

Chapter 2

Evolutionary and Ecological Functions of Dynamic Perceptions of Looming Danger



“The capacity for anxiety, like other normal defenses, has been shaped by natural selection.”

Isaac M. Marks and Randolph M. Nesse, 1994

A useful analogy may help to understand the evolutionary selection pressures that have shaped how humans detect and respond to threats. A rare genetic anomaly on the V chromosome has been found that results in a “movement blindness” in the form of an inability to perceive visual movement (Zeki, 1991; Zihl & von Cramon, 1983). If an individual were to have this genetic defect, the person would only be able to perceive object movement that occurs in the surrounding environment as series of snapshots of static objects rather than as a fluid sequence of dynamic objects that are approaching. Consider how could this inability to perceive the dynamism of visual objects could affect their chances of surviving an encounter with a predator or a car that was careening toward them while they were crossing the street? Similarly, imagine that there were two hypothetical human ancestors, one of whom had our ability to rapidly detect and respond to dynamism and movement of potential predators and one who didn’t. Which one of these potential ancestors are we more likely to be descended from?

As we will attempt to demonstrate in this chapter, a threat-related defensive response to approach movement has an evolutionarily ancient origin. After reading the chapter, we believe it should be obvious that the ability to rapidly detect and respond to approach movement, and dynamic change, has been an important target of selection pressure in our species and other animal species. We will attempt to show in this volume that innate defensive mechanisms, which are ubiquitous observed across the animal kingdom, have been conserved and constitute a part of the basis for human threat processing and anxiety.

This chapter contains three main sections. In the first section, we will begin with a broad discussion of how evolution has shaped the ancient phylogenetic scaffolding

of humans' (and other animals') defense systems. In the second, we will examine concepts of defense repertoires, predatory imminence, and protective space and margins of safety. Then, in the third section, we will review considerable research that has demonstrated the effects of looming stimuli and approach movement in triggering defensive reactions across the whole animal kingdom. The evidence that we present in this chapter implies that the way in which we respond to threats is deeply rooted in our adaptations to evolutionary recurrent threats of predation and other threats in a dynamic world, one in which objects move around and toward us and can cause us harm.

Evolutionary Psychology and Evolutionary Continuity and Change

As Buss (1991) and other evolutionary psychologists (Barrett, 2005; Confer et al., 2010) have noted, the need to escape from predators and other dangers may be the most behaviorally urgent threat to any animal's reproductive success. The need to find solutions to the threat of rapidly approaching dangers is essentially one of the most fundamental and ancient adaptive challenges faced by all animal species. Indeed, even the most primitive multicellular organisms have some kind of biological defense systems for detecting and responding to the dynamic movement of looming threats.

Evolutionary Continuity and Change

How did the human species evolve to what it is today? We should recognize that evolution doesn't proceed by just inventing utterly innovative designs and nervous systems for new animals from out of the blue. To the contrary, evolution can generally only elaborate, modify, or "tinker with what is already there" (Gilbert, 1998). Simply put, earlier design-features are the starting points for continued evolution and tend to be conserved as organisms continue to evolve, even though they may be extended or repurposed for other functions. This conservation of earlier design creates a continuity between the organism's more ancient phylogenetic past and its present. Gilbert (1998, p. 355) used the design of the human spine as an example that aptly illustrates this phenomenon:

"It originated in the sea to act as a 'coat hanger' for the internal organs. Subsequently, it was adapted for walking on four limbs and then later for walking upright. But it does not really work that well for walking on two limbs and bipedalism is responsible for our innumerable back problems. It has also caused serious problems for women. The evolution of larger brain infants and the conflict of this with the size of the birth canal has resulted in billions of females dying in childbirth."

More relevant to our concerns with emotion, a similar conservation mechanism may help to explain the likely evolutionary origins of another presumptively universal and basic emotion—disgust. According to Darwin (1872), the original function of disgust was to prompt animals to physically avoid spoiled or contaminated food, and to expel it—if consumed—by means of spitting or vomiting. Today, however, the function appears to have been *coopted* and expanded to apply to distasteful, repugnant values, ideas, and behaviors that are observed in oneself or others (e.g., child abuse). For example, there is evidence that the same facial expressions and subjective phenomenology that are associated with physical disgust may be implicated in at least some forms or subtypes of moral disgust (Chapman, Kim, Susskind, & Anderson, 2009; LaRosa & Mir, 2013), although not necessarily all (David & Olatunji, 2011).

Another striking illustration of the same conservation phenomenon concerns the molecular mechanisms implicated in the human fear response that humans have to aversive stimuli. As LeDoux (2003) has described, the same molecules that mediate aversive conditioning in snails and fruit flies also mediate fear conditioning, and thus anxiety, in humans and other animals. This striking observation exemplifies the fact that there has even been continuity and conservation of design in anxiety and fear at the molecular level.

Relatedly, Anderson has proposed that “neural reuse” is a basic organizing principle of the brain (Anderson, 2010, 2014). It is normal for an animal’s evolving brain to coopt or reuse neural circuitry that evolved for earlier functions for different purposes. In this chapter, we will demonstrate that even infants, and most, if not all, animals—even invertebrates—respond more negatively with defensive reactions and alarm to perceptions of the dynamism of growing threat and approach movement than to static or to receding physical objects. Accordingly, we will contend that the same phylogenetic mechanisms that are involved in defensive responses of other animals—to dynamic growing threat and approach movement—have been conserved and extended to problems and worries faced in human society today. As a result, ancient biological adaptations have a profound effect on the cognitive processes involved in how we detect and respond to threats today.

Anxiety and Fear as Evolved Defense Systems

Gilbert (1993, 1998) and other scholars including Dixon (1998) and Marks and Nesse (1994) have noted that anxiety and fear are grounded in evolutionarily ancient defense systems. More specifically, according to Gilbert’s (e.g., 1993, 1998, 2001) biosocial model, the human (or animal’s) brain has evolved as a “decision-making organ” for threat assessment. As such, the brain includes stimulus detection systems that are concerned with appraising whether a stimulus is a potential source of “threat/harm, or whether it is neutral, or even a source of reward/benefit.” Paired with this threat assessment system, the brain also has response systems involving species-specific menus of possible options for dealing with the stimuli that have

been detected and coded. Gilbert has proposed that animals select defensive responses from their menus of options that have proven most adaptive in similar circumstances over evolutionary history.

Theorists such as Gilbert (1993, 1998, 2001), Dixon (1998), Marks and Nesse (1994), and others have suggested that the general defensive options for responding to threats that animals can use include escape, aggression, freezing, and submission. According to Dixon (1998, p. 421), escape behavior, which can involve flight, is an emergency response that not only takes precedence over other ongoing activities but encompasses “activities that when performed by an animal serve to remove it from a source of danger or harm.” The simplest form of flight, of course, is escape behavior which serves to physically separate the animal from the source of harm. But as we will see, there are also others such as covert mental strategies.

A second major alternative defensive option is avoidance behavior. The avoidance option has the function of avoiding getting too close to that which threatens. As is true of all defensive behaviors, avoidance and flight have potentially significant tradeoffs and costs (Gilbert, 1998). In many cases, the same situations that threaten an animal, such as social relationships, can also offer potentially significant opportunities (e.g., mates, alliances). Among the tradeoffs and costs of fleeing or avoiding danger is that such behaviors can limit an animal’s abilities to meet other basic needs such as foraging or obtaining food (Nesse, 2001; Ydenberg & Dill, 1986).

Another defense option is aggressive behavior—which represents an “attack-first” strategy that an animal can use when facing threats (Gilbert, 2001). Aggressive behaviors such as bullying, intimidation, or actual attack against others can be an option that could be used in certain circumstances. Obviously, such aggressive strategies are unlikely to be effective for a person who faces others who are far bigger, stronger, faster, or have more lethal weapons for attack. Other options may be preferable in such circumstances.

As Gilbert suggests, another option that is perhaps better in such circumstances is help seeking—seeking protection and alliances from conspecifics and potential allies. One can often best succeed in getting help by making oneself attractive to others as opposed to bullying. By developing friendships or allies, even if by servile submission, one can make threats either less likely or more surmountable. Within this general category of defenses, Marks and Nesse (1994) have identified passivity and subordination as particularly used as a defensive response in the context of social threats.

Dixon (1998) has suggested that the various types of defensive behaviors above can take an altered form when responses are blocked or arrested. “Arrested defenses” occur in several types of circumstances in which primary options are blocked. For example, Dixon suggested (p. 423) that active escape or flight can be prevented by “physical barriers (e.g., confinement, or social constraints), as when the escape route is blocked by a predator or more dominant animal.” A specific example of an arrested defense is “arrested flight” (Gilbert & Allan, 1998) which occurs when an individual is strongly motivated to escape but is blocked, as in the familiar learned helplessness paradigm for understanding depression (e.g., Abramson, Seligman, & Teasdale, 1978; Hiroto & Seligman, 1975; Seligman, 1975). Dixon (1998) sug-

gested that having to stay in an aversive environment while having a “strong desire to escape from it, but feeling unable to” is associated with depression. In other cases, individuals may be strongly motivated to engage in specific defense behaviors, such as aggression or help seeking, but are not able to do so because these behaviors are under inhibitory control. For example, arrested aggression is a defensive pattern which may occur in circumstances in which individuals are frightened of retaliation, or perhaps of potential damage to their alliances. For another example, arrested help seeking occurs when an individual’s desire to seek help or comfort from supportive relationships is stopped because the costs of closeness and support seem to outweigh the benefits. Arrested help seeking can occur if it requires a person to self-disclose things that are personally shameful or where there is strong distrust of others.

When threatened animals cannot reduce the input of an adversary’s disturbing stimuli by escaping, they may resort to defensive “cut-off” actions and postures (Chance, 1962) which serve an analogous function and partially substitute for the actual escape. For instance, the simplest cut-off escape behavior is to physically avert the head away from the source of threat or close or cover the eyes, which reduces the perception of the disturbing stimuli that the adversary represents. The gaze aversion is theoretically adaptive because it reduces the individual’s level of arousal and enhances the person’s chances of switching to a more appropriate behavior when the need arises. Chance states that escape cut-offs such as gaze aversion or perhaps certain forms of postural tension are an indication of incipient flight and their manifestation also implies the presence of perceived danger (p. 423).”

It should be noted that similar arrested defenses can be observed among human beings. For example, some individuals close their eyes (e.g., when watching particularly scary scenes in a horror movie) to reduce arousal produced by threat even when the danger situation is known to be a purely imaginary one. Other arrested defenses take the form of “mental cut-off” strategies such as cognitive avoidance mechanisms or even “ego defense-mechanisms” such as denial and suppression (e.g., Dixon, 1998). From this perspective, worry (Borkovec, Ray, & Stoeber, 1998; Sibrava & Borkovec, 2006) and experiential avoidance (Roemer & Orsillo, 2010) can be reasonably conceptualized as reflecting forms of mental cut-off strategies.

Temporal-Spatial Factors in Defensive Responses: Predatory Imminence Continuum

Theoretical work and research on animal behavior have suggested that spatial-temporal parameters are key determinants of defensive responses. As an example, Fanselow and Lester (1988) proposed the “predatory imminence continuum” hypothesis, which holds that the physical proximity of a predator determines the defensive responses selected by a potential prey animal, such as a rat, in a sequence of predictable phases. Before the potential prey animal encounters a predator, it is

typically engaged in other activities such as exploring surroundings or foraging. When it senses that a predator is near, the animal exhibits freezing or other species-specific defensive reactions that are intended to hinder detection and may facilitate vigilance and threat assessment. Then, once the predator is clearly encountered the animal enters the *circa-strike* phase and defensive responses such as flight or attack become more optimal strategies.

Similarly, some scholars have suggested that there is a “distance-dependent defense hierarchy” (Gallup, 1974; Ranter, 1977). In this hierarchy, animals freeze when they detect a distant predator, whereas they flee a predator that is nearby, and may engage in a defensive attack when the predator is closer and flight is no longer available as an option.

It should be noted that distance isn’t the only spatial-temporal parameter of threat that triggers defensive behavior, but its dynamism, movement, and changing distance are also important. For example, Eilam (2005) described results of a study showing that not only proximity but approach movement predicts defensive behavior. An owl in a birdcage was moved closer toward rodents (voles) on a runway from four meters away. This research revealed that defensive responses of the voles were movement-dependent, not distant-dependent and triggered by the perceived approach movement of the owl, not its proximity.

Approach movement and proximity are distinct although related constructs. They should be distinguished because an animal such as a vole can perceive a threat such as an owl as distant but rapidly approaching, and by the same token, it can perceive the owl as close by but not dynamic or coming any closer. As we shall describe elsewhere (see Chaps. 5 through 7), approaching objects (looming dangers) elicit cognitive, affective, and psychophysiological reactions that are not explained by their physical or temporal proximity alone.

The Margin of Safety and Flight Initiation in Response to the Approach of Threat

The defensive reactions that animals deploy when approached by predators are partly a function of their perceived margins of safety. The related concepts of margin of safety, “buffer zone (Knight & Knight, 1984; Rodgers & Smith, 1995, 1997; Rodgers & Schwikert, 2002), flight zone” (Hediger, 1964), and “flight initiation distance” (Blumstein, 2003; Blumstein, Anthony, Harcourt, & Ross, 2003; Cooper, 1997; Smith, 1997) are similar and refer to the distance that animals require around themselves to feel comfortable and safe around other animals that are in proximity to them (especially predators). These concepts are also related, in human beings, to the concept of personal space that people require to feel comfortable around others (Hall, 1963, 1966).

Generally, animals will tolerate the presence of threats up to a certain point because of the tradeoffs and costs of taking flight. For example, a predator at a distance, and particularly one that is not approaching does not automatically initiate

flight because it would cause the potential prey animal to give up foraging or grazing (Ydenberg & Dill, 1986). However, as the predator gets closer to the flight zone or flight initiation distance (the nature of which may extend either/or both horizontally or vertically from animals) the animals become increasingly vigilant and wary even when they are continuing to eat or graze. Moreover, once the predator reaches their flight initiation zone, they take flight.

Several specific factors determine the size of the margin of safety. For example, the protective space that animals in the wild require around their bodies is greater than the space that domestic animals require. Furthermore, the attributes of the predator, including its dynamism, speed and approach movement, as well as the closeness of a perceived place of safety and refuge, influence the margin of safety and flight initiation distance (Cooper, 1997; Helfman, 1989; Smith, 1997; Stankowich & Blumstein, 2005; Stankowich & Coss, 2006; Ydenberg & Dill, 1986). Thus, animals tend to require a wider margin of safety when they are further away from a place of refuge and when predators are faster moving.

Researchers have found that the distance at which animals begin to actually flee from potential approaching predators, referred to as its “flight initiation distance,” (Blumstein, 2003; Blumstein et al., 2003) can be objectively measured and is associated with other aspects of defensive behavior such as “alert distance,” the distance at which an animal becomes alert to an approaching threat (Fernández-Juricic, Jimenez, & Lucas, 2001, 2002; Fernández-Juricic, Vernier, Renison, & Blumstein, 2005; Rodgers & Smith, 1995, 1997). Moreover, this distance is related to amount of time that the animal spends assessing the movement of the potential threat (assessment time) (Stankowich & Coss, 2006). Notably, researchers use the objectively measured flight initiation distance as an objective behavioral indicator of threat perceptions by nonhuman animals (Gill, Sutherland, & Watkinson, 1996; Stankowich & Coss, 2006). For instance, when prey animals initiate flight more in some circumstances than others after exposure to predators, they are assumed to have greater threat perceptions. Animals also have distinct alert postures when they are attending to approaching threat. Researchers have used this as a measure of the time spent the animal spends on attending to the approaching threat, or elapsed time between alert posture and flight, which is referred to as “assessment time” (Stankowich & Coss, 2006).

In one study that provides a telling example, Stankowich and Coss (2006) examined the “perception of risk” in deer and other animals by the distance at which the deer exhibited defensive behaviors ranging from alertness to actual flight. Several different variables were found to be important determinants of flight distance—including distance from refuge, size, etc.—and the velocity or speed with which the potential predator was one of the important determinants. Deer that perceived a potential predator as rapidly approaching their safety zone responded with greater speed—assumed to represent greater risk perception—than potential predators that moved more slowly toward them or not at all. The latter findings indicated that deer evaluate risk with a variety of different variables—including distance from refuge and rapidly of approach a flight zone—before choosing which of several possible defensive responses that can be deployed (alertness, flight, etc.). Much the same

kinds of findings have been reported for other animals (Cooper, 1997; Fernández-Juricic et al., 2006; Stankowich & Blumstein, 2005; Blumstein, 2006; Ydenberg & Dill, 1986).

As we will now attempt to show, evolutionarily recurrent threats to survival from predators have led all animals to evolve specialized adaptations (Bracha, 2004; Confer et al., 2010). These functional adaptations are specialized to protect animals from rapid gains by dynamically approaching threats approach of threats.

Empirical Evidence of Defensive Looming Responses to Approach Movement in Nonhuman Animals

A wide range of research indicates that all animals have found it necessary to develop specialized survival mechanisms for facilitating the rapid detection and selection of appropriate defensive responses to rapidly approaching, potentially threatening, objects.

Research has found remarkably consistent evidence for the effects of approaching, looming objects in triggering defensive behavioral reaction across the animal kingdom. Some of the earliest evidence for this “looming effect” was presented by Schiff, Caviness, and Gibson (1962), who tested the notion that the changing flow of a visual or optical array (see Gibson, 1979) provided cues that would inform animals about their exposure to danger: the potential approach of dangerous objects and triggered defensive responses. The rapid symmetrical expansion of the visual or optical array signaled the rapid approach of danger and triggered defensive responses, whereas the asymmetrical expansion would signal a near miss, and a shrinking optical display would indicate that the object was receding. In short, an expanding visual optical array presented animals with crucial cues of the approach of danger and elicited subsequent avoidance and defensive responses.

The evidence for the looming effect has been remarkably consistent for both invertebrate and vertebrate animals. For example, defensive responses to the approach movement of looming stimuli have been observed in locusts (Hassenstein & Huster, 1999), flies (Jablonski & Strausfeld, 2000), fruit flies (Card & Dickenson, 2008; Tammero & Dickinson, 2002), locusts (Santer, Simmons, & Rind, 2005; Santer, Rind, Stafford, & Simmons, 2006), cockroaches (Camhi & Tom, 1978; Kramer & Bonenfant, 1997), wood crickets (Casas, Body, & Lazzari, 2011), barnacles (Gwilliam, 1963), crayfish (Glantz, 1974), and crabs (Ball & Tronick, 1971; Hemmi, 2005a, 2005b; Jennions, Backwell, Murai, & Christy, 2003; Oliva, Medan, & Tomsic, 2007). Additionally, they have been observed in vertebrates such as fish (Helfman, 1989; Millot, Bégout, & Chatain, 2009), lizards (Carlile, Peters, & Evans, 2006; Cooper, Martin, & Lopez, 2003) and frogs (Kang & Nakagawa, 2006; Yamamoto, Nakata, & Nakagawa, 2003), birds such as chickens (Jones, Duncan, & Hughes, 1981; Evans et al., 1993), eagles (Knight & Knight, 1984), pigeons (Wang & Frost, 1962; Wu et al., 2005), ducks (Schaller & Emlen, 1962; Schiff, 1965; Hassenstein & Huster, 1999), and gannets (Lee & Reddish, 1981). They have also,

of course, observed in mammals such as mice (Yilmaz & Markus, 2013), woodchucks (Kramer & Bonenfant, 1997), kangeroos (Wolf & Croft, 2001), black-tailed deer (Stankowich & Coss, 2006), and various primates—including rhesus monkeys (Maier & Ghazanfar, 2007; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; King & Cowey, 1992).

These animals exhibit a variety of responses to the visual or auditory approach movement and dynamism of looming stimuli, the nature of which may be both species-specific and exhibit context-sensitivity. For example, chicken's crouch (Jones et al., 1981), and as previously noted, black-tailed deer have been found to exhibit defensive responses that are tailored to the speed of the approach movement, closeness to refuge, and size of the potential predator or enemy (Stankowich & Blumstein, 2005; Stankowich & Coss, 2006). Such context-sensitivity of defensive behaviors is also observed in many invertebrates. For example, as mentioned, barnacles close their shells (Gwilliam, 1963). On the other hand, locusts make evasive responses in which jumps are determined by the angle of the approaching threat (Card & Dickenson, 2008; Gray, Lee, & Robertson, 2001). As further examples of the specificity of defensive reactions to species, some crabs (*Neohelice*) raise their claws aggressively when approached (Scarano and Tomsic, 2014), whereas fiddler crabs hide (Hemmi, 2005a; Hemmi, 2005b; Jennions, Backwell, Murai, & Christy, 2003). In this regard, fiddler crabs run correspondingly faster to an available refuge when a dummy predator approaches them quickly rather than slowly (Hemmi, 2005b).

Defensive Looming Responses to Approach Movement in Primates and Humans

As should be expected, human beings and other primates exhibit defensive behaviors in respond to looming stimuli. For example, monkeys have been found to respond defensively to both visually looming and auditory looming stimuli (Ghazanfar & Maier, 2009; Maier & Ghazanfar, 2007; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; King & Cowey, 1992; Schiff, Caviness, & Gibson, 1962). Likewise, research has documented similar looming effects in human adults (King, Dykeman, Redgrave, & Dean, 1992; Regan & Hamstra, 1993) and their young (Kayed & Van der Meer, 2007; Schmuckler, Collimore, & Dannemiller, 2007). For example, King et al. (1992) found that human adults ducked their heads when presented with looming visual objects. Similarly, developmental psychologists studying stranger anxiety have found that children respond with greater anxiety to a stranger who approaches rapidly rather than slowly (Reingold & Eckerman, 1973; Trause, 1977). A recent study by Schmuckler, Collimore, and Dannemiller (2007) compared the eye blink responses of 4- to 5-month-old infants who were shown stimulus objects that were looming on either collision or near-miss trajectories. Their findings showed that infants showed a greater number of eye blink responses to objects on a collision course than did those on non-collision trajectories. This not

only suggests that infants can discriminate subtle differences in motion direction, but this ability has an innate basis. Indeed, a study by Jouen (1990) (see also Jouen, Lepecq, Gapenne, & Bertenthal, 2000) showed that 3-day-old neonates seemed to orient to looming flow motion patterns by tilting their heads backward. Also noteworthy is that the extent to which these neonates tilted their heads was positively related to the optic flow velocity of the looming stimuli.

Such looming effects have been demonstrated in an auditory as well as a visual modality. Research has demonstrated that behavioral reactions are elicited in human adults by the dynamism of auditory looming sounds (sounds that move closer) that create a sense of looming or receding movement (Bach, Neuhoff, Perig, & Seifritz, 2009; Bach et al., 2008; Neuhoff, 1998, 2001). Similar results have been found in human infants as young as 4–6 months of age, who exhibit avoidance responses to looming sounds but not to other equivalent sounds (Freiberg, Tually, & Crassini, 2001) and discriminate looming sounds better than receding sounds (Morrongiello, Hewitt, & Gotowiec, 1991). In their study, Freiberg et al. tested 4-month-old infants in complete darkness and presented them with auditory stimuli to create the illusion with sound pressure level that a sound source was approaching or receding. They also manipulated the rate at which the auditory stimuli underwent unidirectional changes in the rate at that sound pressure level during trials (fast vs. slow). The researchers assessed the avoidance behavior of the infants by the amount of backward body pressure they exerted in response to the different auditory stimulus presentations. This research showed that avoidance behavior (backward body movement) was associated with sound pressure level increases (i.e., illusory approach) but not sound pressure decreases (i.e., illusory recede) conditions. Moreover, it found that infants engaged in more defensive leaning back in fast change trials compared to slow change trials. Thus, the latter finding indicated that under certain conditions infants can “detect information for changing object distance” just based on auditory looming stimuli.

To conclude, research has thus demonstrated defensive behavioral reactions to looming, approaching stimuli in both nonhuman primates and humans, including human infants, with both visual and auditory stimuli. As will be seen later, looming effects in humans have been studied in relation to attentional and memory processes (see Chap. 6), and approach movement has been shown to have a powerful influence on affective reactions such as fear (Chaps. 5 and 7).

Summary and Conclusions

This chapter has presented extensive evidence that innate survival systems for defending against looming, rapidly approaching threats are ubiquitous across the animal kingdom. Powerful selection pressures due to living in a dynamic environment have apparently led all animals including humans to develop specialized adaptive systems for responding to looming or rapidly approaching threats. As conservation of design is an essential feature of the evolutionary process, we should

hardly be surprised that our human adaptive systems (cognition, emotions, behavior, and physiology) are tightly geared to process information about the dynamism of threats and defend against the approach of threats.

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