

The Evolution of Social Anxiety

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“Understanding the evolutionary history of a trait, how it gives a selective advantage, and the costs it imposes can help to illuminate its design and regulation and can guide research into its mechanisms and control.” (Nesse et al., 2007; p. 965).

Introduction

Social relationships constitute a highly rewarding context for most people, providing a source of support and nurturance, as well as protection against loneliness, depression, and even death (Cacioppo, Hawkey, & Thisted, 2010; Cohen, 2004; Steptoe, Shankar, Demakakos, & Wardle, 2013). Interpersonal relationships can also, however, be stressful. They are marked by periodic conflict with others and entail inherent risks of negative evaluation or criticism (Bertera, 2005; Rook, 1984). Further, social strains contribute to psychological and physical health problems (Seeman, Gruenewald, Cohen, Williams, & Matthews, 2014; Yang, Schorpp, &

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Harris, 2014). It is thus not surprising that interpersonal difficulties constitute one of the most common reasons that people seek psychological treatment (Bankoff, 1994; Benton, Robertson, Tseng, Newton, & Benton, 2003; Pledge, Lapan, Heppner, Kivlighan, & Roehlke, 1998). One particularly common manifestation of such difficulties is social anxiety (SA), defined as an excessive fear of negative evaluation that can lead people to avoid social engagement. Its associated behavior patterns may result, in the most severe cases, in a clinical diagnosis of social anxiety disorder¹ (SAD, formerly called social phobia; APA, 2013). Indeed, this disorder is common. Approximately 7–8% of adults meet the criteria for SAD in a given year (Kessler, Chiu, Demler, & Walters, 2005), and an additional 10–11% have at least some impairing symptoms (Fehm, Beesdo, Jacobi, & Fiedler, 2008).

Not surprisingly, given both its ubiquity and its negative effects, SA has been the focus of much research. Despite this work, it remains difficult both to predict who will develop the condition and, for many affected individuals, to treat SA successfully. Indeed, although researchers have identified a range of genetic, temperamental, and environmental risk factors (Bas-Hoogendam et al., 2016; Spence & Rapee, 2016), we do not fully understand how these interact to precipitate SA. Further, even when gold standard treatments, such as cognitive behavioral psychotherapy, are applied reliably, roughly half of the adults with SA fail to show a meaningful response (Loerinc et al., 2015).

In recent years, due at least in part to frustration with persistent limits to their ability to predict and treat SA, researchers have begun to explore alternate approaches to understanding this condition. Of these, the most relevant for our purposes is the hypothesis that, although SA certainly has detrimental effects that require treatment, it is an adaptive behavior pattern that has been selected for the benefits that it may have provided and that continue to be relevant. In other words, SA may be, at its core, a behavior pattern that was selected in our evolutionary history because it has useful properties, rather than a psychopathology stemming from novel cultural expectations and environmental factors in modern Western environments. If this is the case, then understanding why this suite of traits was under positive selection pressure not only would provide a better understanding of when to expect SA symptoms (i.e., those that match the conditions under which there was positive selective pressure), but also may help us decide when treatment is needed and, when indicated, to more successfully treat severe manifestations (i.e., by eliminating or modifying the core circumstances that elicit symptoms, as opposed to just treating the symptoms themselves). Indeed, this approach has coincided with a general appreciation for the idea that considering the evolutionary history of behavior helps us to better understand the trait in question. As is evident in this volume, there has been substantial interest in the evolutionary history of psychopathology, in general, and more specifically in the possibility that psychopathology may be adaptive in some circumstances (Brüne, 2015; McGuire & Troisi, 1998).

¹Throughout the text, we refer to social anxiety, or SA, by which we mean the cluster of anxiety-related symptoms, but do not mean that there is a clinical diagnosis unless otherwise specified.

In this chapter, we first summarize the history of thought surrounding SA, and then outline the evolutionary frameworks that scholars have proposed. We next discuss the ways in which recent work on social behavior in animals, particularly other primates, affects our understanding of these models. In particular, although the original models focused on aggression and dominance as key issues in eliciting interpersonal difficulties, more recent work emphasizes the formation and maintenance of peaceful social relationships and highlights situations in which it may be to an individual's substantial advantage to hesitate in social circumstances. Indeed, new research demonstrates that there are times when appeasing or avoiding is highly beneficial. Building from this more recent work in primates, we outline an updated model. We include a series of open questions around SA, and its evolutionary history, that will need to be answered to better prediction and treatment of SA.

Just because it's unpleasant doesn't mean it's pathological: The Importance of an Evolutionary Approach to Psychopathology.

"The ubiquity of the illusion that defenses are abnormalities arises from several sources. First, defenses are often associated with some kind of suffering and therefore seem maladaptive. Unfortunately, however, discomfort is itself probably one aspect of a mechanism that makes it useful. Second, they are reliably associated with disadvantageous situations, so the association bias makes it seem as if they are the problem. Finally, it is possible to use drugs to block the expression of many defenses with very little harm, completing the illusion that defenses are useless." (Nesse & Young, 2000, p. 79).

Psychopathologies, including SA, are not fun. They feel bad, and commonly occur in situations that we did not want to be in to begin with. People wish the symptoms to end, which is sometimes possible with easily obtained and well-tolerated medications. As a result, we tend to focus on the resulting *symptoms*, rather than their causes. We act as if the symptoms alone are the problem, rather than also recognizing them as *expressions* of the actual problem. But why is this an important distinction? If we can decrease symptoms by simply taking a pill, why not do it?

First of all, because it is not always so easy to relieve psychological problems. Despite substantial research into treatments (medication and other) for psychopathologies, and evidence that these treatments have lasting benefits for a substantial proportion of people, they do not work well, or at all, for many others. In a given year, roughly 60% of people with SA do not receive treatment at all. Of those who do get help, only about a third get treatment that has been shown in clinical trials to work well (Wang et al., 2005). Even medications and other first-line interventions, such as cognitive behavioral therapy, fail to relieve symptoms in at least half of the treated cases, and cure even fewer than that (Loerinc et al., 2015; Ravindran & Stein, 2010).

Second, without effective treatment, there is a high likelihood of developing more debilitating symptoms (Wittchen, 1998; Wittchen & Fehm, 2003). As an example in the physical realm, imagine that you are a marathon runner and you develop a stress fracture. You have qualified for a major race, so you choose to take painkillers and run through the pain. There are two likely outcomes. First, you probably will not do well in your race, due to the fact that your body is not functioning

at its full level of ability. Second, you will probably make the injury worse, possibly resulting in a long period while you recover in which running is impossible. The same is true in the psychological realm. Attempting to soothe symptoms with medication may provide temporary relief, but if the root causes of symptoms are not addressed, they will continue to cause problems, and may indeed cause even worse ones. This is perhaps the most devastating effect because, as Nesse indicates in the quote above, efforts to relieve distress can hide the real problem.

So how does considering SA from an evolutionary perspective address these issues? If one approaches SA with a focus on how it may be adaptive, one can reconceptualize the condition as serving both useful and impairing functions, rather than simply the latter. Clinicians can then work collaboratively with affected people to identify the sources of anxiety symptoms and to develop treatment plans that take these into account and, potentially, address them along with symptoms. Although attention to the contexts in which symptoms arise is common in psychotherapy, particularly CBT (Mennin, Ellard, Fresco, & Gross, 2013), an evolutionary approach is grounded in comparative data that can be used to generate a road map of likely causes, that is, situations and contexts that lead to an increase in anxiety-related symptoms in other species. An evolutionarily informed perspective regarding the social circumstances that trigger anxiety and why they might do so can assist the practitioner in predicting the onset of symptoms and determining if they reflect adaptive or maladaptive processes.

But how does one do this effectively? An evolutionary approach only works if it is evidence based. So-called Just So Stories—in which creative but unsupported causes are hypothesized for selective pressures behind traits—are ineffective and, because they misdirect research and treatment, possibly dangerous. Instead, any such hypotheses need to be empirically grounded and rigorously tested. This is challenging if one is looking only at people in a modern, Western world that may not particularly resemble the environment in which humans evolved (Henrich, Heine, & Norenzayan, 2010). Indeed, it is virtually impossible to come up with good hypotheses without having broad insight into environmental and social pressures across multiple groups. One solution is to look across cultures, to find underlying commonalities that may indicate shared causes (e.g., Dinnel, Kleinknecht, & Tanaka-Matsumi, 2002). Although useful, even this approach limits research to shared causes within humans, and may mask fruitful avenues that are shared more widely across the animal kingdom. Thus, the comparative approach, in which we look at other species for insight into our own behaviors, holds distinctive value.

Indeed, the comparative approach has been immensely useful in generating insight into the evolution of a wide variety of human social and cognitive behaviors (Brosnan & de Waal, 2014; DeAngelo & Brosnan, 2013; Kappeler & Van Schaik, 2005; Kornell, 2009; Wiley, 1983), as well as human physical health (Merlo, Pepper, Reid, & Maley, 2006; Nesse et al., 2010; Williams & Nesse, 1991) and mental health (Brüne, 2004, 2015; Crow, 1995; Grinde, 2005; McGuire & Troisi, 1998; Nesse, 1998; Nesse & Young, 2000). An evolutionary perspective offers a new way of thinking about behaviors that too often seem only problematic (i.e., morning sickness is unpleasant, but may protect the fetus; Flaxman & Sherman, 2000). Such

a view may not only help those with SA understand their suffering in a more nuanced and accurate way, but also may lead to novel interventions that, as we argued previously, can take into account and address the roots of symptoms rather than simply provide a “Band-Aid” to fix them. Finally, although much has changed in humans’ evolutionary trajectory since our lineage split from the other great apes, we nonetheless share many of the same issues. Like us, other primates are highly social, highly reliant on their friendships for their health, well-being, and longevity, and suffer from a suite of anxiety behaviors that are ameliorated by changing circumstances and, in some situations, drugs, indicating the possibility of similar underlying mechanisms.

Below we expand on these ideas and argue that by considering the evolutionary angle we may be better able to thoroughly define the contexts in which SA symptoms arise and why they do so. Specifically, understanding the settings in which SA occurs, and the selective pressures that led to it, may help us to provide a more precise, evidence-based diagnostic criterion for when the experience of SA reaches a clinical threshold and when it is “normal.” Critically, this means both better understanding of how to treat SA and insight into *when SA might be worth not treating, or even fostering*. This latter perspective is often underemphasized in approaches to psychiatric disorders, yet it could be an important one for appropriately targeting and tailoring interventions.

The Benefits of Studying SA in Nonhuman Species

Humans are not the only species that experience anxiety; indeed, if we are to explore the evolutionary correlates of SA comparatively it is critical to be able to identify SA-like behavior in other species. Much work demonstrates that other primates show anxiety-related symptoms, in situations that, from a human perspective, appear to be stressful. Further, these symptoms can be alleviated using the same medications that humans use (implying the same, or at least similar, underlying mechanisms). A review from 2002 identifies almost 70 studies on fear and/or anxiety in nonhuman primates (primarily rhesus macaques, *Macaca mulatta*, squirrel monkeys, *Saimiri spp.*, and common marmosets, *Callithrix jacchus*, although other model species are also mentioned; Barros & Tomaz, 2002). Tests ranged from traditional conflict tests to more ethologically appropriate models (social interaction, involuntary isolation) and found that in about half of these anxiolytic drugs decreased anxiety-related symptoms. This is a relatively widespread effect, and argues for the utility of studying anxiety in other primates. The effectiveness of the anxiolytic drugs also hints at a common underlying mechanism. Indeed, research on macaques shows that selective bilateral lesion of the amygdala led to a lack of both fear and social inhibition in rhesus macaques, just as it does in humans (Amaral, 2002), indicating a similar neurobiology.

Conveniently for such work, the key behavioral measure for primate anxiety comprises displacement activities (i.e., self-grooming, self-scratching, body-shaking,

yawning; Gabriele Schino, Perretta, Taglioni, Monaco, & Troisi, 1996). Such behaviors are easy to observe and therefore function as a noninvasive assay for anxiety. Indeed, numerous studies have used self-directed behaviors (SDB) to index distress in social contexts. For example, in wild olive baboons, females increase SDBs by approximately 40% when the nearest neighbor is dominant to them as compared to when the nearest neighbor is subordinate (Castles, Whiten, & Aureli, 1999). Rough self-scratching has been used to assess social anxiety in wild chimpanzees, and research indicates that there is a sex difference; among males, performance of this SDB was related to rank order (higher ranking males performed less scratching), but in females, social proximity, rather than low rank, increases SDBs. In neither sex, however, did the rank of individuals in social proximity influence SDB rate (Kutsukake, 2003). Chimpanzees also show SDBs during difficult tasks, although interestingly the increase occurs only when the task becomes harder, and no decrease is seen when subjects start with a hard version that then becomes easier (Leavens, Aureli, Hopkins, & Hyatt, 2001). However, care must be taken to disentangle anxiety from other environmental factors. A recent study of Japanese macaques indicates that one SDB, self-scratching, is most closely related to environmental factors (lice load), whereas another, self-grooming, may be more closely related to displacement behavior in the context of social uncertainty (Dubocq, Romano, Sueur, & MacIntosh, 2016). Although this balance will vary across contexts and species, it is important to consider other causes of these displacement behaviors. When possible, for example, researchers can correlate changes in SDBs with changes in stress-related hormones (i.e., cortisol).

Of course, the clear advantage of SDBs as a behavioral assay for studying SA in primates is that they appear to be a relatively consistent measure of anxiety in uncertain contexts (social and nonsocial) that can be assessed without interfering with ongoing activity. This means that an SDB assay is appropriate for ongoing social interactions, which it might not be desirable (or possible) to interrupt in order to obtain a physiological measure or a sample for hormonal assay. SDB assays are also good options for studying social behavior and distress in wild populations where more invasive interventions may not be possible or ethical. Indeed, these situations are exactly the ones that we need to know more about, if our interest is in understanding the evolution of SA. It is key to know the natural contexts in which SDBs occur, as well as the impact of the social environment, neither of which is amenable to studies of isolated individuals.

Aside from providing data about the evolutionary history of SA, these studies strongly support nonhuman primates as an excellent model for human anxiety-related behavior. There are multiple advantages to studying questions about SA in other species. Practically speaking, in an ideal circumstance we can use a model species to ask questions that are impractical or impossible, or are unethical, to ask with humans. For example, it is difficult and expensive to get high-quality, longitudinal data on humans. However, there are primate social groups that have been studied for decades, and whose entire social history, including the frequency of both positive and negative social interactions, personality, health, and kinship, has been documented for the whole social group (most of these social groups are closed,

meaning that we also do not have to contend with the influences of extraneous relationships). Such detailed long-term data about individuals and their social relationships are virtually impossible to obtain in humans, and yet may be key in unlocking the causes of SA. In studies of nonhuman primates, we can also manipulate social environments (e.g., by adding or removing individuals), which allows us to directly test hypotheses about the influence of various factors on anxiety and also to determine whether and why some individuals are more resilient in the face of social stress than others.

Additionally, although interviews with humans give insight into what they are thinking and feeling, such interviews may also be misleading, as people inadvertently or intentionally misreport motivations and behaviors (Liang, 1988). Studying animals by necessity focuses the inquiry to actual observed behaviors, which may make it easier to observe unexpected behaviors or contexts that can be used to develop predictions in humans (Brosnan, Newton-Fisher, & van Vugt, 2009). Although of course this can be done in humans, in animals there is no other way, which may lead to creative ways to “ask” questions through observational studies. Finally, in nonhuman primates, we can gain access to physiological data that may be difficult to obtain from humans. For example, cortisol or testosterone levels can be obtained simply and noninvasively from primate social groups, and both can be used to explore everything from the endocrinology of cooperative interaction to social stress related to dominance interactions (Trumble, Jaeggi, & Gurven, 2015; Wheeler, Tiddi, & Heistermann, 2014).

Building an Evolutionary Model of Social Anxiety

One of the primary motivating factors for human behavior is a need to belong, or to form relationships with others that are strong and enduring (e.g., Baumeister & Leary, 1995). As Baumeister and Leary (1995) specified, this need to belong is distinct from an indiscriminate need for social interchange; instead, it constitutes a “need for regular social contact with those to whom one feels connected” (p. 501). From an evolutionary perspective, such a powerful drive for consistent connection with valued others makes sense, given that individuals embedded in mutually supportive social networks should have preferential access to resources needed for survival and reproduction (Leary, 2001). Indeed, other primates also show such close ties, and new evidence shows unequivocally that, as with humans, relationship quantity and quality affect everything from longevity to offspring survival (Palombit, 2001; Seyfarth & Cheney, 2012; Silk, 2007; Silk, Alberts, & Altmann, 2003, 2006; Silk, Seyfarth, & Cheney, 2016; Silk et al., 2010; Smuts, 1985).

Not surprisingly, then, it is common for humans to experience social anxiety, or fears that others may evaluate them negatively and consequently ridicule or reject them—such experiences signal risk for exclusion from valued resources or for loss of rank or status (Leary, 2001). Consequently, when they feel socially anxious, people behave in ways that presumably help them to avoid such unpleasant outcomes

(Rinck et al., 2010). Such avoidant patterns commonly encompass deferential, withdrawn, and a broad range of other “safety” behaviors (Cuming et al., 2009).

The term “social anxiety” is commonly used in the psychological literature to refer to extreme manifestations of fear of negative evaluation and its associated behavior patterns. When SA leads to lasting distress across a broad spectrum of social settings, it can impede professional and academic advancement, prevent healthy relationship formation, and increase risk for substance abuse and depression (Ruscio et al., 2008; Schneier, Johnson, Hornig, Leibowitz, & Weissman, 1992; Stein & Kean, 2000). Such impairing symptoms cluster under the diagnosis of SAD, which is among the most common of all psychological disorders (Kessler et al., 2005). For individuals with severe or clinically significant SA, fears of rejection or negative evaluation are reinforced and perpetuated by cognitive biases to interpret ambiguous social cues through a negative lens and to assume that aversive social outcomes are highly probable and, when they occur, costly in terms of their likely effects on status and connection (Foa & Kozak, 1986; Stopa & Clark, 2000).

However, although the behaviors associated with SA can be problematic if selected in excess or in contexts in which alternate responses would lead to better outcomes, each is also a normal part of a healthy social repertoire. Deference and withdrawal, for instance, can confer advantages in some situations, by decreasing the risk that one will enact antisocial or otherwise inappropriate behaviors (Hermans & van Honk, 2006) or enabling one to escape from conflicts with dominant others (Weeks, Rodebaugh, Heimberg, Norton, & Jakatdar, 2009). Thus, transient and/or mild social fear, which most people experience to varying degrees in response to real social threats or challenges, likely has adaptive value.

Clinical Models of SA

Researchers have proposed numerous models to explain how and why SA develops and persists among humans (Clark & Wells, 1995; Heimberg, Brozovich, & Rapee, 2010; Hofmann, 2007; Moscovitch, 2009; Rapee & Heimberg, 1997; Schlenker & Leary, 1982). Schlenker and Leary (1982) were among the first to propose a conceptually integrated model, which centered on the idea that SA arises when people want to make good impressions on others, but lack confidence that they will be successful in doing so. This self-presentation model, which is rooted in social learning and interpersonal theories, shifted the focus from a traditional, psychodynamic view of “anxiety as drive” to a perspective in which anxiety is a constellation of emotional, cognitive, and behavioral responses that arise from a mismatch between perceived abilities and desired outcomes (Schlenker & Leary, 1982, 1985).

In the 1990s, researchers proposed two additional models, both of which revolved around the roles of attention and perception in the generation and maintenance of SA (Clark & Wells, 1995; Rapee & Heimberg, 1997). These distinct, but compatible, models both emphasize the role of attention to cues indicating social threat in both precipitating and perpetuating socially anxious behaviors and feelings,

particularly in people who assume that others will be critical and will hold them to unrealistically high behavioral expectations. Clark and Wells' (1995) model is built around the idea that signals of threat that are internal to the self (e.g., aroused autonomic responses in social settings) preferentially capture socially anxious people's attention. In other words, SA results when attention to the self is enhanced and processing of cues from the external world that might disconfirm social fears is diminished. In Rapee and Heimberg's model (Heimberg et al., 2010; Rapee & Heimberg, 1997), attention to both internal and external cues that social threats are present is considered important for the emergence and perpetuation of SA. Thus, socially anxious people persistently scan their internal and external environments for evidence that they are performing poorly and will be judged harshly or that they performed well, which could set the performance bar even higher. Further, this model proposes that a tendency to dwell ruminatively and vividly on negative aspects of behavior after social events increases the likelihood that socially anxious people will view themselves through a biased lens. Note that both self-presentational and cognitive models of SA are compatible with evolutionary perspectives.

Evolutionary Models of SA

In his presidential address to the Society for Psychophysiological Research in 1985, Öhman (1986) sketched out a model of SA that underscored the idea that this type of anxiety emerged as a function of specific biological pressures. In laying groundwork for his model, Öhman (1986) contrasted human responses to escaping an angry conspecific by running away with those to escaping a wild animal by running away. He argued that whereas the escape from a wild predator might lead to relief, the escape from an angry human might instead elicit shame or humiliation. An evolutionary perspective that takes into account the distinct behavioral systems that drive these two distinct responses to frightening stimuli provides one way to understand why fear of people might have evolved. In particular, Öhman (1986) contended that social fear constitutes the opposite pole of social dominance and that individuals within a group engage in complementary interactions distributed along this dimension in order to establish and maintain a stable social hierarchy that ensures social order. Within these interactions, social submissiveness serves to "avert attack by dominant conspecifics" (Öhman, 1986, p. 130).

In a more thoroughly defined evolutionary model of SA, Gilbert and colleagues (Gilbert, 2014; Trower & Gilbert, 1989) proposed, broadly, that a socially anxious pattern of emotional and behavioral response constitutes a vestigial response to social threat. Within this model, competition for social status engenders a particularly salient type of threat—status loss—and those with high levels of SA are considered to be acutely attuned to indicators that such loss is impending. Gilbert and colleagues' model is rooted in defense approaches that are adaptive in the context of social groups that revolve primarily around hierarchy, like those observed in some other species and much like those based in the dominance/submission system

around which Öhman's model is built. More specifically, Gilbert and colleagues argue that humans with SA operate interpersonally from a competitive stance that would be better suited to a purely hierarchical context. They thus fail to engage with others in friendly and affiliative ways that might actually better serve their goals of belonging, or being included and valued.

More recently, Gilboa-Schechtman, Shachar, and Helpman (2014) proposed an evolutionary model that resembles Gilbert and colleagues' model in that it encompasses both social rank and affiliative elements. Grounded in research on the expression and processing of emotional cues that signal warmth or dominance, this model draws upon Leary's (2001) idea that SA may alert individuals to threats to their integration within a valued social group. According to this model, fears of both exclusion and defeat are salient for the socially anxious person. Gilboa-Schechtman and colleagues contend that these fears may be adaptive in the context of unstable or volatile hierarchies, but in more stable and cohesive communities they may lead to problematic behavior.

Notably, these models are grounded largely in research on humans; although Gilbert draws upon the nonhuman primate research literature, he and his colleagues focus primarily on studies of dominant/submissive behavior in other species, with less attention devoted to research on affiliation and other types of positive interaction. If we aspire to develop a thorough and fully accurate evolutionary model of SA, it is important that we integrate up-to-date research on both humans and related species and take account of the ways that new findings shift our understanding.

Challenges to Existing Evolutionary SA Models

The Reality of Primate Conflict Behavior

One key problem with the current evolutionary models of SA is an incomplete view of primate behavior. As noted earlier, only Gilbert and colleagues' model draws heavily from research on nonhuman primates; however, their model was originally developed in the late 1980s. In the intervening 30 years, there has been a fundamental shift in how primate social behavior is perceived, which is not reflected in this model. At the time they developed it, research on nonhuman animals was primarily focused on aggression and striving for dominance, and little interest or thought was given to other aspects of social behavior. Around this time, researchers began to focus on more "positive" aspects of social behavior, demonstrating that animals maintain long-term, and apparently valuable, friendships; that these friendships enhance longevity and health; and that although conflicts certainly do occur, the animals work hard to repair and maintain their beneficial relationships.

One of the first well-known discussions of this shift in perspective came from Frans de Waal, an influential Dutch biologist. In the early 1980s, he published years' worth of observations of a large, multi-male, multi-female captive colony of chimpanzees at Berger's Zoo in Arnhem, the Netherlands. His report, entitled *Chimpanzee*

Politics, showed a markedly different side of these apes' behavior (1982). They were, indeed, focused on dominance, particularly the males, but dominance was not achieved by sheer force; instead, the apes developed a series of alliances that they carefully manipulated to gain and maintain power. In a dramatic example of this, when the leading males' coalition collapsed, within a day, the third male—who was individually stronger than either of the coalition partners—became the alpha.

As has gradually become clear, relationships are critical in nonhuman primates (Silk et al., 2006; Smuts, 1985). In most species, individuals begin life with a set of relationships derived from their mothers' social networks. These relationships are not static, however; individuals maintain these connections and develop new ones through grooming and other prosocial (i.e., positive) behaviors that strengthen social ties. Moreover, having such positive relationships is critical. For example, data from long-term field studies with baboons demonstrate that primates with more social ties are longer lived and have better infant survival than those with fewer such ties (Silk et al., 2003, 2010). Other evidence shows that nonhuman primates work hard to nurture their relationships; for example, baboons use vocalizations flexibly to build and maintain connections to others (Silk et al., 2016). This focus on building and maintaining *positive* relationships is different from the focus on aggression and dominance as the key to understanding primate social behavior that was predominant when Gilbert and Trower were developing their model.

Moreover, even the dominance hierarchy itself functions differently than research in the 1980s suggested. At that point, the hierarchy was conceived as a mechanism by which more dominant individuals were able to control access to resources (i.e., food, mates, sleeping sites) at the expense of more subordinate individuals. Of course, that is true to some extent. However, the degree to which it is true varies depending on the social structure of the species in question. Some species, like rhesus macaques, have strict, linear, despotic dominance hierarchies in which the more dominant can take anything that they wish. Others, however, such as chimpanzees, have much more relaxed hierarchies that both lack strict linearity (dominance relationships often depend on which other individuals are present) and are much more tolerant. In chimpanzees and capuchin monkeys, another tolerant species, subordinates can expect to maintain possession of resources. In chimpanzees, there is impartial support in conflicts, especially by high-ranking individuals breaking up fights among others (von Rohr et al., 2012). Indeed, even in the more despotic social systems we see policing, in which dominant individuals intervene impartially in fights to restore peace (Flack, de Waal, & Krakauer, 2005; Flack, Girvan, de Waal, & Krakauer, 2006).

In fact, the existence of the hierarchies themselves provides a stabilizing function as a mechanism for reducing conflict in day-to-day interactions among group members. Groups that have a strong, stable dominance hierarchy have few actual fights; incipient conflicts are ameliorated through a series of standardized signals and norms that resolve the conflict in ways that are predictable. These include, for example, unilateral, unambiguous submission signals that indicate that an individual is subordinate; a subordinate who gives such a signal is telling the dominant "I know you are dominant, we don't have to have a fight!" On the other hand, groups with

unstable dominance hierarchies endure repeated fights, lessened grooming, and substantially increased tension. Indeed, observers can predict when a dominance hierarchy is about to shift through increases in aggression and changes in the frequency and direction of these standardized signals (de Waal, 1982). A strong dominance hierarchy also reduces day-to-day aggression, because it obviates the need to fight each day to reestablish the hierarchy. Indeed, it is not *dominance* that leads to fights and conflict, but *uncertainty* about dominance that does so.

Moreover, once there has been conflict, animals work hard to repair relationships; again, it is not the relationships themselves—positive or negative—that appear to cause stress. Rather, it is uncertainty about where the relationship stands, or the risk that a positive relationship will not be repaired following a conflict (it is difficult to distinguish these two underlying motivations²). Reconciliation is defined as increased positive contact, as compared to baseline, between two former combatants. It is measured using an approach called the post-conflict/matched-control (PCMC) method (de Waal & van Roosmalen, 1979). In this, subjects are observed for some time period (typically 10–30 min) following a fight (post-conflict) and all instances of affiliation are recorded. Then subjects are recorded for another period of the same duration, at the same time of day, on a subsequent day when there was not a preceding fight in the group. Preferably, this second observation occurs the next day, but if these conditions are not met, it is done on the soonest subsequent day that meets those criteria (matched control). Subjects are considered to show reconciliation if they exhibit increased grooming in the period following conflict as compared to the matched control period. Using this methodology, reconciliation has been found to be widespread in primates (i.e., Cords, 1993; de Waal & Ren, 1988; Palagi, Antonacci, & Norscia, 2008; Pereira, Schill, & Charles, 2000) as well as other highly social nonprimate vertebrates (i.e., Schino, 1998; Wahaj, Guse, & Holekamp, 2001). Some have even argued for consolation, or positive contact with the victim by a third party (Romero, Castellanos, & de Waal, 2010; but see Koski & Sterck, 2007).

Overall, the updated view of primate social behavior focuses heavily on affiliation, not conflict, and on the role of positive relationships in everything from offspring survival to longevity. If anything, the new data emphasize the role of uncertainty in causing stress and anxiety; subjects appear to be most disturbed when

²There is an important distinction in evolutionary biology that deserves clarification here. When biologists talk about *evolutionary function* they mean the reasons why a given trait was selected (i.e., the evolutionary history and evolutionary function from Tinbergen's famous four questions; Tinbergen, 1963). An evolutionary mechanism, on the other hand, is the underlying architecture that enables the behavior (i.e., cognitive—Was it learned? Socially or individually?—mechanisms, neural architecture, hormonal underpinnings) and how the behavior developed. A related, but not entirely overlapping, point is that a mechanism does not imply any knowledge or intention. Therefore, if we say that an organism reconciles to reduce the uncertainty in the relationship, this simply mean that animals have been selected to perform certain behavior patterns that reestablish positive bonds, which is beneficial for their long-term fitness and is caused in the short term by the negative affect that accompanies the uncertainty. Note that the organism does not need to understand this or even have any goals; although this could certainly be a part of it, and is in some species, including humans, it need not be for the behavior to function as such.

the relationship is unknown rather than when the relationship is marked by a sharp difference in dominance. Moreover, the behaviors associated with anxiety may function not only to appease, but also to solicit positive contact. The good news is that this revised model of primate social behavior looks substantially more like human behavior than did the previous, despotic view. Further, evidence that primate social behavior more closely resembles that of humans raises the possibility that the evolutionary approach is even more relevant than previously believed. Nonetheless, this new information requires a rethinking of how we perceive the role of relationships and dominance in the evolution of SA.

Nuances of Social Behavior in Human SA

In addition to the deeper understanding that we have acquired regarding primate social behavior, new knowledge about SA has emerged over the past few decades that must be taken into account in evolutionary models. First, whereas early conceptualizations focused on fear of negative evaluation as the core cognitive component of SA, more recent research suggests that people with SA also fear positive evaluation (Weeks & Howell, 2012, 2014). Weeks and colleagues have suggested that those who see themselves as low ranking engage in a reflexive calculus aimed at ensuring not only that they avoid sinking to the bottom of the hierarchy, but also that they avoid *rising* to a status level that invites dominant peers to view them as threats (Weeks & Howell, 2012). Thus, SA may function to help preserve stability of the social hierarchy in both upward and downward directions.

This desire to “fly under the radar” and maintain the social status quo may relate to a second advance in our understanding of SA: as recent studies demonstrate, people with this condition call on a varied repertoire of behaviors to avoid losing or gaining social status. Early research on interpersonal behavior in SA focused on identifying behavioral deficits (Arkowitz et al., 1975), such as difficulty reading or producing social cues (Beatty & Beatty, 2001; Schroeder, 1995), and submissive “safety” behaviors (Daly, 1978; Fromme & Schmidt, 1972; Fugita, 1974). More recently, however, researchers have shifted attention to interpersonal behavior patterns and styles that characterize those with SA, and have used their data to paint a more complex and nuanced picture.

Findings suggest, first and foremost, that a strict focus on submissive actions or social ineptitude fails to capture the full range of social behavior associated with SA. Instead, there appear to be striking variations in interpersonal styles both across and within individuals with SA. Studies show that people with SA cluster into broad stylistic categories, with some interacting in a cold/quarrelsome way (e.g., demanding reassurance with increasing hostility) and others displaying a more friendly/submissive style (Cain, Pincus, & Grosse Holtforth, 2010; Kachin et al., 2001). Failure to show warmth to others appears to be particularly problematic. Rodebaugh and colleagues have found evidence, for example, that such interpersonal constraint, especially when combined with a tendency toward vindictiveness, leads people with SA to show progressively less generosity toward friends over a series of interactions

(Rodebaugh, Heimberg, Taylor, & Lenze, 2015; Rodebaugh et al., 2013). Further, people with SA who exhibit a friendly submissive style appear to respond better to psychotherapy, showing fewer symptoms and better adjustment after treatment than peers with a cold interpersonal demeanor (Cain et al., 2010).

An intriguing line of research into the degree to which individual people's social behavior vacillates across time and settings suggests that anxious people not only show elevations in both quarrelsomeness and submission, but also shift markedly—and more than depressed peers—among agreeable, dominant, and submissive behavior both during the course of a single event and across events over time (Rappaport, Moskowitz, & D'Antono, 2014). These data, although not specific to SA per se, suggest that at least some socially anxious people do engage in affiliative and cooperative ways. However, they may do so indiscriminately or unpredictably, potentially shifting away from approaches that might have been useful for deepening or enhancing relationships had they been used consistently.

Several areas of research into social behavior thus converge to suggest that people with SA engage in a broad range of behaviors that function in the short term to circumvent evaluation by others, but in the long term to keep the individual predictably situated in the social hierarchy, which is not always desirable. These behaviors vary among avoidant, hostile, and affiliative gestures; indeed, some evidence suggests that a fluid and variable interpersonal style may serve as a characteristic marker of anxious individuals. The degree to which context shapes both an anxious person's choice of behaviors and the regularity with which that individual engages in any given type of behavior remains unclear; clarifying the ways in which different people with SA respond to varying pressures in different social environments and community structures will be an important next step.

An Updated Model of SA

Clearly, an evolutionary perspective is critical for helping us to both understand the causes of SA and make better decisions about how to manage it. By highlighting the adaptive, as well as the maladaptive, aspects of SA, an evolutionary perspective could also help shift perceptions of this condition and decrease the stigma that affected individuals often face or fear. In this section, we update existing evolutionary models, taking into account the previously discussed changes in our understanding of primate social life, particularly the importance of developing and maintaining a strong set of positive relationships, and of human SA and how it relates to distinct patterns of interpersonal behavior. But before we outline the model, we address one area that we have alluded to, but not addressed in detail, the critical role that we hypothesize is played by the degree of uncertainty within the given social context.

The Important Role of Uncertainty

Clearly any updated evolutionary model needs to take into account new knowledge about primate relationships. In addition, however, it must also incorporate the best available evidence about what environmental challenges might engender SA or related emotional states. This evidence, for primates, points to uncertainty (i.e., about the social hierarchy or one's place in it) as a key challenge that warrants attention, consistent with existing evolutionary models of SA (Gilboa-Schechtman et al., 2014; Trower & Gilbert, 1989). If animals (including humans) cannot make reasonable guesses about where they stand and what will happen, how can they make reasonable guesses as to what to do next? Such uncertainty is distressing. Indeed, a growing literature identifies "intolerance of uncertainty" as an important predictor or correlate of SA in humans (Carleton, Collimore, & Asmundson, 2010; Teale Sapach, Carleton, Mulvogue, Weeks, & Heimberg, 2015).

Notably, as Grupe and Nitschke (2013) point out in their cogent model of the neural basis for anxious responses to uncertainty, the anticipatory cognitive and emotional processes that we engage when we are trying to ward off or lessen the impact of possible threats are typically adaptive. In other words, picking up on a real threat before it happens seems likely to enhance fitness and survival. Similar reactions to improbable threats, however, are less useful and may instead impede healthy functioning if they occur with excessive frequency or intensity. Thus, assuming that every instance of uncertainty will have negative consequences is, under most circumstances, going to be maladaptive. Grupe and Nitschke (2013) also note that uncertainty combined with uncontrollability is a particularly strong trigger for anxious responses. Indeed, this pairing has been linked with anxiety and distress across decades of research (Havranek et al., 2016; Miller, 1979; Mineka & Kihlstrom, 1978). The degree to which individuals see themselves as capable of managing, or at least responding effectively to, uncertain social contexts may thus also help determine how distressing those contexts are.

When Do We Expect Increases in the Expression of Anxiety?

Overall, then, we argue, consistent with existing evolutionary models of SA, that the core feature that elicits anxiety (in any situation) is uncertainty. When animals or people do not know where they stand, what is happening, or what the future will hold, they become anxious. In the social realm, this sequence may manifest in several ways.

First, we expect anxiety to be the most common when formerly stable relationships become unstable. This may occur as a consequence of conflict, but can also simply reflect the introduction of new and unfamiliar individuals to a group or the departure of familiar conspecifics. Note that we expect some level of anxiety in the face of instability in any relationships, not simply good ones or bad ones. Knowing that one has a poor relationship with another individual is better than not being sure whether the other individual will groom you or bite you; however, we would

nonetheless expect higher levels of anxiety when valuable relationships are unstable, regardless of the valence of interactions among the individuals involved.

Second, we expect that anxiety should increase in the context of aggression primarily when aggression is unexpected or when it is not properly reconciled. Unfortunately, however, it is difficult to measure this, as reconciliation reduces not only uncertainty about the relationship, but also anxiety, through grooming and other affiliative behaviors. Indeed, it is hypothesized that both uncertainty and inadequate reconciliation necessarily contribute to anxiety (see Fraser, Stahl, & Aureli, 2008; Kutsukake & Castles, 2001, for evidence that both of these factors are key, the so-called integrated hypothesis). However, there is some evidence that uncertainty plays a role distinct from the anxiolytic effects of positive contact. Even the aggressor seems to find the uncertainty of conflict stressful, and to show larger reductions in SBD after reconciled conflict than unreconciled ones; in this case, though, body contact with other individuals did not reduce SBDs, indicating that the effect is specific to the individual with whom there was a conflict (Das, Penke, & Van Hooff, 1998). This supports a primary role of uncertainty reduction.

Finally, we expect anxiety in all individuals, dominant or subordinate, in situations of social uncertainty. Very low rank is certainly stressful, but even high-ranking individuals may suffer from extremely high levels of stress (Sapolsky, 2004). Susceptibility to stress for individuals of high rank may be greatest when their rank is unstable (i.e., they are ascending, being challenged, or are young; Knight & Mehta, 2017). Further, at these inflection points, individuals of all ranks may be especially doubtful that their social context is within their control, because shifting circumstances may call for them to use new or unpracticed social skills.

When Does Anxiety Become Pathological?

Of course anxiety in these contexts is not pathological; it's completely typical. And that is a key point—some anxiety is not only expected, but also beneficial. Much like pain lets you know to pull your hand away from the fire, anxiety lets you know it is time to seek out the object of your anxiety and see if you can (re)establish, and potentially improve, the relationship's parameters.

But when does such anxiety become pathological? We argue that pathological SA occurs when this system goes into overdrive, with subjects failing to establish stable relationships, perceiving uncertainty in relationships that are not actually there, or overreacting to even subtle cues of instability. When these missteps occur repeatedly, which may be especially likely to happen in uncertain contexts, individuals may become increasingly prone to read others' cues through a biased lens, which results, in turn, in recurrent failure to recognize opportunities to form relationships or instances when relationships are not stable. These failures are likely to have negative repercussions that provoke distress. In such cases, we would expect high levels of anxiety-related behaviors (SBDs such as self-scratching, self-grooming, yawning, or body shaking) or hormones (i.e., cortisol), atypically large spikes following moderately uncertain situations, or spikes in situations to which

other individuals (or the same individual, in secure contexts) do not react. These are all empirically testable questions, allowing us the opportunity to test and refine this hypothesis.

One additional thing to remember—following the tradition of behavioral phylogeny, what we are outlining is the early stages of the evolution of SA, with the ultimate goal of understanding how this developed into the suite of emotional and behavioral patterns that we see in humans with SA today (i.e., Brosnan & de Waal, 2014; Brosnan et al., 2009). Humans, with our substantially more complex cognition and social environments will have developed additional symptoms, situations that elicit SA, and so forth. What is important, though, is to break SA into its component parts in order to determine the original function of (non-pathological) SA, to delineate how it was originally expressed pathologically, and then to figure out how human clinical SA developed from this. Mel Konner (2002) has likened this process of discovery to considering how a bird caught in a thicket could escape; in principle, the bird has limitless options, but in reality, the ways in which its wings are tangled constrain it to a few realistic choices. Much as with the bird's wing, we need to figure out not the limitless ways SA *could* have evolved, but the constraints that forced it into the current path (Konner, 2002). Only in this way can we understand the root causes of the condition and its associated behaviors and then trace the key aspects that developed along the way.

What Makes Humans Stand Apart?

Humans express SA differently than other primates, so one important key will be determining which aspects of distinctively human behavior and cognition were critical in reshaping SA. For example, although some primates, and in particular apes, appear to have a limited theory of mind (Boesch, 1992; Hare, Call, Agnetta, & Tomasello, 2000), most lack the sophisticated sense of self that humans possess. Nonhuman primates are thus not likely to be as vulnerable as are humans to distress associated with insult to one's self. One key question when considering human SA is the degree to which this uniquely human vulnerability to insults to the self combines with discomfort with uncertainty to underpin SA.

In addition, humans have evolved two more distinctive capacities that add nuanced layers to the basic foundation of SA. First, we have a complex sense of "other" that engenders an advanced type of empathy (Watt & Panksepp, 2016). Although empathy is, in many contexts, helpful for strengthening social ties, a growing body of research suggests that it can also be problematic by leading to distress (Tone & Tully, 2014). How this ability to place ourselves vividly in others' shoes interacts with the tendency to experience distress in contexts of social uncertainty remains unclear and warrants further investigation. For example, highly empathic people may overread others' subtle cues (Chikovani, Babuadze, Iashvili, Gvalia, & Surguladze, 2015), thus potentially picking up on evaluative signals that were not intended to be public and consequently responding in unwanted ways. These people may also, due to their sensitivity to others' distress, respond

preferentially to others' evaluative cues in a friendly submissive way that has its own distinctive set of risks and rewards from that associated with a cold/quarrelsome style. Empirical work examining how individual differences in empathy relate differentially to SA and related behavior across species and social contexts is a potentially useful next step.

Humans' ability to look forward in time and anticipate how a behavior in the moment might affect future outcomes is particularly sophisticated (Roberts, 2002). This ability to project oneself forward in an abstract and hypothetical way may make humans more acutely aware of the uncertainty inherent in social life—unlike members of other species, we must grapple not only with today's instability, but also the instability that might arise tomorrow and the next day. Although being able to imagine that the future has clear advantages, it also sets humans up to brace for negative outcomes that may never occur. Members of more present-oriented species thus play on a necessarily simpler field, with only immediate social cues to take into account when evaluating where one stands in the hierarchy.

Not only do humans have some characteristics that vary markedly from those of other species, but we also live in social structures that differ in key ways from other primates'. In particular, we relate to strangers in a much more complicated way than do members of most other species. In primates, interactions with strangers are basically consistent—you generally want to keep them away or get away from them. In humans, in contrast, interactions with strangers are more of a gamble. They can be advantageous, opening one up, for example, to new resources and avenues of support, or may be dangerous. Humans thus have additional decisions to make about when social environments are safe and they also face a constant stream of threats to the stability of their social hierarchies, given the fluidity with which strangers enter social groups.

Conclusion

Humans have developed what may be the most flexible social system of any animal, but with this flexibility come costs; we also suffer greater uncertainty as to our place in that system, and how we influence or are influenced by other humans. When considering this, it is not surprising that socially mediated anxiety is so common. Our goal in this chapter has been to emphasize ways in which taking an empirically informed evolutionary perspective can help us to better understand SA, better predict the contexts and individuals in which it will emerge, and better determine when it is appropriate to treat the symptoms, versus the cause, versus neither.

Of course, we cannot yet answer that question. Thus, our secondary goal was to provide a hypothesized framework that could be used as a starting point to test specific predictions that will further refine our understanding. Some of these studies will need to be done with nonhuman species, to better understand how our reactions fit with the animal kingdom or to utilize a model systems approach to study questions that are not empirically tractable in humans, and some will need to be done

with humans. Each will provide a better way of understanding the ways in which SA is derived from what we believe were (and are) rational and beneficial reactions.

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