, moderate susceptibility to, and duration of the TI response.

Thus, individuals who perceive an event as more unpredictable and uncontrollable as a result of situational elements and individual differences (e.g., preexisting memory networks) may be more likely to perceive a situation as inescapable, regardless of environmental contingencies. In some cases, minimal physical contact coupled with extreme fear may be sufficient to induce TI in certain individuals. As such, when discussing TI in humans, it may be appropriate to conceptualize "restraint" broadly to include entrapment and the perception of inescapability coupled with physical contact.

Along these lines, Fusé et al. (2007) found that two cognitive experiences, namely, fear for one's life and feeling detached from oneself (depersonalization), were associated with TI in female survivors of sexual assault. These findings suggest that general fear and panic are insufficient for the induction of TI. The more critical elements were perceived or actual threat to life coupled with circumstances that prevent escape. One obvious problem with this interpretation is that most animals are not thought to be able to distinguish between fear and fear for one's life. This report or appraisal, in turn, may be different than actual threat to one's life. This view is consistent with basic conceptualizations of TI and findings from the animal literature, noting that TI is more probable under conditions of predation and the possibility of harm or death (Gallup, 1977). Thus, extreme fear may be on a separate dimension from immobility, and require the addition of physical restraint or circumstances that function to prevent escape in order to induce TI in humans.

Among humans, depersonalization (but not derealization) may be a by-product, or even a component of TI (Fusé et al., 2007). For instance, a sense of "self" detachment may occur during TI, in part, because individuals are attending to the external environment more sharply. Animals in TI remain acutely aware of their surroundings, carefully scanning the environment for signals indicating the possibility for successful escape (Gallup, 1977). Although research clearly shows that dissociation can occur apart from immobility, it is unclear whether TI increases the likelihood of dissociative experiences. Fusé et al. (2007) and Heidt et al. (2005) provided evidence that symptoms of dissociation were associated with TI. Although the exact relation between TI and dissociation is unclear, a number of researchers have demonstrated that peritraumatic dissociation is a potent risk factor for PTSD (e.g., Ozer, Best, Lipsey, & Weiss, 2003). The problem of directionality remains an issue that prospective strategies may help to resolve. These and other cognitive sequelae to TI are difficult to study in nonhuman species.

Tonic Immobility and Psychopathology

Results from the Heidt et al. (2005) study indicated that TI occurring in response to an episode of CSA was associated with long-term psychological distress; yet, the mechanism by which this experience affects psychological functioning is unclear. One possibility, first suggested by Suarez and Gallup (1979), is that TI may contribute to feelings of self-blame and guilt for not having done more to prevent or limit the attack (e.g., Metzger, 1976). This possibility was corroborated by Mezey and Taylor (1988), who found that women who felt paralyzed during rape were more likely to self-blame and report higher levels of guilt than women who did not feel paralyzed during an assault. Self-blame and guilt, in turn, have been shown to be related to poorer recovery from sexual assault (Frazier, 1990; Ullman, 1997).

Self-blaming is often compounded by attributions of responsibility made by those around the victim (e.g., family, friends, and the legal system), such as "Why didn't you fight back?" or "You obviously asked for this." In support of this view, McCaul, Veltum, Boyechko, and Crawford (1990) compared attributions of blame in college students across nine rape scenarios. The scenarios differed in terms of extent of early signs of danger and active resistance (e.g., fighting back). Results demonstrated that participants were more likely to blame the assailant when the victim exhibited more active resistance, whereas victims were more likely to be blamed when there was little evidence of active struggle (McCaul et al., 1990). Consequently, TI assault survivors may experience less emotional and social support for not doing more to prevent or escape from the assailant. Poor-quality support, in turn, may place such individuals at greater risk for more severe PTSD symptomatology (Zoellner, Foa, & Brigidi, 1999). These and other unresolved issues demand more serious consideration, as they will likely inform the psychological treatment of sexual assault survivors, as well as legal and social policy decisions in the arena of sexual victimization.

Others have suggested that the freezing that occurs during TI may itself promote the emergence of PTSD and other posttraumatic sequelae (e.g., Levine, 1997; Ogden & Minton, 2002). Specifically, these authors suggest that the TI response thwarts other more active and adaptive defensive responses from occurring during and after trauma. These failed responses, along with the inability to modulate arousal, can be sources of distressing bodily experiences and ultimately lead to trauma symptoms.

Importantly, the conditions that elicit TI (restraint and high levels of fear) are the same conditions that have been found to be risk factors for PTSD following sexual trauma (Ozer et al., 2003). Given that restraint and fear are the antecedent conditions necessary to produce TI, Bovin et al. (2007) evaluated whether TI mediated for the relation between fear, restraint, and PTSD symptomatology. Results showed that the initial conditions for mediation were met. When all variables were entered into the model, TI fully mediated the relation between restraint and PTSD symptom severity and partially mediated the relation between fear and PTSD symptom severity. These preliminary findings suggest that TI may be an important causal factor in determining whether or not survivors develop PTSD and other psychopathology in the wake of a sexual assault. Specifically, the TI experience itself might be so aversive and frightening that having such an experience promotes the onset of posttraumatic stress symptomatology. This possibility is consistent with other data showing that 47% of a sample of rape survivors who experienced TI symptoms reported these symptoms to be extremely frightening. Importantly, given the retrospective nature of these data, the exact relation between TI and PTSD remains unclear. An alternate possibility is that TI and PTSD are by-products of the same experiences, namely, changes in limbic system functions and serotonin and neuroendocrine levels (Maser, Gallup, & Hicks, 1975; Moskowitz, 2004; Shin, Rauch, & Pitman, 2005; Yehuda, 2002) that may occur during, and as a result of, sexual assault. Likewise, both PTSD and TI have been associated with particular genetic predispositions (e.g., Jones, Mills, & Faure, 1991; McGraw & Klemm, 1973; Segman & Shalev, 2003), and it is possible that the same genetic predisposition may be responsible for the elicitation of TI and subsequent psychopathology.

CONCLUSIONS AND FUTURE DIRECTIONS

The accumulation of nearly 400 years of research has established TI as a widely exhibited and well-understood defensive reaction. The behavioral characteristics of the response have been examined in numerous species distributed throughout the phylogenetic scale and, with few exceptions, are consistent across the various species studied. Similarly, the relative consistency of the response across species is apparent in empirical investigations, demonstrating that comparable induction conditions reliably elicit the response, that habituation occurs across trials, and that central processing, learning, and memory remain intact during TI.

To date, the FH represents the most comprehensive and parsimonious account of TI and provides an explanatory framework that can be applied at several levels of analysis, including developmental, genetic, behavioral, neurological, chemical, and ethological. Yet, fear alone is not a sufficient condition for TI and, thus, a complex, multidimensional model incorporating psychobiological and experiential variables occurring before, during, and following TI in humans is warranted. Although the possibility that humans may exhibit TI has been suggested since the late 1970s, little research has examined this issue. To date, most studies of human TI have utilized retrospective self-report methodologies assessing the prevalence and correlates of rape-induced paralysis. The absence of experimental work examining TI in humans, including its relation with other forms of trauma beyond sexual assault, limits the ability to draw firm conclusions. We speculate that TI ought to be moderated and expressed somewhat differently in humans relative to nonverbal organisms. This notion fits with what we know about the role of human verbal–cognitive activity in regulating the experience and expression of emotional responses. More pointedly, everything we know from the animal and human literature to date suggests that the TI response itself may be traumatic.

Investigations of survivor behavior during rape and sexual assault tend to focus on psychological responses (i.e., telling oneself to remain calm) or overt behaviors (i.e., fighting back or screaming), and particularly how these reactions influence postassault adjustment. TI, however, is a response to trauma that requires consideration of (a) the circumstances of the trauma, and (b) how those conditions affect survivor reactions. We need to understand TI in humans, particularly the psychophysiological differences between survivors who experience TI and those who do not. Likewise, research evaluating TI during other traumatic events should clarify whether TI is specific to sexual assault conditions or occurs when the powerful action tendency to fight or escape is unsuccessful. TI would be expected to occur in high-threat situations involving restraint or circumstances that preclude escape more generally, not just during sexual assault (Gallup, 1974b).

It is necessary to explore the extent to which humans and nonhuman animals differ with respect to certain important characteristics of the TI experience. For example, it would be important to know whether, among humans, TI serves an adaptive function during sexual victimization and other forms of trauma. Might such a response under those conditions reduce the likelihood that a perpetrator will complete a sexual assault? Might it reduce the likelihood that a perpetrator will seriously injure an individual during a sexual assault? Another important question concerns the nature of TI itself. Certainly, the presence of TI among nonhuman animals is unambiguous, as the animal is either in TI or not, as defined by the lack of the righting response. However, for clinical purposes, it may matter less if TI among humans is an "all or none" phenomenon, as the intensity of the TI response among humans may be an important factor in the onset and maintenance of posttrauma psychopathology.

Other important unanswered questions about TI among humans concern the extent to which fear and restraint are needed to induce the response, whether TI habituates after repeated trauma, and whether TI can be reinstated after a subsequent aversive experience. Further research on human TI should also examine individual differences in the susceptibility to, and expression of, the response as a function of various biological, psychological, and social variables. Also, it is important to know whether or not the propensities to experience TI change as humans develop verbally and cognitively. These and other unresolved questions point to the need for future research to better understand the nature and phenomenology of TI across the trauma spectrum. Such research ought to help clarify important boundary conditions that may moderate human TI expression, thus informing the development of an explanatory framework for human TI. It is also important to disentangle the unique contribution of TI to the development of short- and long-term posttrauma difficulties as well as the mechanism(s) through which TI may promote poor posttrauma functioning.

The presence of an immobility reaction during a sexual assault may have important implications for treatment of postassault psychopathology. For example, like peritraumatic dissociation (e.g., Griffin, Resick, & Mechanic, 1997; Lanius et al., 2002), TI may be associated with suppression of autonomic arousal to trauma reminders. Such a possibility is consistent with findings from studies with nonhuman animals that have shown that TI is associated with decreased autonomic arousal (e.g., chickens—Gentle, Jones, & Wooley, 1989; Nash, Gallup, & Czech, 1976—and pointer dogs—Reese, Newton, & Angel, 1982). Cognitive-behavioral treatments for PTSD generally aim to decrease physiological arousal to trauma-related cues through strategies such as exposure, relaxation, and cognitive restructuring (Foa & Rothbaum, 1998). Although these strategies may prove effective in many cases of PTSD, they may not be appropriate for cases of PTSD in which the client responded to the trauma with reduced physiologic arousal and motor inhibition (such as in TI), as well as suppressed arousal to subsequent trauma reminders. Indeed, some have argued that those who respond to trauma reminders with blunted physiological responding may not be the best candidates for exposure-based therapies (e.g., Hembree, Rauch, & Foa, 2003).

Perhaps treatment aimed at increasing arousal to trauma cues would be more appropriate for clients who experienced TI coupled with sexual assault. This alternative is consistent with other already existing treatment approaches for trauma survivors that emphasize experiencing the somatic sequence of an active defensive response through the tracking of physical sensations and increasing arousal (e.g., Levine, 1997; Ogden & Minton, 2002). Importantly, these alternative treatment approaches have not yet been empirically established through independent replications.

Finally, there is a need for greater public education. Widespread acknowledgment and understanding of the TI response may lead to an increased capacity for assault survivors to feel more comfortable disclosing aspects of their experience (specifically, the inability to fight back), and may also foster a more supportive environment that is sensitive to this dimension of trauma response and its consequences. In this context, it is also critical for therapists working with sexual assault survivors to include assessment of TI as part of their clinical practice, recognizing that this response is common, associated with negative outcomes, and likely will impact outcomes in those seeking professional help for their sexual assault–related difficulties.

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