Evolutionary Perspective on Social Anxiety

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The social world is a perilous place. With few lions in sight, and too much sweet and caloric food around, it is people, rather than predators or hunger, that constitute the main perils of modern life. New acquaintances may be hostile and sardonic. Potential romantic partners might ignore or reject our advances outright. Friends may find us lacking in social graces. Audiences may mock us as we make our speeches. Our bosses might jeopardize our efforts to ascend on the corporate ladder. It is therefore not surprising that in modern societies fear of public speaking is more prevalent than fear of snakes or spiders (e.g., Fredrikson, Annas, Fischer, & Wik, 1996; Stein & Walker, 1996).

AN EVOLUTIONARY PERSPECTIVE ON SOCIAL LIFE

Like most primates, humans live in groups. Given the stability of this arrangement, it can be assumed that the advantages of group living outweigh their disadvantages. Group living is thought to confer significant survival advantages through facilitation of resource acquisition, the protection it offers against predators (Silk, 2007), and the secondary benefits of territory defense and alloparenting (Dunbar, 1988). However, such advantages come at a cost, most of which seem to be related to the hierarchical nature of the group (Buss, 1991). In order to maintain stability, hierarchy is achieved by displays of social dominance on the one hand, and submissiveness on the other (Sapolsky, 2005). To successfully navigate in the interpersonal world, one needs to resolve the inherent tensions in group living by being able to cooperate with others, while still defending one's social standing. Inability to successfully traverse this complexity results in fewer social contacts and in a decline in prestige, both of which are associated with reduced health and well-being (Baumeister & Leary, 1995; Rivers & Josephs, 2010). Socially anxious individuals appear to suffer from difficulties in achieving this balance.

Examining the functioning of the two-biobehavioral systems may facilitate the understanding of the core mechanisms in social anxiety: social rank (including dominance, competence, agency, power, instrumentality, and authority) and affiliation (including communion, safety, warmth, morality, and expressiveness). Indeed, the realization that two similar fundamental dimensions (the "Big Two") underlie much of social judgment and social behavior has been integrating several lines of research in basic and applied psychology (Abele & Wojciszke, 2013).

Social rank and affiliation biobehavioral systems

Over the evolution of human sociality, individuals have taken part in several social structures (e.g., Bugental, 2000). The two most prominent ones are affiliative and hierarchical relationships. The need to affiliate with or belong to a social group is considered one of the central social motives across species, with systems in place monitoring both inclusionary status (Baumeister & Leary, 1995) and social rank (Sapolsky, 2005). Social exclusion (i.e., ostracism or social rejection) and social submission (e.g., being defeated or disgraced) may threaten one's place within a social group, decreasing one's chances of obtaining influence and collaboration and, thereby, access to group resources. In contrast, social acceptance and social ascendance increase one's chances of flourishing socially.

Social rank biobehavioral system (SRBS)

Social hierarchies are ubiquitous among social species (Silk, 2007). In order to gain access to resources such as food and mates, group members engage in competition, and dominant members of the group gain advantage. Such competition can lead to aggressive interactions (West-Eberhard, 1979). Stable social organization reduces the costs of social competition (e.g., Sloman, Atkinson, Milligan, & Liotti, 2002). Humans and other mammals appear to have developed a specialized biobehavioral system that monitors for social status, referred to as rank regulation system (Zuroff, Fournier, Patall, & Leybman, 2010), the hierarchical domain (Bugental, 2000), power system (Shaver, Segev, & Mikulincer, 2011) or the dominance behavioral system (Johnson, Leedom, & Muhtadie, 2012). The social rank system is conceptualized as a special biologically-based behavioral system, which constantly monitors one's standing in relation to others and uses that information to guide behavior (e.g., Johnson & Carver, 2012).

Neuroimaging evidence supports the role of several limbic as well as cortical circuits in the processing of social rank among humans (Beasley, Sabatinelli, & Obasi, 2012; Chiao et al., 2009). The most frequently studied biochemical substrate related to SRBS is testosterone (e.g., Schultheiss & Wirth, 2008). Testosterone has been found to correlate with self-report, observational, and cognitive measures of dominance in men and women alike (e.g., Archer, 2006;

Sellers, Mehl, & Josephs, 2007). Recent findings also point to the importance of estradiol in female social rank and dominance (Stanton & Schultheiss, 2009). The SRBS is geared to coordinating responses to changes in social power structures, emerging early in development (Thomsen, Frankenhuis, Ingold-Smith, & Carey, 2011), monitoring non-verbal signals such as gaze, voice, gestures, and postures (e.g., Cheng & Tracy, 2013; Hodges-Simeon, Gaulin, & Puts, 2010; Strongman & Champness, 1968; Weisfeld & Beresford, 1982), and operating automatically (e.g., Moors & De Houwer, 2005). In sum, SRBS appears to be a coherent system organizing behavior-concerning changes in the hierarchical organization of a group.

Affiliation biobehavioral system (ABS)

Cooperation with others and close social bonds play a key role in increasing the chances of survival across species. Indeed, an evolutionarily based biobehavioral system designed to gauge inclusionary status is postulated to be constantly operating among social species (Baumeister & Leary, 1995). The need to belong is so basic, that thwarting it is found to activate neural circuits that partially overlap with those of physical pain (e.g., Dewall et al., 2010; Eisenberger, Lieberman, & Williams, 2003). Neurally, exclusion and rejection have been associated with activation in limbic and cortical regions (Cristofori et al., 2012). Individual differences in sensitivity to social exclusion are associated with greater neural reactivity in these regions (e.g., DeWall et al., 2012).

Two major endocrine substrates have been associated with affiliative behavior: oxytocin, a neuropeptide, and progesterone, a steroid gonadal hormone. Baseline levels of oxytocin have been found to correlate with self-report, observational, and cognitive measures of affiliation in men and women (see Feldman, 2012), to enhance attention to social cues (Norman et al., 2011), and to regulate interpersonal stress (Taylor et al., 2000). Progesterone has been associated with affiliative experiences, covarying with time spent alone or with others (Brown et al., 2009) and with affiliative motivation (Schultheiss et al., 2004). Such evidence points to the existence of a complex affiliation system involved in coordinating the response to ruptures in, and opportunities for social bonds.

Evolutionary models of social anxiety from the perspective of the two biobehavioral systems

Several evolutionary models emphasized the role of the social rank system in social anxiety. Öhman (1986) postulated that the evolutionary origin of social fears lies in a dominance-submissiveness system. Encounters geared to establish social hierarchy may include symbolic gestures of dominance directed towards acquiring high rank, as well as submissive gestures aimed to avoid harm. Öhman argues that these submissive gestures epitomize social anxiety.

Trower & Gilbert (1989) proposed that socially anxious individuals tended to be "locked into", or over-utilize the social rank system, and under-utilize the affiliation system. Socially anxious individuals are attuned to cues and signs of dominance and to the competitive dynamic of the social world, frequently at the expense of the attunement to signals of affiliation. Because socially anxious individuals evaluate themselves as low in social attractiveness, they fear making bids for status or approval, since these claims are associated with conflict, disgrace, or rejection. The fear of competition on the one hand, and the need to remain in the social arena on the other hand, lead them to recruit verbal and non-verbal submissive behaviors to manage these conflicts (e.g., eye-gaze avoidance, self-derogation) (Gilbert, 2001). Multiple recent investigations supported this account (Aderka, Weisman, Shahar, & Gilboa-Schechtman, 2009; Sturman, 2011; Weeks, Heimberg, & Heuer, 2011; Weisman, Aderka, Marom, Hermesh, & Gilboa-Schechtman, 2011; Zuroff et al., 2010).

Hermans and van Honk (2006) highlight the possibility that, under certain circumstances, social anxiety may be adaptive. They propose that the adaptive function of social anxiety is rooted in ancient communicative systems that regulate social order and inhibit inappropriate and antisocial behaviors. Weeks and colleagues (2008) elaborate this line of thinking, suggesting that the tendency to avoid evaluations and to exhibit submissive behaviors helped some individuals to cope with social threats by dodging conflicts with powerful others. Whereas submissive behaviors may be adaptive in aggressive environments, in prosocial environments fear and submissiveness are potentially unattractive, and may hinder the individual in fulfilling various social goals such as attracting peers and partners or impressing powerful others (e.g., Taylor & Alden, 2011; Weeks, Rodebaugh, Heimberg, Norton, & Jakatdar, 2008).

Leary's account (Leary, 2001) proposes that social anxiety functions as a mechanism designed to prevent social rejection or exclusion, thus linking social anxiety to the functioning of the affiliation/belongingness system. According to his model, one of the individual's main social tasks is to monitor their level of relational value in the eyes of others. In order to do so, a specific motivational-affective system (sociometer) has evolved (see Leary & Jongman-Sereno, 2013, Chapter 20). Acting in continuous and automatic fashion, the sociometer serves as part of an exclusion warning system, which also motivates the organism to take corrective actions in order to ensure that they remain a valued relationship partner. Social anxiety may represent an overly sensitive sociometer system that generates many "false alarms." A warning signal from the sociometer leads to a wide gamut of negative feelings, as well as a rise in self-awareness. Heightened self-awareness is experienced as troubling, and prevents socially anxious individuals from devoting their full attention to the tasks at hand. However, enhanced concern regarding one's relational value may jeopardize one's ability to initiate and maintain social bonds.

In our view, social anxiety is characterized by (1) a thin-skinned disposition to matters of social rank; (2) a propensity to respond to social rank changes by lowering one's social profile (aka submissiveness, subordination), and (3) an

enhanced *coupling* of the ABS and SRBS systems, such that a negative change in one system carries over to the other. For example, social anxiety might involve linking exclusion to demotion and defeat to rejection. We agree with the emphasis on the role of the social rank system in social anxiety (e.g., Aderka, Weisman, Shahar, & Gilboa-Schechtman, 2009; Haker, Aderka, Marom, Hermesh, & Gilboa-Schechtman, 2013). However, like Leary (2001), we recognize the involvement of the affiliation system as well. From an evolutionary point of view, it seems reasonable that the linkage between the two systems contributes to "social cautiousness" (or to the sensitivity of the sociometer) in that it alerts the individual to changes in social fortunes. Clearly, while such sensitivity may be advantageous in unstable hierarchies and shifting alliances, it may backfire in moderately benevolent and cohesive social groups.

To examine this proposition, we review research from a wide array of empirical findings. Firstly, we focus on the perception and expression of non-verbal cues, conveying information regarding emotions and social intentions. Next, we explore the ways in which socially anxious individuals form impressions of others. We then briefly explore the developing understanding regarding the translation of these evolutionarily based systems into the online social sphere. Finally, we outline findings concerning the reactions of socially anxious individuals to events signaling changes in social standing and belongingness.

PROCESSING AND EXPRESSION OF EMOTIONAL SIGNALS

Affection and dominance are frequently expressed nonverbally via face, voice, and posture (e.g., App, Reed, & McIntosh, 2012). Until recently, research on the processing and expression of emotional signals has focused on the perception of emotional facial expressions (EFEs), and the expression of emotions by facial changes such as eye gaze. The past decade has witnessed an increase of interest in vocal and postural expressions of emotions as well.

Faces

Most research on the perception of emotional facial expressions (EFE) in social anxiety has examined biases in the perceptions of EFEs conveying threat or disapproval (Heinrichs & Hofmann, 2001; Staugaard, 2010). In no-stress conditions, social anxiety is associated with generalized reactivity to emotional and neutral faces alike. In addition, in some, but not all tasks, social anxiety is associated with selective processing of threatening EFEs (e.g., Gilboa-Schechtman et al., 1999; Schofield, Johnson, Inhoff, & Coles, 2012) and this bias appears to be modulated by the direction of the targets' gaze (e.g., Roelofs et al., 2010). Thus, socially anxious individuals appear to be hyper-sensitive to expressions connoting dominance.

Smiling facial expressions sometimes lead to reactions that are similar to the reactions to threatening EFEs. For example, Gilboa-Schechtman and

colleagues found that individuals with SAD had greater difficulty to disengage from smiling, as well as from angry facial expression (Gilboa-Schechtman, Foa, & Amir, 1999). Campbell and colleagues (2009) found that individuals with SAD rated smiling faces as less approachable than did normal controls. Using a priming task, Yoon & Zinbarg (2007) found that social anxiety was associated with a faster latency to correctly label angry and disgust expressions when primed by neutral expressions. Moreover, this association was also found when disgust expressions primed smiling expressions. On approach-avoidance task, Heuer, Rinck, & Becker (2007) found that highly socially anxious individuals exhibited avoidance for smiling, as well as for angry faces, as reflected by faster pushing than pulling of these faces when presented on a screen. Roelofs et al. (2010) replicated and extended those findings, using facial expressions with direct and averted gaze. Compared to individuals low in social anxiety, highly socially anxious individuals tended to avoid smiling faces irrespective of gaze direction, but avoided angry expression only when direct (versus averted) gaze was present.

It has been commonly assumed that smiles are "positive" stimuli, because smiles are the most common visual expressions of affiliative intent. Yet, smiles are intrinsically ambiguous as they may convey contrasting intentions such as enjoyment and affiliation, as well as dominance (Niedenthal, Mermillod, Maringer, & Hess, 2010). It has also been suggested that certain smiles may represent the facial component of pride expressions (Tracy & Robins, 2008). The similarity of socially anxious individuals' responses to smiles and to angry expressions can be conceptualized as the propensity to mistake signals of affiliation for displays of dominance.

Social intent and motivations are frequently expressed by the eyes (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). Avoidance of eye contact may be a central characteristic of SAD (e.g., Schneier, Rodebaugh, Blanco, Lewin, & Liebowitz, 2011). Indeed, this avoidance is consistently found to be associated with the severity of social anxiety (e.g., Stein, Kasper, Andersen, Nil, & Lader, 2004).

Eye contact has been found to increase with successful treatment (e.g., Schneier et al., 2011). Eye tracking studies have shown less gaze fixations on the eyes when facial expressions have been presented for relatively long time intervals (e.g., Moukheiber, Rautureau, Perez-Diaz, Jouvent, & Pelissolo, 2012). Importantly, gaze avoidance has been linked to submissive behavior in a variety of species (e.g., Mazur & Booth, 1998). The findings of the gaze literature are consistent with the view that socially anxious individuals tend to respond to interpersonal challenges by lowering social profile.

Voices

Prosody has been the main variable of interest in the perception of vocal features. It informs others about the emotional state of the speaker, thus enhancing

the ability to appropriately react and interact in social contexts (see Bostanov & Kotchoubey, 2004). The first study to examine interpretation of vocal expressions of emotion found that individuals with SAD tend to over-label various utterances as fearful or sad (Quadflieg, Wendt, Mohr, Miltner, & Straube, 2007). A follow-up study found that people with SAD exhibited increased neural activation to angry versus neutral prosody (Quadflieg, Mohr, Mentzel, Miltner, & Straube, 2008).

SAD is not only associated with biased perception or interpretation of threatening vocal features, but also with a distinct pattern of vocal expression. Average fundamental frequency of speech (mF0) is an objectively measured variable, subjectively perceived as pitch. Bigger body size is associated with lower mF0, and by lowering mF0 organisms appear larger than they are (Ohala, 1984). It has been argued that low pitch is associated with higher levels of dominance and therefore constitutes a potential threatening signal in various species (e.g., Puts, Gaulin, & Verdolini, 2006). Several studies have found that social anxiety is associated with high mF0 in both planned and spontaneous speech. Weeks and colleagues found higher levels of mF0 in SAD individuals during a public speech (Weeks et al., 2012), a tendency which appeared to subside following pharmacological treatment (Laukka et al., 2008). In a study assessing features of male voices under competition over female attention, Weeks, Heimberg, & Heuer (2011) demonstrated an increase in mF0 in highly socially anxious men, while men low in social anxiety showed the opposite trend. Social anxiety was also associated with higher mF0 for command versus neutral sentences in nostress conditions (Galili, Amir, & Gilboa-Schechtman, 2013). Combined, these studies suggest that social anxiety is associated with hyper-responsivity to the perception of vocal signals of dominance, as well as with a propensity to respond with appearement in the face of dominance activation.

Body and posture

Body movements and postures are additional aspects of non-verbal social cues conveying social standing in various species (e.g., Hinde & Rowell, 2009). In humans, body movements have been established as an effective tool in conveying and recognizing affective states (Bianchi-Berthouze, Cairns, Cox, Jennett, & Kim, 2006). Dominant postures, for instance, were accurately judged even after a brief exposure of 40 milliseconds (Rule, Adams, Ambady, & Freeman, 2012).

A handful of studies assessed the perception of postures as signaling social threat (such as dominance or anger) in socially anxious individuals. Pitterman and Nowicki (2004) found that correct labeling of postures depicting various emotions was negatively associated with fear of negative evaluation. Errors in identifying angry postures were also evident in highly socially anxious children (Walker, Nowicki, Jones, & Heimann, 2011). Although preliminary, these findings suggest that social anxiety may be associated with biased processing of dominant postures.

Weeks and colleagues found that social anxiety was associated with an increase in body collapse in men during competition situations (Weeks et al., 2011). Other studies argued that socially anxious individuals exhibited more bodily discomfort during social or performance tasks, such as rigidness and fidgeting (e.g., Heiser, Turner, Beidel, & Roberson-Nay, 2009; Voncken & Bögels, 2008). These behaviors may be seen as signs of anxiety, thus conveying a less dominant and threatening body language.

As in the case of facial and vocal signals, the findings with respect to posture seem to strengthen the link between social anxiety and hyper-responsivity to the perception of dominance signals. Moreover, social anxiety is associated with difficulty in conveying dominance even in non-evaluative conditions, as well as with a propensity to respond with appeasement in the face of social rank challenge. So far, no study assessed the vocal and postural properties of affiliative perception and expression in social anxiety. Examining these links is important for understanding whether, and under what conditions, affiliative processing and behavior are compromised in social anxiety.

PERSON PERCEPTION

People use non-verbal information to form impressions about others' momentary emotional states, as well as about their traits. Indeed, impression formation or person perception is one of the first steps in establishing a relationship. In the context of social anxiety, perceiving others as judgmental, critical, or domineering can lead to protective behaviors such as withdrawal or lack of self-disclosure. These protective behaviors might in turn lead to interpersonal rejection (Alden & Bieling, 1998).

In the dynamic social world, individuals are typically not passive recipients of information, but rather engage in an active process of information gathering. Actively seeking information about others is a central process of impression formation (e.g., Smith & Collins, 2009). In a recent study, we engaged individuals with clinical SAD as well as non-anxious controls in an impression formation task (Aderka, Haker, Marom, Hermesh, & Gilboa-Schechtman, 2013), with the ultimate goal of forming an impression regarding several protagonists. Participants were instructed to obtain as much information as possible in order to rate these protagonists on social rank and affiliation related traits. We found that, compared to non-anxious individuals, individuals with SAD sought less information about others. This tendency was especially pronounced when the initial information about the protagonist was focused on their social-rank aspects. We also found that individuals with SAD-rated protagonists described as dominant during the information gathering stage as being higher in social rank as compared to non anxious individuals.

In a follow-up study, we also examined how people update their impressions once they receive additional information concerning an individual (Haker et al., 2013). SAD individuals rated dominant others more extremely on the

social rank dimension than did non-anxious controls. Importantly, individuals with SAD revised their impressions of others to a greater extent than did non-anxious individuals, thus exhibiting enhanced reactivity to social rank information. Finally, individuals with SAD rated others as lower in affiliation than did non-anxious individuals. The latter finding suggests a negative bias in the evaluation of affiliation in individuals with SAD.

Combined, our findings suggest that socially anxious individuals are likely to err on the over-cautious side when estimating other people's social status (and over-estimate their own). Indeed, recent studies show that erring on the "overly-confident" side may lead to significant social costs (e.g., Anderson, Ames, & Gosling, 2008). Specifically, individuals who overestimated their social standing were evaluated as less amicable and more disruptive (Anderson et al., 2008). Constantly monitoring others' social rank may help avoid conflict and prevent defeat. However, this cautiousness may come at a cost, as it may thwart socially anxious individuals' aspirations of getting some of the social limelight.

SELF-PRESENTATION IN THE VIRTUAL SPHERE

As modern technology evolves, the social and collaborative functions of the Internet are expanding. In fact, the social arena has partially migrated to the digital sphere with the emergence of social network sites and the reliance on computer-mediated communication. Social boundaries are redefined and the constraints of previously known social structures (e.g., schools, neighborhoods etc.) are alleviated.

In this context, threats to social belongingness and status may be compounded and reinterpreted. Non-verbal cues of dominance and affiliation are substituted with graphic and verbal cues, which developed in the unique climate of computer-mediated communication (for example, comments on a Facebook status, or "likes" on a photo). These convey important information regarding the inclusionary status of a group member as well as his or her social rank. As in the case of face-to-face communication, accurately responding to these cybersignals is crucial for a successful social outcome. For instance, social exclusion and rejection may have a poignant effect when transmitted through various online behaviors, regarded as cyberbullying (DeAndrea, Tong, & Walther, 2011).

Social sites' profiles are an important aspect of social living in today's world, as they are common means through which interactions are managed. One of the major challenges in online social interactions is self-presentation in the absence of many non-verbal signals. Visual and verbal cues presented by the user are the prism through which one's personality is communicated. Indeed, visual factors of Avatars were found to accurately predict users' personality. For instance, wearing a pink shirt or high heels were linked to the female users' extraversion (Bélisle & Bodur, 2010). Objective measures of Facebook profiles were found to accurately predict personality characteristics (Back et al., 2010; Buffardi &

Campbell, 2008). Similarly, Fernandez, Levinson, and Rodebaugh (2012) demonstrated that levels of social anxiety were accurately predicted from Facebook profiles, based both on subjective impressions and objective measures.

These findings suggest that Facebook is not as far from the proverbial ancestral caves as might be expected. The new media are still a fertile ground for the display of one's inclusionary status, attractiveness, and social aspirations.

RESPONSES TO EVENTS CONNOTING CHANGE IN SOCIAL STATUS

Loss of social status: Shame, humiliation, and defeat

Shame and humiliation are self-conscious emotions, evoked in social situations and associated with submissiveness (Gilbert, Pehl, & Allan, 1994; Keltner & Harker, 1998). Defeat is frequently followed by shame and humiliation as it typically results in a decrease in one's social standing.

Shame is conceptualized as the perception that one's personality characteristics, attributes, or behaviors are inadequate and inferior. Shame is related to self-criticism and self-blame, and was found to relate to social anxiety (e.g., Gilbert & Miles, 2000; Shahar, Soffer, & Gilboa-Shechtman, 2008). This association remains significant even after controlling for depression and other anxiety symptoms (Gilbert, 2000). Additionally, patients with SAD demonstrated a reduction in self-reported shame ratings following a CBT intervention (Hedman, Ström, Stünkel, & Mörtberg, 2013). The expression of shame has been linked to non-verbal behaviors conveying submissiveness, such as eye gaze avoidance, speech disturbances, and slumped postures (Keltner & Harker, 1998). Self-report scales also demonstrate a consistent link between shame and submissive behavior (Gilbert & Allan, 1996; Gilbert & Miles, 2000).

Humiliation is defined as "[a reduction] to a lower position in one's own or other's eyes" (Merriam-Webster Dictionary). Humiliation has been found to be associated with intense feelings of anxiety, shame, anger and depression (e.g., Kendler, Hettema, Butera, Gardner, & Prescott, 2003). Although humiliation appears in the very definition of social anxiety disorder (APA, 2000), no existing studies we are aware of specifically tested whether socially anxious individuals are more likely to experience social encounters as humiliating. Given the centrality of status concerns in social anxiety, humiliation appears to be a central emotion to be explored among individuals with this disorder.

Being defeated in a head-to-head competition has been shown to lead to a host of psychologically and physiologically negative outcomes (e.g., Mehta, Jones, & Josephs, 2008; Sturman, 2011; Wirth & Schultheiss, 2007). In one of the only studies to explore how socially anxious individuals cope with defeat, Maner and colleagues examined the responses of individuals to a defeat in a face-to-face competition with a same-sex confederate (Maner, Miller, Schmidt, & Eckel, 2008). They found that socially anxious men exhibited a drop in

testosterone following a defeat, while men with low social anxiety did not. Such hormonal responses are consistent with submissiveness and a motivation to avoid further competition, possibly reflecting an appearement strategy of dealing with conflict.

Social power or leadership

Recent research suggests that social anxiety might impair people's ability to experience the psychological benefits typically associated with the experience of power. For example, Maner and his colleagues found that socially anxious individuals tended to mention fewer feelings of control, authority, or influence following a recollection of an experience involving power or following an imaginary leadership encounter (Maner, Gailliot, Menzel, & Kunstman, 2012). Moreover, Maner and his colleagues assigned individuals to a managerial position based on their responses to a questionnaire ostensibly measuring leadership ability. Following this assignment, participants interacted with an oppositesex confederate either as equals, or under conditions in which participants had power over their partner. They then evaluated the participants' assessments of the partners' sexual interest in them. While under conditions of power, individuals low in social anxiety experienced an increase in perceived attractiveness, while individuals high in social anxiety exhibited an opposite tendency. Based on these findings, the authors suggest that social anxiety insulates individuals from interpreting their environment as socially rewarding.

The "insulating" effects of social anxiety are also consistent with the findings on the interactive effects of testosterone and cortisol (Mehta & Josephs, 2010). Leadership performance of men and women with high levels of testosterone was related to higher observer's ratings of dominance when cortisol was low, whereas this relationship was either blocked or reversed in individuals high in cortisol. Because high levels of cortisol are strongly associated with anxiety severity and with social avoidance, these results can be seen as supporting the role of social anxiety as impairing or down-regulating the observed rewards of social ascendance.

Taken together, these findings suggest the need to explore the potentially regulatory effects of social anxiety on the experience of, and reactions to elevations in social rank. Specifically, endocrinological markers of SRBS (e.g., testosterone and estradiol) may interact with markers of general anxiety to hinder the hedonic and agency-enhancing effects of social ascendance and social attention.

Pride

Pride has been conceptualized as a self-conscious emotion that signals the accomplishment of a valued task to members of the group, enabling an individual to improve their social standing within the social hierarchy (Tracy &

Robins, 2007). Recent findings link depression to a decreased propensity to experience pride as assessed by self-report and experimental manipulation (e.g., Gruber, Oveis, Keltner, & Johnson, 2011). Given the high comorbidity between social anxiety and depression on both a symptom and a syndrome level (Brown, Campbell, Lehman, Grisham, & Mancill, 2001), it seems especially important to examine the association of pride and social anxiety.

Evidence thus far suggests that social anxiety is associated with more intense reactions to loss of status coupled with diminished reactions to social ascendance. Future research may examine whether loss of social status is associated with changes in belongingness and motivation for the formation and enhancement of close social bonds. Given the propensity of socially anxious individuals to engage in upward social comparison (Antony, Rowa, Liss, Swallow, & Swinson, 2005), and the possible detrimental effects of such comparisons on social bonds (Nicholls & Stukas, 2011), this line of research may extend our understanding of the affiliative impairments in social anxiety.

RESPONSES TO CHANGES IN BELONGINGNESS

Social Exclusion

Social exclusion has been found to profoundly affect individuals' subjective, cognitive, behavioral, physiological, motivational, and endocrine responses (e.g., Wesselmann & Williams, 2011; Wirth & Schultheiss, 2006). Given the possibility of social acceptance, excluded individuals are likely to attempt to reconnect, whereas when such a possibility is not forthcoming, such attempts may be abandoned (DeWall & Richman, 2011).

Social anxiety was found to affect the intensity, persistence, and nature of a wide gamut of affective reaction to social exclusion. Specifically, Oaten and colleagues found that highly socially anxious individuals differ from individuals low in social anxiety in their ability to self-regulate following exclusion (Oaten, Williams, Jones, & Zadro, 2008). Furthermore, research in temperamentally shy children found more intense emotional upheaval and poorer vagal regulation in response to peer rejection. In a recent study we examined the response of socially anxious individuals to social exclusion and social acceptance (Gilboa-Schechtman, Galili, Sahar, & Amir, under review). While there were no differences in the way individuals high and low in social anxiety perceived the reality of the interactions, highly socially anxious individuals reported lower self-esteem following exclusion than following acceptance as compared to individuals low in social anxiety. These results are consistent with previous findings demonstrating that social anxiety in children was associated with greater changes in self-esteem following rejection (Reijntjes et al., 2011).

Social anxiety appears to affect not only the quantitative, but also the qualitative nature of coping with exclusion. While following interpersonal rejection, individuals low in social anxiety behaved more prosocially on a reward

allocation task, and individuals high in social anxiety responded by exhibiting less prosocial behavior. In addition, Mallott and colleagues examined non-verbal characteristics of self-presentation of individuals high and low in social anxiety following interpersonal rejection (Mallott, Maner, DeWall, & Schmidt, 2009). They found that observers' ratings of vocal and eye-gaze performance were strongly inversely related to social anxiety severity in highly anxious individuals, and moderately positively related to social anxiety in individuals low in social anxiety. While Mallott and his colleagues interpret the latter finding as suggestive of deficiencies in restoring affiliative tendencies, it is also possible that rejection leads to submissive behavior through the enhanced coupling of the affiliation and the social rank systems.

Recently, we examined the subjective and expressive responses of high and low socially anxious individuals to exclusion, acceptance, and popularity induced by participation in an online ball-tossing task (Gilboa-Schechtman et al., 2013). Participants read aloud neutral and command utterances before and after the manipulation. Among individuals low in social anxiety, exclusion promoted increased vocal confidence, as indicated by decreased mF0 and increased vocal intensity in uttering commands. Highly socially anxious individuals exhibited an opposite reaction, responding to exclusion by decreased vocal confidence. Insofar as acoustic parameters are seen as proxy for interpersonal strategies, our study suggests that social anxiety is linked to a propensity to react to social exclusion by self-effacement. Put differently, while non-socially anxious individuals appear to compensate for loss of belongingness by increasing their social standing, individuals high in social anxiety show a spill-over from "belongingness wounds" to social status threats.

Popularity

Events connoting social acceptance or popularity are commonly experienced as positive by non-socially anxious individuals. This is not necessarily the case for socially anxious individuals (e.g., Weeks and Howell, 2012). In fact, several researchers (e.g., Alden and Taylor 2004; Gilboa-Schechtman et al., 2000; Gilboa-Schechtman et al., 2013; Weeks and Howell 2012) proposed that socially anxious individuals exhibit biased processing of cues or events connoting enhanced social acceptance, or popularity. Socially anxious people appear to be less successful in making the most of these experiences than are individuals low in social anxiety (e.g., Gilboa-Schechtman et al., 2000; Kashdan et al., 2011).

In one of a handful of experimental studies examining the effects of positive social attention on social anxiety, Alden and colleagues examined the impact of positive feedback following a social interaction. They found that individuals with high levels of social anxiety expected to experience greater levels of anxiety regarding future social interactions (Alden et al., 2004), predicted that their partners would expect more from them in such interactions, and that they

would fall short of those expectations (Alden and Wallace 1995; Wallace and Alden 1997). In a study mentioned earlier, we examined subjective (and vocal) reactions to popularity in high and low socially anxious individuals (Gilboa-Schechtman et al., 2013). Popularity was manipulated by the amount of attention given by other "players" in a ball-tossing task. We found that while social anxiety did not affect men's self-esteem ratings in response to popularity as opposed to acceptance, high, but not low socially anxious women reported *decreases* in mood and in self-esteem in such conditions. High socially anxious men were found to be more affectively responsive to popularity than to acceptance as opposed to men low in social anxiety. It appears that high socially anxious men are more dependent on external feedback than are men low in social anxiety. While popularity and social visibility may not carry negative costs for men, it may incur negative consequences for women, who may consequently seek to affirm obedience to the group norms (Cillessen and Borch 2006; Benenson, 1990).

CLINICAL IMPLICATIONS

Core features of SAD

Conceptualizing SAD as defined by parameters of sensitivity, reactivity, and interdependence of the dominance and the affiliation systems may broaden and refine our understanding of this condition. Firstly, the model of SAD can be expanded beyond sensitivity to social threat to include biased processing of signals of affiliation and of enhanced social rank (e.g., admiration). Moreover, broadening the notion of SAD sensitivity and reactivity to socially affiliative as well as social rank cues may further contribute to the understanding of the comorbidity between social anxiety and related affective and personality disorders. Secondly, the examination of the multi-modal communication of social rank and of affiliation may be useful in pinpointing the idiosyncratic ways in which social anxiety is expressed in a particular individual. Thirdly, examining gender differences in the interpersonal and endocrine expression of social anxiety seems called for, given the gender differences in the hormonal bases of dominance and affiliation (Schultheiss & Wirth, 2008; Stanton & Schultheiss, 2007) and the formation and maintenance of hierarchies in women and in men (Benenson, Antonellis, Cotton, Noddin, & Campbell, 2008; Schmid Mast, 2001). Finally, the examination of the interdependence between the social rank and the affiliation systems may enrich our understanding of the maintaining factors of SAD. Specifically, the failure of socially anxious individuals to recover from negative changes in their social status or affiliative bonds may relate to the spill-over from dysregulation of one system to the dysregulation of the other. Combined, this conceptualization represents a shift towards a theory-based, rather than a symptom-based approach to this disorder.

Treatment implications

Our review highlights the interplay between the social rank and the affiliation systems in social anxiety. Cognitive-behavioral interventions could be conceptualized as "re-tuning" the functioning of the social rank system. Specifically, these interventions can be seen as geared to decreasing the "thin-skinnedness" (by such mechanisms as attentional retraining and cognitive restructuring) and practicing the high-profile rather than low-profile behaviors while dealing with social rank challenges (Clark, Ehlers et al., 2006; Hofmann, 2010). Interpersonal interventions can be thought of as enhancing the functioning of the affiliative system and possibly contributing to the decoupling between the affiliation and the social rank systems by focusing on friendly interpersonal exchanges (e.g., Alden & Taylor, 2011). More generally, creating a personalized profile of the functioning of social rank and affiliative system may create more effective treatment interventions.

From the perspective of the present conceptualization, reviewing events related to loss of social status or belongingness in treatment may help to articulate the coping strategies individuals use to deal with such challenges, and, when needed, to develop more flexible and pro-social strategies of this type. If especially painful events involving loss of status are part of a person's history, statusenhancing interventions (e.g., Bergner, 1999) or trauma-focused exposure techniques might prove useful in their therapy (Wild, Hackmann, & Clark, 2008).

The relationship of subjectively perceived and externally assessed social rank and well-being is well documented (Firebaugh & Schroeder, 2009; Hammer & Good, 2010). Acknowledging the importance of social rank, respect, and prestige for well-being may also be helpful in adopting a more self-accepting and self-compassionate approach to distress experienced by socially anxious individuals (Gilbert & Procter, 2006).

Finally, an emphasis on the misinterpretation of affiliative signals, and down-regulation of events connoting social ascendance or acceptance, suggests an enhanced focus on helping socially anxious individuals to bolster affiliative gestures, savor popularity and acceptance, and extract the potential benefits from power-loaded events. This emphasis harmonizes with the growing body of research on positive psychology in general and the positivity impairment in social anxiety in particular.

SUMMARY

While our quest for attention and affection from the chosen few (otherwise known as love) is socially acceptable and well charted, our quest for attention from a group tends to be less explored. In the present chapter, we proposed an evolutionary view on social anxiety, bridging, through the operation of two basic biobehavioral systems, the normative and the maladaptive routes to social attention. In our view, socially anxious individuals are not only thin-skinned and

interpersonally cautious but also suffer from difficulties in disentangling social rank and affiliation threats. Being affected by changes in affiliative relationships, viewing rejection and exclusion as challenges not only to social bonds, but also to social standing is likely to take a toll on one's sense of self and efficacy. Conversely, experiencing loss in competition as potentially straining one's intimate relationships can erode the feelings of closeness and companionship.

Evolutionary explanations of almost any human activity are in vogue: within the past two years, evolutionary explanations have been applied to the study of tattoos in Western Cultures (Carmen, Guitar, & Dillon, 2012), the characteristic of literary heroes created by women and by men (Ingalls, 2010), the significance of the female orgasm (Puts, Dawood, & Welling, 2012), and the nature of virtual communication (Crosier, Webster, & Dillon, 2012). With the net cast that wide, a common reservation regarding evolutionary explanations is that of falsifiability. Are evolutionary approaches an exercise in scientifically informed story-telling? We think not. Evolutionary approaches have the capacity to seamlessly integrate findings from endocrinology, neuroscience, cognition, primatology, and sociology. In this chapter we argued that this conceptual framework is uniquely positioned to inform and direct empirical research on social anxiety.

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