COGNITION AND EMOTION
https://doi.org/10.1080/02699931.2024.2314987

Routledge
Taylor & Francis Group

Altered mechanisms of adaptation in social anxiety: differences in adapting to positive versus negative emotional faces

Erinda Morina[a], Daniel A. Harris[a,b], Sarah A. Hayes-Skelton[c] and Vivian M. Ciaramitaro [a]

[a]Developmental and Brain Sciences, Department of Psychology, University of Massachusetts Boston, Boston, MA, USA; [b]Division of Epidemiology, Dalla Lana School of Public Health, University of Toronto, Toronto, ON, Canada; [c]Clinical Psychology, Department of Psychology, University of Massachusetts Boston, Boston, MA, USA

ABSTRACT
Social anxiety is characterised by fear of negative evaluation and negative perceptual biases; however, the cognitive mechanisms underlying these negative biases are not well understood. We investigated a possible mechanism which could maintain negative biases: altered adaptation to emotional faces. Heightened sensitivity to negative emotions could result from weakened adaptation to negative emotions, strengthened adaptation to positive emotions, or both mechanisms. We measured adaptation from repeated exposure to either positive or negative emotional faces, in individuals high versus low in social anxiety. We quantified adaptation strength by calculating the point of subjective equality (PSE) before and after adaptation for each participant. We hypothesised: (1) weaker adaptation to angry vs happy faces in individuals high in social anxiety, (2) no difference in adaptation to angry vs happy faces in individuals low in social anxiety, and (3) no difference in adaptation to sad vs happy faces in individuals high in social anxiety. Our results revealed a weaker adaptation to angry compared to happy faces in individuals high in social anxiety (Experiment 1), with no such difference in individuals low in social anxiety (Experiment 1), and no difference in adaptation strength to sad vs happy faces in individuals high in social anxiety (Experiment 2).

ARTICLE HISTORY
Received 9 June 2022
Revised 19 December 2023
Accepted 16 January 2024

KEYWORDS
Faces; emotions; adaptation; perceptual bias; social anxiety

Introduction

Successful identification and interpretation of emotional stimuli plays an important role in everyday life (Itier et al., 2006; Luo et al., 2010; Öhman, 1986; Öhman et al., 2001; Ran et al., 2014). Inaccurately identifying and interpreting emotions can hinder social interactions, which comes with its own social cost (Leber et al., 2009). One clinical condition where emotional processing has been shown to be disrupted is social anxiety (Yoon & Zinbarg, 2007).

Social anxiety is one of the most common types of anxiety (Kessler et al., 2005; Stein et al., 2017) and is characterised by the continuous fear of being negatively evaluated by others and avoidance of social situations (American Psychiatric Association, 2013). The personal, social, and economic costs of social anxiety, and its comorbidity with other mental health disorders, have been well studied and documented (Kessler et al., 2005), but the underlying cognitive mechanisms contributing to the maintenance of this condition are still unclear. Hirsch and Clark (2004) suggest that the persistence of fear characterising social anxiety is unlikely to be maintained solely by avoiding social situations (e.g. Wells et al., 1995) because socially anxious individuals often have some form of regular social interaction. Rather, it has been suggested that biases in information-processing may play an important role in the maintenance of social anxiety (for a review see Peschard & Philippot, 2016). Cognitive models of social anxiety suggest that individuals high in social anxiety exhibit negative biases in perceiving and processing social cues, including social cues from emotional information, which may contribute to the

CONTACT Vivian M. Ciaramitaro Vivian.Ciaramitaro@umb.edu Department of Psychology, Developmental and Brain Sciences, University of Massachusetts, 100 Morrissey Boulevard, Boston, MA 02125, USA

maintenance of anxiety symptoms (e.g. Clark & Wells, 1995; Hirsch & Clark, 2004; Morrison & Heimberg, 2013; Rapee & Heimberg, 1997).

Biases in information processing investigated in social anxiety include attentional biases (Amir et al., 2003; Fox et al., 2002), memory biases (e.g. Hope et al., 1990; LeMoult & Joormann, 2012; Mellings & Alden, 2000), and perceptual biases in interpreting social cues, especially cues related to threat (e.g. Amin et al., 1998; Gutiérrez-García & Calvo, 2017; Huppert et al., 2007; Moser et al., 2012; Murphy et al., 2007). For instance, social cues can include: (1) Social Scenarios: Individuals with social phobia demonstrate a negative bias, more often choosing a negative interpretation for an ambiguous social scenario despite a positive or neutral interpretation being available (Amin et al., 1998). (2) Words and Sentences: Individuals high in social anxiety demonstrate a negative bias by resolving ambiguous sentences regarding a social situation using negative words, unlike individuals low in social anxiety (Huppert et al., 2007). (3) Eye Gaze: Individuals high versus low in social anxiety show greater avoidance and higher physiological and neuronal responsiveness when using direct eye gaze compared to averted eye gaze (e.g. Roelofs et al., 2010; Schneier et al., 2009; Wieser et al., 2010). (4) Faces: Over the past two decades, more ecologically valid stimuli, such as expressive faces, have been the focus of research (for review see Staugaard, 2010). Interpretation and representation of facial expressions are particularly relevant in social anxiety because they provide a medium through which positive and negative evaluations by others can be expressed, and fear of negative evaluation contributes to the development and maintenance of different psychopathologies, including social anxiety (American Psychiatric Association, 2013; Miller, 1995; Reiss, 1991).

Cognitive models suggest that socially anxious individuals perceive social cues, such as emotionally charged faces, as threatening (Clark & Wells, 1995; Rapee & Heimberg, 1997). Although most studies find that socially anxious individuals do not differ from non-socially anxious controls in their ability to accurately decode emotional information in faces or judge the emotion in faces, (Bell et al., 2011; Heuer et al., 2010; Philippot & Douilliez, 2005), it appears there might be differences in sensitivity to threatening stimuli, which may lead to misclassification and overestimation of threatening emotions.

One well-studied bias in individuals with social anxiety is a tendency to interpret ambiguous expressions, including morphed and blended facial expressions, as more negative compared to non-anxious individuals (for review see Mobini et al., 2013). A possible reason for such a bias is that ambiguity allows for more open interpretation, and socially anxious individuals are prone to fear negative evaluations and tend to interpret ambiguous social cues in a negative light, for example as a sign of disapproval (Clark, 2001). Compared to non-socially anxious controls, socially anxious individuals tend to show a negative bias; they interpret and misclassify neutral faces as expressing threatening emotions, such as anger (e.g. Bell et al., 2011; Gutiérrez-García & Calvo, 2017; Heuer et al., 2010; Joormann & Gotlib, 2006; Peschard & Philippot, 2016; Yoon et al., 2014; Yoon & Zinbarg, 2007, 2008), while interpreting ambiguous smiles as less positive (Gutiérrez-García & Calvo, 2014, 2016). Generally, there seems to be an attribution of threat and increased sensitivity for anger but not other negative emotions, such as fear or sadness (Bell et al., 2011; Gutiérrez-García & Calvo, 2017; Joormann & Gotlib, 2006).

However, the tendency of socially anxious individuals to interpret ambiguous emotional faces as more threatening, a negative bias, is not found consistently across the literature. Some studies of socially anxious individuals find only partial evidence of a negative bias for more ambiguous faces, including faces of lower emotional intensity, (Frenkel & Bar-Haim, 2011; Rossignol et al., 2007), or no negative bias for ambiguous faces (Button et al., 2013). Such discrepancies might arise from differences in experimental design, such as the presence or absence of mood induction or differences in state affect at the time of the experiment.

We sought to investigate one potential mechanisms which could maintain a negative bias, altered adaptation to emotional information in socially anxious individuals Adaptation allows for recalibration of perceptual systems based on the influence of recent sensory exposure. Behaviourally, adaptation refers to a process by which repeated exposure to a stimulus feature results in a perceptual change, temporarily altering the sensitivity of the system to generate a bias towards the opposite feature, an aftereffect (Grill-Spector et al., 1999; Rhodes, 2017; Webster, 2015). For instance, when participants are repeatedly exposed to a face feature such as face sex, specifically stereotypically female faces, they demonstrate a bias away from female faces, such that they perceive androgenous faces as more stereotypically male (Little et al., 2013). Originally, adaptation aftereffects had been described for low-level visual features, such as colour, form, and motion, but they are also present for high-level visual stimuli, such as faces (for a review see, Webster & MacLeod, 2011). Different aspects of a face can be adapted, including age (e.g. Little et al., 2008; Schweinberger et al., 2010), ethnicity (e.g. Jaquet et al., 2008), attractiveness (e.g. Anzures et al., 2009), and emotional content (e.g. Hsu & Young, 2004; Rutherford et al., 2008), as well as combinations of features, as evident in contingent adaptation aftereffects (e.g. Harris & Ciaramitaro, 2016; Ng et al., 2006).

The strength of adaptation has been found to be altered in several disorders where social information processing is compromised. For example, compared to typically developing children, children with autism spectrum disorder (ASD) show reduced adaptation to face identity (Pellicano et al., 2007) for upright, but not inverted, faces (Ewing et al., 2013), and even show aftereffects in the wrong direction, such as a bias to see a neutral face as angrier following adaptation to negative emotions (Rutherford et al., 2012), when one would expect a bias to see a neutral face as happier following adaptation to negative emotions.

Given evidence for altered adaptation to emotional faces in other mental health and neuropsychiatric conditions, such as ASD, and the commonality of negative biases in social anxiety, we investigated whether mechanisms of adaptation to emotional information were altered in socially anxious individuals. Individuals high in social anxiety tend to perceive social situations more negatively, showing a maintained sensitivity to negative information or a negative bias. A negative bias could be perpetuated by weakened adaptation to negative emotional information, by strengthened adaptation to positive emotional information, or by a combination of both mechanisms. The current experiments aim to extend previous research by (1) quantifying the magnitude of adaptation to faces displaying threatening negative compared to positive emotional information in individuals high in social anxiety (Experiment 1), and by considering two control conditions (2) quantifying the magnitude of adaptation to faces displaying threatening negative compared to positive emotional information in individuals low in social anxiety (Experiment 1) and (3) quantifying the magnitude of adaptation to faces displaying non-threatening negative compared to positive emotional information in individuals high in social anxiety (Experiment 2). We predict that individuals high in social anxiety will show weakened adaptation to angry emotions and/or strengthened adaptation to happy emotions. We predict our control conditions will show no overall difference in the strength of adaptation to positive versus negative emotional faces. More specifically, we predict that individuals low in social anxiety will not show weakened adaptation to angry compared to happy emotional faces and that individuals high in social anxiety will show no overall difference in the strength of adaptation to sad versus happy faces, given that sadness is not threatening. *Overall, we predict that mechanisms of adaptation to emotional information will be selectively altered in social anxiety based on emotional valence (positive vs negative) as well as the threatening nature of the emotional content (threatening vs non-threatening).* Ultimately, differences in adaptation to emotional stimuli can clarify underlying mechanisms which might maintain sensitivity to negative and threatening emotional information and perpetuate information processing biases in social anxiety.

Experiment 1

Methods

Participants

In Experiment 1, we collected data from 85 participants, 18–61 years of age, recruited from the University of Massachusetts Boston community by email or announcements in psychology classes. Our final sample included 76 participants, who were predominately female (64.47%) and white (57.89%) with a mean age of 25.23. The final sample included 37 participants classified as *low* in social anxiety (LSA: 20 females; mean age = 26.03 years, SD = 9.72, range = 18–54) and 39 participants classified as *high* in social anxiety (HSA; 29 females; mean age = 24.46 years, SD = 8.41, range = 18–61). Of the 85 participants who contributed data, 9 participants were excluded due to: an insufficient number of valid trials (trials with valid responses, made while the question mark appeared on the screen), fewer than 30 out of 64 valid trials (2), biased behavioural responses, where 80% happy faces were judged happy less than 75% of the time or 80% angry faces were judged happy more than 25% of the time, during either baseline or adapt (5), not following instructions (1), comorbidity with other disorders, such as ADHD or learning disabilities, via personal report (1) (see Table 1 for details on demographics and measures). Participants reported normal or corrected-to-normal vision, provided written informed consent, and were compensated with $18 or course credit for eligible undergraduate psychology classes. All experimental procedures and protocols (protocol number: 2013148), were approved by the University of Massachusetts Boston Institutional Review Board and complied with the Declaration of Helsinki.

Measures

BFNE

The Brief Fear of Negative Evaluations (BFNE; Leary, 1983) was used to asses social anxiety. The BFNE is a 12-item self-report measure examining participants' fears of being negatively evaluated using a 1 (not at all characteristic) to 5 (extremely characteristic) Likert scale. The BFNE has excellent internal consistency ($\alpha = .96$), excellent reliability and validity (Leary, 1983), good test retest reliability ($r = .75$), and good convergent and divergent validity (Leary, 1983). We used the 8 straightforward items of the BFNE (BFNE-S; Rodebaugh et al., 2004) to classify individuals as high in social anxiety (*HSA* group; scores > = 25) or low in social anxiety (*LSA* group; scores < = 12; based on criterion described in Carleton et al., 2011; Weeks et al., 2012). Similar cut-offs from measures from the BFNE-S have been used in undergraduate populations (Rodebaugh et al., 2004) and clinical samples (Weeks et al., 2012). Individuals who met qualifying scores were contacted and followed up with a phone interview to verify social anxiety status. The phone interview consisted of two questions: (1) participants had to reflect on their feeling in certain social situations, such as speaking in a classroom or attending a party, where they are unfamiliar with most of the attendees and (2) participants had to reflect on how they would react when they found themselves at the centre of attention. Those whose responses were aligned with their social anxiety group classification from the online survey were subsequently invited to partake in the laboratory portion of the study.

DASS

The *Depression Anxiety Stress Scale–21-item version* (DASS; Lovibond & Lovibond, 1995) was used to assessed depression. The DASS is a self-report scale with separate, reliable, and valid scales for depression, anxiety, and stress (Antony et al., 1998; Bottesi et al., 2015; Henry & Crawford, 2005; Sinclair et al., 2012; Vasconcelos-Raposo et al., 2013). The subscales have demonstrated good internal consistency and construct validity (Antony et al., 1998). We used the 7-item Depression subscale to determine depression status and excluded participants scoring above 17 in depression. A score of 17 represents the middle of the moderate range (14–20) on this measure of depression (Lovibond & Lovibond, 1995).

PANAS

The *Positive and Negative Affect Schedule – State Version* (PANAS: Watson et al., 1988) was used to measure current state affect (i.e. whether participants were feeling generally more positive or negative in the present moment), and was completed immediately before data collection. PANAS is a 20-item scale used to measure current affective state, separated into negative affect (PANAS-NA) and positive affect (PANAS-PA), which are designed to be orthogonal (Watson et al., 1988). For each item, participants indicate on a 5-point Likert scale how much they are experiencing each emotion (e.g. distressed, excited, etc.). We used the PANAS subscales to assess state-level affect at the beginning of the experimental protocol. The psychometric properties of the PANAS have been deemed acceptable in samples of anxiety and depression (Watson et al., 1988).

The BFNE and DASS were completed via an online survey, a few days to 1–4 weeks before the in-person study, whereas PANAS was completed when the participant arrived in the laboratory, before data collection (see Table 1).

PSE

The *Point of Subjective Equality (PSE)* was used to quantify the strength of adaptation, i.e. the strength of the perceptual aftereffect. The PSE was measured uniquely for each participant before and after adaptation. The PSE is the unique neutral point, where a face is judged emotionally neutral, equally likely to be seen as happy or angry, or judged happy on 50% of trials for a given facial expression. Participants viewed neutral faces as well as faces of various intensities of anger or happy emotions (see Stimuli section below). Responses to these faces, judging the face as happy or angry, were recorded and data fit with a mathematical function to determine the face that

Table 1. Characteristics of individuals high and low in social anxiety in Experiment 1, grouped by adapt condition: angry adapt and happy adapt.

	High Social Anxiety (HSA) ($n = 39$)		**Low Social Anxiety (LSA)** ($n = 37$)	
Conditions	Angry Adapt ($n = 19$)	Happy Adapt ($n = 20$)	Angry Adapt ($n = 17$)	Happy Adapt ($n = 20$)
	Mean (SD; Range)	**Mean (SD; Range)**	**Mean (SD; Range)**	**Mean (SD; Range)**
Age	21.63 (3.55; 18–30)	27.15 (10.67; 18–61)	24.18 (7.85; 18–50)	27.60 (11.01;19–54)
BFNE	31.89 (4.55; 25–39)	32.40 (3.82; 26–39)	10.12 (1.69; 8–12)	10.15 (1.46; 8–12)
DASS	9.05 (5.08; 0–17)	8.60 (5.20; 0–17)	5.06 (4.94; 0–13)	5.70 (4.49; 0–14)
Positive Affect[1]	29.35 (14; 18–45)	30.17 (8.67; 13–46)	31.59 (8.14; 19–46)	33.70 (8.25; 21–50)
Negative Affect	14.00 (2.92; 10–20)	13.33 (3.05; 10–19)	11.29 (1.53; 10–15)	12.00 (2.34; 10–18)
	***n* (% total N)**	***n* (% total N)**	***n* (% total N)**	***n* (% total N)**
GENDER				
Female	14 (73.68%)	15 (75.00%)	8 (47.06%)	12 (60.00%)
Male	5 (26.32%)	5 (25.00%)	9 (52.94%)	8 (40.00%)
ETHNICITY				
White	13 (68.42%)	12 (60.00%)	9 (52.94%)	10 (50.00%)
Latino/Hispanic	0 (0.00%)	1 (5.00%)	0 (0.00%)	6 (30.00%)
Asian–American	3 (15.79%)	5 (25.00%)	1 (5.88%)	0 (0.00%)
Black/African–American	2 (10.53%)	1 (5.00%)	6 (35.29%)	2 (10.00%)
Multi–Racial	1 (5.26)	0 (0.00%)	0 (0.00%)	0 (0.00%)
Unspecified	0 (0.00%)	1 (5.00%)	1 (5.88%)	2 (10.00%)

Notes: SD = standard deviation; BFNE = Brief Feat of Negative Evaluations; DASS = Depression Anxiety Stress Scale–21-item version.
[1]Four participants did not report Positive and Negative Affect, two from adapt happy and two from adapt angry in the HSA group.

would support 50% performance (see Data Analysis: Quantifying Adaptation Strength). We controlled for pre-existing biases by normalising the strength of adaptation for each individual by their own perceptual bias at baseline, before adaptation (see Data Analysis: Quantifying Adaptation Strength). This is important because negative perceptual biases can be found in individuals with social anxiety at baseline, before adaptation. Finally, our use of psychophysical methods allows us to compute not only PSE, but also slope at the PSE. Slope estimates provide additional insight into the nature of perceptual biases, measuring the degree to which the representation of emotional information is more categorical versus continuous. Steeper slopes indicate more categorical perception, with clearer demarcations between emotional faces, while shallower slopes indicate more continuous perception (Roesch et al., 2010). We report on slope as an additional metric and exploratory analysis.

Determining adaptation strength

Apparatus

Face stimuli were presented on a Nexus CRT monitor. All participants were seated 45cm from the monitor and used a chin and forehead rest to maintain a fixed distance from the screen. Responses were made via key press on a laptop keyboard or a Cedrus Response Box (RB-844) and recorded using MATLAB and the psychophysics toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Participants wore noise-cancelling headphones (3M-Peltor headset), which presented auditory stimuli while reducing distractions from ambient sounds.

Stimuli

Adaptation stimuli

We selected 30 unique face identities (15 female and 15 male; 21 White, 3 Asian and 6 Black) from the NimStim face database, closed mouth version (Tottenham et al., 2009). Stimuli depicted a 100% emotional face, had validity ratings for a given emotion of 75% or higher, were grey-scaled to 50% and embedded within a grey oval to eliminate distracting features, such as hair. Stimuli were 595 × 595 pixels and subtended 19.8 degrees of visual angle.

Test stimuli

A subset of the adaptation faces was used as test faces. Test faces were generated by morphing different proportions of a 100% angry face and the corresponding neutral face or a 100% happy face and the corresponding neutral face to create an emotional continuum for a given identity (80, 40, 20 and 10% angry, neutral, and the complementary 80, 40, 20 and 10% happy). MorphMan software (STOIK Imaging, Moscow, Russia) was used to morph faces by selecting points on prominent face features, such as the eyebrow, nose, eyes, and mouth (for sample faces showing selection points see Harris & Ciaramitaro, 2016).

We used 8 unique identities to quantify perceptual biases (4 females & 4 males; 5 White, 2 Asian, & 1 Black) and created 9 test faces (4 angry morphs, 4 happy morphs, and 1 neutral) for each of the 8 unique identities, for a total of 72 possible faces (see Figure 1 for the 9 morphs ranging from angry through neutral to happy, for one sample test face).

Procedure

First, participants were familiarised with the task and timing of responses, completing a minimum of 2 practice trials. Practice trials consisted of an auditory alerting cue, followed by a blank oval (1 s), then a question mark (1.5 s), during which time participants had to press a button to practice the timing of when to indicate their judgment. The practice session was followed by the experiment, which consisted of a baseline condition (15 min) and an adapt condition (15 min), separated by a 5 min break (see Figure 2).

Baseline condition

At baseline, participants were instructed to fixate their gaze on the centre of a blank grey screen for the duration of the experiment, but eye position was not monitored. The experiment began with a fixation cross at screen centre (180 s). After the 180 s fixation period, a trial began as indicated by an auditory cue (500 Hz), which alerted the participant that they would need to start judging the emotion of faces presented on the screen. Specifically, a trial consisted of a 1sec fixation period, an alerting auditory cue, followed by a test face, 1 of the 72 possible morphs, presented at random (1 s), which was then followed by a question mark (1.5 s). While the question mark was visible, the participant had to judge if the test face they had seen was happy or angry. Judgments were recorded via a button box; one button was pressed for happy judgments and another button was pressed for angry judgments. If the participant responded outside the 1.5 s when the question mark was visible, too early or too late, their response was excluded from analysis. In between each test face, a grey screen with a fixation cross (8 s) was presented.

A total of 64 test trials were presented at baseline (8 trials for happy and angry face morphs (40%, 20%, 10%), 8 trials for neutral faces, and 4 trials for happy and angry face morph (80%)). Baseline data were

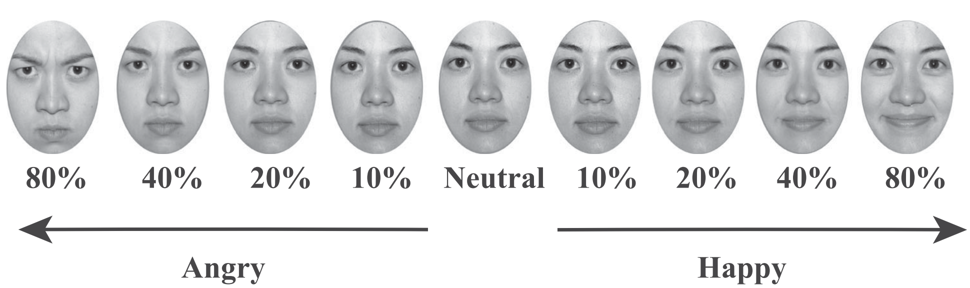

Figure 1. Sample Angry-Happy Face Morphs.

Note: An example of an angry-happy continuum of faces for a single identity. During baseline and post-adaptation participants judged a total of 64 faces morphed along an angry-happy continuum, from 80, 40, 20 and 10% angry to neutral and from neutral to 10, 20, 40 and 80% happy.

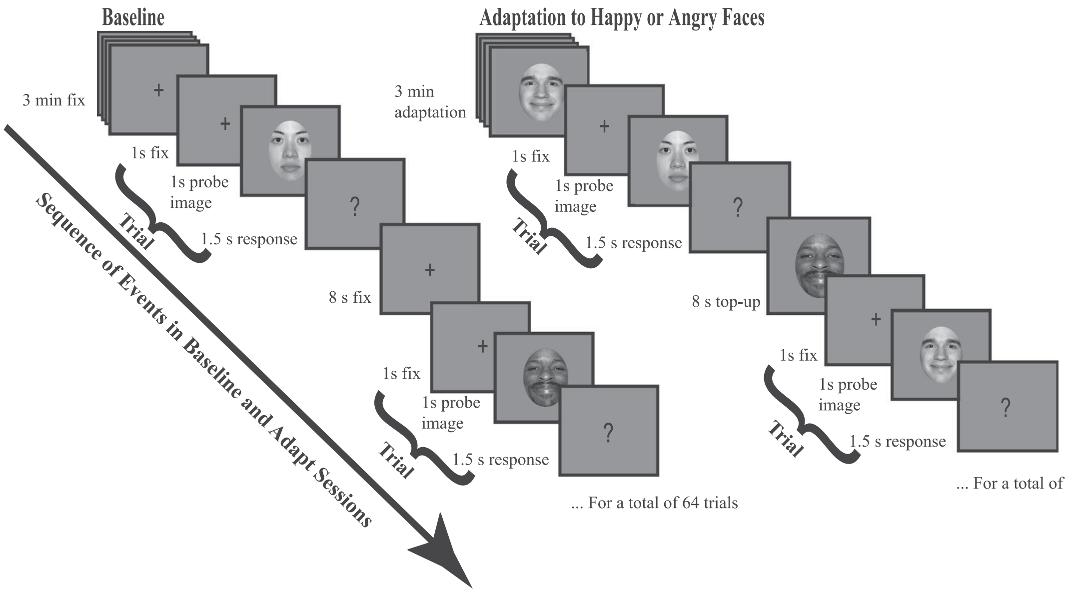

Figure 2. Experimental Design.

Note: Baseline started with fixation (3 min), during which participants were instructed to gaze at the cross. Then, an auditory beep and a test face were presented (1 s), followed by a question mark (1.5), during which participants had to judge the emotion of the face presented as happy or angry. Following baseline there was a break (5 min) and then adaptation. Adaptation started with exposure to either 100% happy or angry faces (3 min). Participants then viewed the same test faces (1 s each) as during baseline but after each test face was judged a series of 8 100% happy or angry faces, the same as during the initial 3 min adaptation was presented. Each participant was assigned randomly to one of the two adapt conditions: (1) Happy Adapt, or (2) Angry Adapt.

used to determine each participant's pre-existing bias in judging faces and to normalise adaptation strength for each participant.

Adapt conditions

Adaptation followed the same sequence of events in time as baseline; however, instead of a fixation cross, emotional faces were presented during the initial 180 s period (*initial adaptation*) and during the 8s period between each test face after the face was judged (*top-up adaptation*). During initial adaptation, a total of 180 male and female faces at 100% of a given emotion (1 s per face; either happy or angry) were presented and then participants made judgments for the test faces presented during baseline. During top-up adaptation a total of 8 100% emotional faces (1 s per face) were presented to maintain adaptation effects (as used in Izen et al., 2019; Izen & Ciaramitaro, 2020; Ng et al., 2006).

Two adaptation conditions were tested in a between-subjects design (1) Happy Adapt: 100% happy faces were presented during initial and top-up adaptation or (2) Angry Adapt: 100% angry faces were presented. After adaptation, a total of 64 test faces were presented and judgement of these test faces was used to determine adaptation strength (see Figure 2).

Data analysis

Transparency and openness

Data and analysis code are available on Open Science Framework via this link: https://osf.io/fmtah/. The study design and analysis were not pre-registered. G* power (version 3.1) was used to determine sample size. We had explicit predictions in testing for differences between two independent means, our two adapt conditions, within each social anxiety group and planned a one-tailed test, medium effect size = 0.7, alpha = 0.05, and power = 0.8. Required sample size was 26 participants for each of the two adapt conditions within each anxiety group. From this estimate for 104 total participants, we collected data from 85 participants with a final sample of 76.

Quantifying adaptation strength

All data were analysed using MATLAB (The MathWorks, Inc., Natick, MA, USA) and psignifit (http://bootstrap-software.org/psignifit/), which implements the maximum-likelihood method described by Wichmann and Hill (2001), to fit the data for each adapt condition (angry and happy), for each participant, at baseline and post-adapt. Responses were plotted such that the emotional morph continuum was plotted along the *x*-axis: happy emotions plotted as positive and negative emotions as negative, and the percentage of trials the participant responded that a given face morph appeared happy was plotted along the *y*-axis. Data were fit to a cumulative normal function to determine PSE, the morph supporting 50% performance, which defines the face perceived as emotionally neutral. Given that we plotted happy emotions to the right of 0 and angry to the left of 0, a positive PSE indicates that more happiness is required to see a face as neutral, a negative perceptual bias. Conversely, a negative PSE indicates that more anger is required to see a face as neutral, a positive perceptual bias.

To quantify adaptation strength, we measured how each participant's judgments of the face considered emotionally neutral at baseline changed post-adaptation. We subtracted the *y*-value, or happy judgments, for the PSE at baseline (defined as 0.5) from the *y*-value for the same face after adaptation (as used in Harris & Ciaramitaro, 2016; Izen & Ciaramitaro, 2020; Ng et al., 2006). Importantly, such a measure normalises for baseline biases and allows quantification of perceptual biases using the linear range of the *y*-axis, indicating how much happier a face appears after adapting to happy versus angry emotions. This is advantageous over using shifts along the *x*-axis, which is in mathematical, not perceptual, units of % emotion in a face.

Figure 3 provides hypothetical predictions for the strength of adaptation following adaptation to 100% happy versus 100% angry face in individuals high (HSA) vs low (LSA) in social anxiety. The direction and the magnitude of changes in perception from baseline to post-adapt (PSE shift) are depicted using an arrow. The direction of the arrow demonstrates the direction of adaptation and the length of the

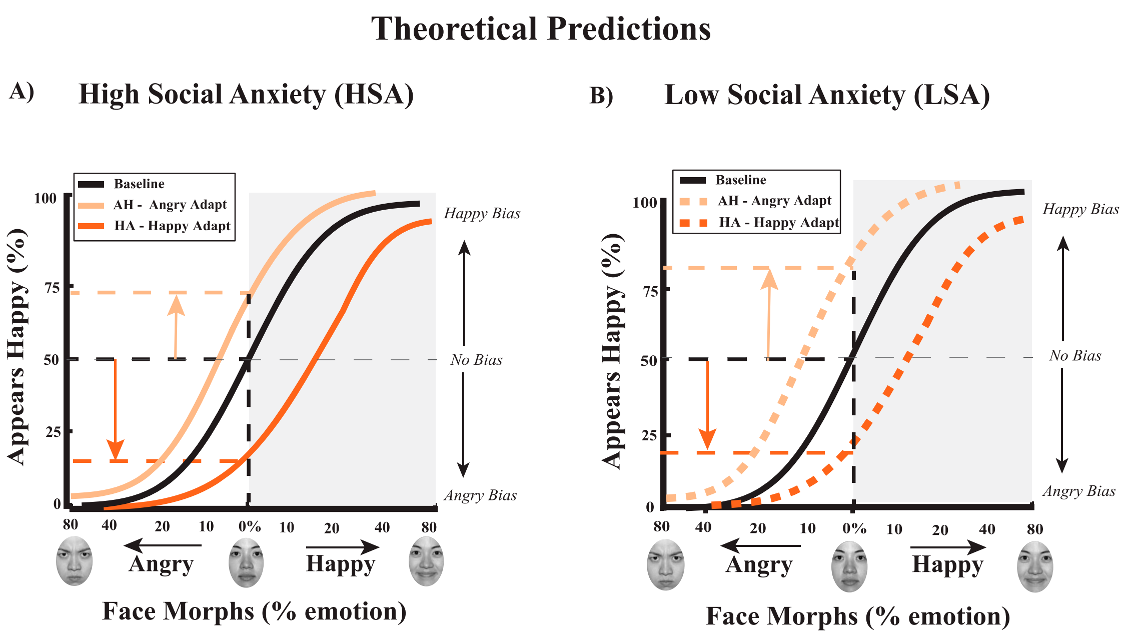

Figure 3. Theoretical Predictions in HSA and LSA for Adapting to Happy vs Angry.

Note: The *x*-axis represents faces morphed along a continuum from 80% angry (left of 0), through neutral (0% emotion) to 80% happy (right of 0), whereas the *y*-axis represents the percent at which a certain face morph is judged happy. The grey shaded area highlights happy face morph data, with 0 indicating the standard neutral face, as defined by the NimStim dataset. For each participant, we measured the Point of Subjective Equality (PSE) or the face equally likely to judged happy or angry. The black curve represents a cumulative normal fit to judgements of face morphs at baseline, whereas the yellow and the orange line represent the fit to judgements of the same face morphs after adaptation to angry or happy faces, respectively. The predicted direction and magnitude of perceptual changes from baseline to post-adapt (PSE shift) are depicted in the direction and magnitude of the arrows. We quantified how judgments of the face considered emotionall neutral at baseline changed after adaptation. (A) We predicted that HSA individuals would show a stronger magnitude of adaptation to happy relative to angry faces (B) We predicted that LSA individuals would not show a significant difference in the magnitude of adaptation in the expected direction to happy vs angry faces.

arrow indicates the magnitude of adaptation. As depicted in Figure 3, adaptation should yield perceptual aftereffects, with happy adaptation yielding a negative shift and angry adaptation yielding a positive shift. To consider adaptation strength *in the expected direction*, we evaluated the difference of shifts after angry adaptation and the additive inverse of shifts after happy adaptation. We predicted that (1) HSA individuals would show weaker adaptation in the expected direction to angry vs happy faces while (2) LSA individuals would show no difference (see Figure 3).

Statistical analysis

Throughout the results section, data were normally distributed, skew/kurtosis +/−2, and parametric statistics were applied. Our main dependent variable was adaptation strength, quantified as the PSE after vs before adaptation. Our second dependent variable was slope, after vs before adaptation. Our main independent variable was social anxiety group.

We had an *a priori* expectation that the strength of the perceptual shift in the expected direction would be weaker in HSA individuals when adapting to angry and/or stronger when adapting to happy faces, with no such differences expected in LSA individuals, as explained in Figure 3. To compare the overall strength of adapting to happy vs angry faces in our between-subject design, we considered PSE shifts *in the expected direction* for each adapt condition for each individual, with variance computed across individuals. More specifically, we compared the strength of adaptation to happy versus angry faces among HSA and among LSA individuals separately, using two-tailed independent samples t-tests. This approach is preferable to first collapsing data across individuals within a given adapt condition and a given social anxiety group, and then fitting group data to determine overall PSE, as such a method does not take into account individual differences in perceptual biases at baseline. This issue has been highlighted before, (e.g. Turi et al., 2015), and is particularly relevant for socially anxious individuals who have negative perceptual biases at baseline (e.g. Gutiérrez-García & Calvo, 2014; Yoon et al., 2014).

Although not our main dependent measure, we also estimated changes in slope at the PSE, for each participant, by calculating the difference between post-adapt and baseline measures of slope. Slope is informative in terms of perceptual bias since it indicates the rate of change in the categorisation of emotional information (Roesch et al., 2010). Independent samples t-tests were conducted using IBM SPSS Statistics (Version 19) for both PSE and slope measures.

Given our between subject design our data are underpowered, but we considered an exploratory analysis, using bootstrapping (10,000 iterations with replacement) to compare differences in adapting to angry vs happy faces between HSA and LSA individuals.

Results

Our final sample of 76 participants completed a total of 4357 baseline and 4583 adapt trials. Trials where participants did not respond during the 1.5 s response interval were excluded. Of the 64 test faces presented to determine the PSE, HSA participants in the adapt happy condition provided valid responses in an average of 55.90 baseline trials (SD = 9.75; range = 30–64), and 60.55 post-adaptation trials (SD = 3.35; range = 52–64), and those in the adapt angry condition provided valid response in an average of 58.00 baseline trials (SD = 5.36; range = 48–64), and 59.00 post-adaptation trials (SD = 6.02; range = 45–64). LSA participants provided valid response in an average of 58.65 baseline trials (SD = 6.39; range = 39–64), and 61.55 post-adapt trials (SD = 2.78; range = 54–64) in adapt happy and an average of 56.71 baseline trials (SD = 8.23; range = 37–64), and 60.00 post-adapt trials (SD = 5.39; range = 45–64) in adapt angry. There was no significant difference in the overall number of valid baseline trials (independent samples Mann–Whitney U Test, 2-sided; U = 704, p = .855, η^2 = .00045) or adapt trials (independent samples Mann–Whitney U Test, 2-sided; U = 616.5, p = . 269, η^2 = .016) in HSA vs LSA individuals. Furthermore, we found no significant difference in age between LSA (Mean = 26.03; SD = 9.72) and HSA (Mean = 24.46; SD = 8.41) individuals (independent samples t-test, 2-sided; t(74) = .752, p = .454, Hedge's g = .173) nor in participant gender (X^2 (1) = 3.42, p = .093). Additionally, there was a significant difference in age between adapting to angry versus happy in HSA individuals (angry (Mean = 21.63; SD = 3.55) vs happy (Mean = 27.15; SD = 10.67); independent samples t-test, 2-sided; t(37) = −2.14, p = .039, Hedge's g = .687), but no significant difference in LSA individuals (angry (Mean = 24.18; SD = 7.85) vs happy (Mean = 27.60; SD = 11.01); independent samples t-test, 2-sided; t(35) = −1.07, p = .292, Hedge's g = .353). Finally, we found no significant differences in participant gender when adapting to happy versus angry faces for HSA ($X^2(1)$ = .009, p = .925) or LSA ($X^2(1)$ = .62, p = .431) individuals.

We also found no significant differences in measures for anxiety, depression, and state affect, when adapting to angry versus happy faces in HSA individuals (BFNE: angry (Mean = 31.89; SD = 4.55) vs happy (Mean = 32.40; SD = 8.82); independent samples t-test, 2-sided; t(37) = −0.377, p = .709, Hedge's g = .122), DASS: angry (Mean = 9.05; SD = 5.08) vs happy (Mean = 8.60; SD = 5.20; independent samples t-test, 2-sided; t(37) = 0.275, p = .785, Hedge's g = .088), PA: angry (Mean = 29.35; SD = 8.19) vs happy (Mean = 30.17; SD = 8.67; independent samples t-test, 2-sided; t(33) = −0.285, p = .777, Hedge's g = .097), and NA: angry (Mean = 14.00; SD = 2.92) vs happy (Mean = 13.33; SD = 3.05; independent samples t-test, 2-sided; t(33) = .660, p = .514, Hedge's g = .224). Correspondingly, no significant differences were found in LSA individuals (BFNE: angry (Mean = 10.12; SD = 1.69) vs happy (Mean = 10.15; SD = 1.46); independent samples t-test, 2-sided; t(35) = −0.062, p = .951, Hedge's g = .019), DASS: angry (Mean = 5.06; SD = 4.94) vs happy (Mean = 5.70; SD = 4.49; independent samples t-test, 2-sided; t(35) = −.414, p = .682, Hedge's g = .136), PA: angry (Mean = 31.59; SD = 8.14) vs happy (Mean = 3.70; SD = 8.25; independent samples t-test, 2-sided; t(35) = −0.781, p = .440, Hedge's g = .257), or NA: angry (Mean = 11.29; SD = 1.53) vs happy (Mean = 12.00; SD = 2.34; independent samples t-test, 2-sided; t(35) = −1.064, p = .440, Hedge's g = .353).

Figure 4 shows the mean PSE shift across individuals in each anxiety group. Each individual's post-adapt PSE was normalised by each individual's pre-adapt PSE, at baseline. We found no significant difference in baseline PSE between LSA (Mean = 3.04; SD = 11.88) and HSA (Mean = 5.82; SD = 12.67) individuals (independent samples t-test, 2-sided; t(74) = −.986, p = .327, Hedge's g = .023). Furthermore, within the HSA group, there was no significant difference in baseline PSE when adapting to angry (Mean = 3.83; SD = 13.99) vs happy (Mean = 7.71; SD = 11.32) faces (independent samples t-test, 2-sided; t(37) = −0.953, p = .347, Hedge's g = .306). The LSA group also showed no significant difference in baseline PSE when adapting to angry (Mean = 3.50; SD = 12.47) vs happy (Mean = 2.65; SD = 11.67) faces (independent samples t-test, 2-sided; t(35) = .216, p = .830, Hedge's g = .071).

We used a two-tailed independent sample t-test to test if adaptation strength in the *expected direction* differed between adapt happy and adapt angry. We compared the strength of adaptation *in the expected direction* by evaluating the difference between perceptual shifts after adapting to angry and the additive inverse of perceptual shifts after adapting to happy. It was necessary to consider the magnitude of the shift in the *expected direction* as adapting to emotions of opposite valence (i.e. angry vs happy) yields shifts in

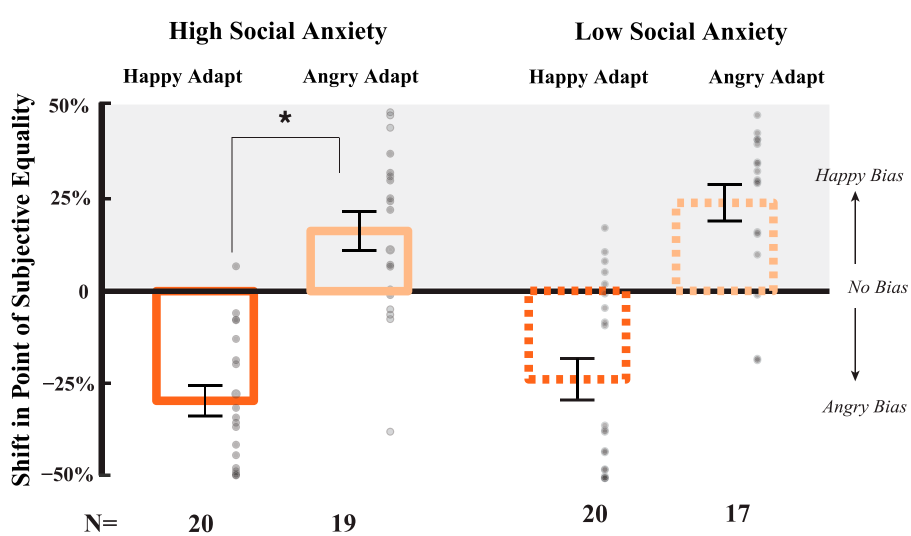

Figure 4. Effects of Adaptation to Happy vs Angry Faces in HSA and LSA.

Note: Perceptual Shifts in the expected direction in HSA and LSA individuals, for the Happy Adapt and Angry Adapt conditions. Results showed stronger adaptation to happy vs angry faces in HSA individuals (p = .038), and no significant difference in adaptation to happy vs angry faces in LSA individuals (p = .446).

opposite directions as seen in the sample individuals, and would yield significant differences simply based on shift direction when what is important is shift magnitude. Overall, HSA individuals showed significantly weaker adaptation in the *expected direction* after adapting to angry (Mean = .16; SD = .23) vs happy faces (Mean = .30; SD = .18; independent samples t-test, 2-sided, $t(37) = -2.149$, $p = .038$; Hedge's g = −.67). LSA individuals showed no significant difference in the *expected direction* after adapting to angry (Mean = .23; SD = .20) vs happy (Mean = .24; SD = .25) faces (independent samples t-test, 2-sided; $t(35) = -.016$, $p = .987$, Hedge's g = −.043).

We found no significant difference in change in slope after adapting to angry (Mean = −.024; SD = .23) vs happy (M = .027; SD = .26) faces ($t(37) = -.636$, $p = .53$; Hedges' g = −.20) in HSA individuals, nor between adapting to angry (M = −.022; SD = .19) vs happy (M = .12; SD = .26; $t(35) = -1.85$, $p = .072$; Hedges' g = −.60) in LSA individuals (data not shown).

We also compared the difference in adapting to happy vs angry faces, *in the expected direction*, between HSA and LSA, using a bootstrap analysis, 10,000 iterations with replacement. The mean difference in adapting to happy vs angry between HSA and LSA was 0.1382, which was not significant, since the bootstrapped confidence interval included 0 [−0.0476–0.3247].

Discussion

In Experiment 1, we investigated if adaptation to emotional information was altered in individuals high in social anxiety, a mechanism that could serve to maintain negative perceptual biases. We proposed that altered adaptation could maintain enhanced sensitivity to negative information such as angry faces by reducing the strength of adaptation to this emotion, or by enhancing the strength of adaptation to positive emotions, as conveyed by happy faces. To test that the difference between adapting to angry vs happy faces would be evident only in individuals with high social anxiety, we included a control group of low social anxiety individuals. We then quantified the strength of adaptation to angry versus happy emotional faces by measuring the PSE (Point of Subjective Equality) for a perceptual aftereffect in each individual. We predicted a significant difference in adaptation strength to angry vs happy faces in individuals high in social anxiety, while expecting no difference in adaptation to angry vs happy faces in individuals low in social anxiety. our findings suggest that (1) mechanisms of adaptation to emotional information appear to be altered in social anxiety such that individuals with social anxiety show weaker adaptation to angry faces compared to happy faces; a difference in adaptation that was not observed in the control group of individuals low in social anxiety, and (2) angry faces carry important threating information for HSA individuals, observed through a weakened strength of adaptation to angry relative to happy faces.

As shown previously by Rhodes et al. (2011), attention enhances adaptation, however in the HSA group we observed reduced adaptation for angry faces compared to happy faces, potentially suggesting that some avoidance attentional mechanisms might be playing a role in weakening adaptation effects. This avoidance attentional pattern has been observed in previous studies. For instance, one study using eye-tracking in a visual search task, found that compared to controls, individuals with social anxiety disorder showed reduced fixation duration to angry faces (Wermes et al., 2018). However, in the context of our study, it is still not clear how attentional biases play a role in altered mechanisms of adaptation, specifically in weakened adaptation to angry faces. Thus, future studies should explore this question using eye-tracking data and measures such as reaction time.

Another important issue to consider is related to the influence that anger, as a type of negative emotion, has on social anxiety. Would we observe altered adaptation for other negative emotions, such as sadness, in individuals with high social anxiety, or are the results particular to a threatening negative emotion such as anger? We explore this question further in Experiment 2, where we test adaptation to sad and happy faces in an HSA group.

Experiment 2

In Experiment 2 we tested a new sample of HSA individuals considering adaptation to non-threatening negative emotions, and quantified adaptation to happy versus sad faces in a between-subjects design. As mentioned in the introduction, and further tested in our first experiment, research has shown that HSA individuals show an increased sensitivity and a general attribution of threat to anger, but not to other negative emotions such as sadness (e.g. Bell et al., 2011; Gutiérrez-García & Calvo, 2017; Joormann & Gotlib, 2006). In our first experiment, we observed altered adaptation, specifically weakened adaptation to angry relative to happy faces, however considering that sad faces might not be conveying rejection, threat or hostility, we predict that there is going to be no difference in adaptation strength when adapting to sad versus happy faces in a high social anxiety group.

Methods

Participants

In Experiment 2 we collected data from 48 participants, 18–38 years of age, recruited from the University of Massachusetts Boston community by either email notices or announcements in Psychology classes. Our final sample consisted of 40 individuals classified as *high* in social anxiety (HSA: 30 females; 2 transgender individuals: mean age = 26.90 years, SD = 9.97, range = 18–38). Of the 48 participants who contributed data, 8 participants were excluded due to: an insufficient number of valid trials (3), biased behavioural responses (4), and participant error, such as pressing the wrong button (1). As in Experiment 1, the final sample included predominately female (75%) and white (57.5%) participants with a mean age of 23.08 (see Table 2). Participants were screened for social anxiety status, depression, and for current state affect as described for Experiment 1.

Table 2. Characteristics of individuals high and low in social anxiety in Experiment 2, grouped by adapt condition: adapt sad and adapt happy.

	High Social Anxiety (n = 40)	
Conditions	Sad Adapt (N =21) **Mean (SD; Range)**	Happy Adapt (N = 19) **Mean (SD; Range)**
Age [1]	23.10 (5.31; 18–38)	23.06 (4.12; 18–33)
BFNE	30.38 (4.74; 25–40)	33.00 (5.26; 25–40)
DASS	5.62 (4.57; 0–15)	7.05 (4.35; 0–14)
Positive [2]**Affect**	26.21 (7.22; 14–44)	26.56 (8.08; 16–41)
Negative Affect	14.84 (3.98; 10–26)	13.28 (2.52; 10–18)
	***n* (%N)**	***n* (%N)**
GENDER		
Female	14 (66.67%)	16 (84.21%)
Male	6 (28.57%)	2 (10.53%)
Transgender	1 (5.26%)	1 (5.26%)
ETHNICITY		
White	11 (52.38%)	12 (63.16%)
Latino/Hispanic	1 (4.76%)	1 (5.26%)
Asian–American	4 (19.05%)	3 (15.79%)
Black/African–American	1 (4.76%)	1 (5.26%)
Pacific Islander	1 (4.76%)	0 (0.00%)
Multi–racial	0 (0.00%)	1 (5.26%)
Unspecified	3 (14.29%)	1 (5.26%)

Notes: SD = standard deviation; BFNE = Brief Feat of Negative Evaluations; DASS = Depression Anxiety Stress Scale 21-item version.
[1]One participant in the HS condition did not report age.
[2]Three participants did not report Positive and Negative Affect, two in the adapt sad condition and one in the adapt happy condition.

Measures

As described in Experiment 1.

Apparatus, procedures for stimulus presentation including experimental design, data analysis, and statistical analysis are as described in Experiment 1. The one difference: instead of angry faces, we presented sad faces in a sad to happy continuum (see Figure 5 for a sample test face).

Data analysis

Figure 6 provides hypothetical predictions for adaptation strength following repeated exposure to 100% happy vs 100% sad faces in HSA. The direction of adaptation to happy versus sad faces, is, by definition, in opposite directions, with happy adapt yielding a negative shift and sad adapt yielding a positive shift. For statistical analysis, we evaluated the difference between shifts after adapting to sad and the additive inverse of shifts after adapting to happy, which considers adaptation strength in the expected direction as a function of emotional valence (happy/sad). We predicted that HSA individuals would show no difference in adaptation strength, in the expected direction, to sad vs happy faces, since sad faces are not threatening (see Figure 6).

Results

Our final sample of 40 participants completed a total of 2433 baseline and 2497 adapt trials. Of the 64 possible trials presented during baseline and post-adaptation, HSA individuals adapted to happy provided valid responses on an average of 61.00 baseline trials (SD = 3.56; range = 49–64), and 62.42 post-adaptation trials (SD = 1.71; range = 57–64). HSA individuals adapted to sad provided valid responses on an average of 60.67 baseline trials (SD = 4.71; range =

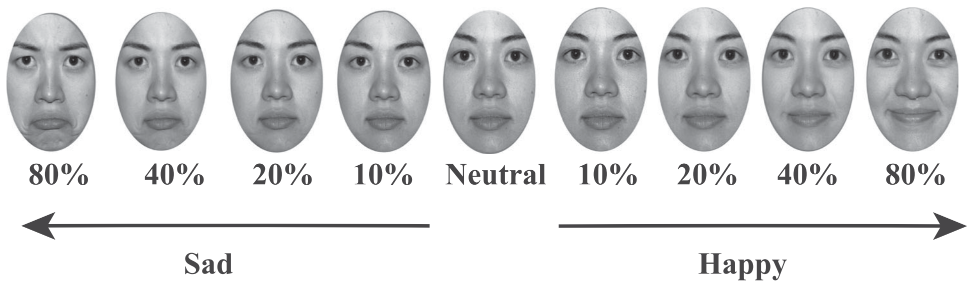

Figure 5. Sample Sad-Happy Face Morphs.

Note: An example of a sad-happy continuum of faces for a single identity. During baseline and post-adaptation participants judged a total of 64 faces morphed along a sad-happy continuum, from 80, 40, 20 and 10% sad to neutral and from neutral to 10, 20, 40 and 80% happy.

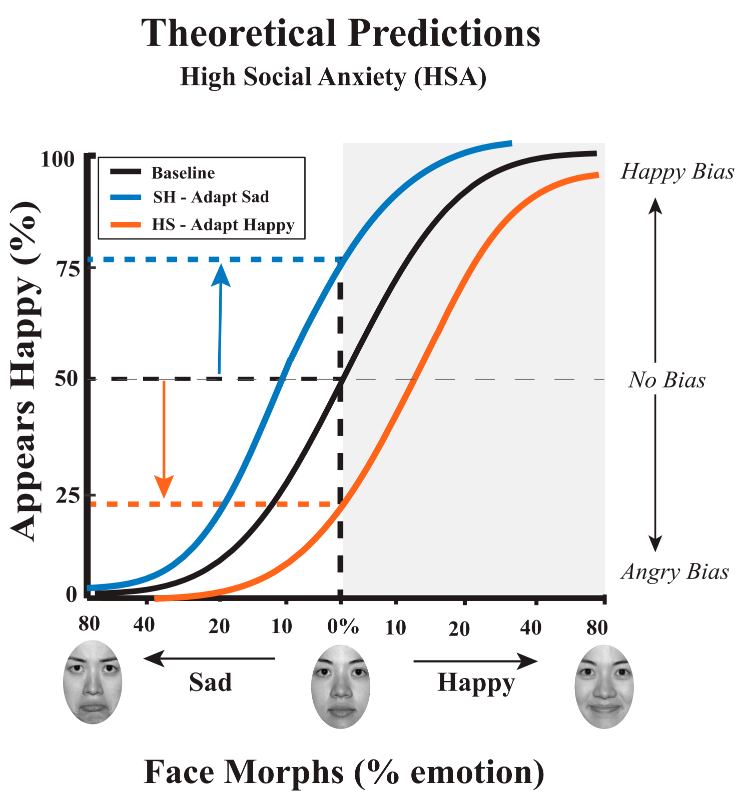

Figure 6. Theoretical Predictions in HSA for Adapting to Happy vs Sad.

Note: In this figure, the *x*-axis represents morphed faces in the continuum from 80% sad (left of 0), to 80% happy (right of 0), whereas the *y*-axis represents the percent at which a certain face morph is judged as happy. For each participant, we measured the Point of Subjective Equality (PSE), the face equally likely judged happy or sad. The black curve represents a cumulative normal fit to judgements of each face morph at baseline, whereas the blue and the orange curves represent the cumulative normal fit to judgements of each face morph after adapting to sad and happy faces, respectively. The predicted direction and magnitude of perceptual changes from baseline to post-adapt (PSE shift) are depicted in the direction and magnitude of the arrows extending from the baseline curve to the post-adapt curve. We predicted no significant difference in the magnitude of adaptation, in the *expected direction*, to happy vs sad faces.

47–64), and 62.43 post-adaptation trials (SD = 2.20; range = 57–64). We found no significant difference in the number of baseline trials (independent samples Mann–Whitney U Test, 2-sided; U = 192.5, $p = .848$, $\eta^2 = .001$) or adapt trials (independent samples Mann–Whitney U Test, 2-sided; U = 177, $p = .527$, $\eta^2 = .009$) between HSA individuals adapted to sad vs happy faces. There were no differences in age between individuals adapting to sad faces (Mean = 23.10; SD = 5.31) and individuals adapting to happy faces (Mean = 23.06; SD = 4.12) (independent samples t-test, 2-sided; t(37) = .026, *p* = .980, Hedge's g = .008), and no differences in gender distribution ($X^2(2) = 2.04$, *p* = .361).

We also found no significant differences in measures for anxiety, depression, and state affect, when adapting to happy versus angry faces in HSA individuals (BFNE: sad (Mean = 30.38; SD = 4.74) vs happy (Mean = 33.00; SD = 5.26); independent samples t-test, 2-sided; t(38) = −1.657, *p* = .106, Hedge's g = .525), DASS: sad (Mean = 5.62; SD = 4.57) vs happy (Mean = 7.05; SD = 4.35; independent samples t-test, 2-sided; t(38) = −1.014, *p* = .317, Hedge's g = .32). PA: sad (Mean = 26.21; SD = 7.22) vs happy (Mean = 26.56; SD = 8.08; independent samples t-test, 2-sided; t(35) = −.137, *p* = .892, Hedge's g = .046), and NA: sad (Mean = 14.84; SD = 3.98) vs happy (Mean = 13.28; SD = 2.52; independent samples t-test, 2-sided; t(35) = 1.421, *p* = .164, Hedge's g = .465).

Figure 7 shows mean PSE shift. Each individual's post-adapt PSE has been normalised by their pre-adapt PSE at baseline. Using a two-tailed independent sample t-test, we tested for baseline differences in PSE between adaptation conditions (adapt sad vs happy). We found no significant difference in baseline PSE between HSA individuals adapting to sad (Mean = 15.87; SD = 5.59) vs happy (Mean = 12.42; SD = 10.28) faces (independent samples t-test, 2-sided; t(38) = 1.339, *p* = .189, Hedge's g = .423). HSA individuals also showed no significant difference in the strength of adaptation in the *expected direction* after adapting to sad (Mean = .27; SD = .11) vs happy (Mean = .28; SD = .24) faces (independent samples t-test, 2-sided, t (38) = −.135, *p* = .894, Hedges' g = −.05).

We did find a significant difference in slope after adapting to sad (Mean = −.12; SD = .19) vs to happy (Mean = .16; SD = .24; independent samples t-test, 2-sided, t(38) = −.135, *p* < .001, Hedges' g = −1.28), such that adapting to happy yielded a steeper change in slope after adaptation, compared to adapting to sad.

Discussion

In experiment 2 we further tested the idea that altered adaptation might help maintain sensitivity to negative emotional faces but only to emotions conveying threat such as anger and not to other negative emotions such as sadness. Thus, using a between-subject design, we collected data only on an HSA group, and compared the adaptation to sad vs happy faces, testing the hypothesis that the strength of adaptation to sad faces would not differ from the

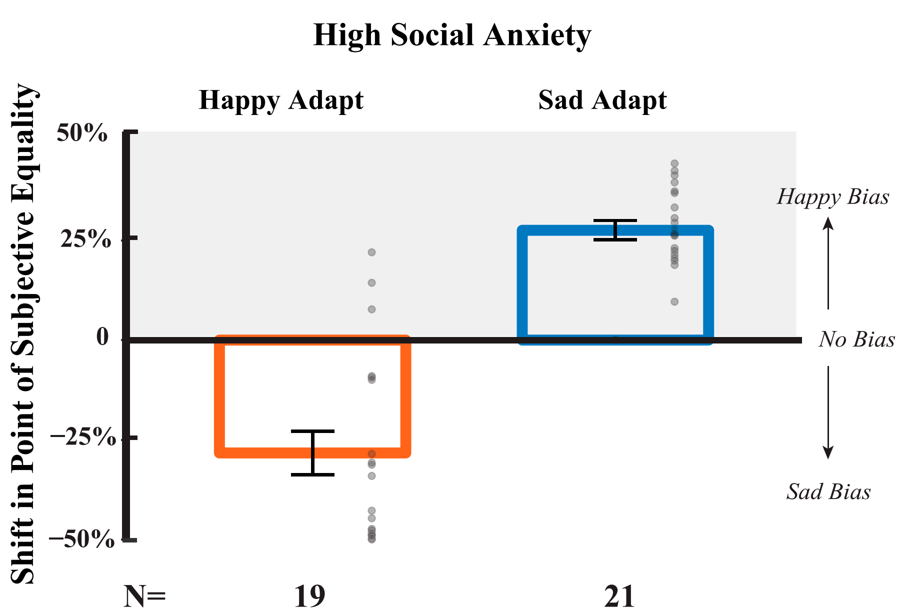

Figure 7. Effects of Adaptation to Happy vs Sad in HSA.

Note: Perceptual Shifts in the expected direction in HSA individuals in the Adapt Happy and Adapt Sad conditions. As expected, we found no significant difference in adaptation to happy vs sad faces (*p* = .20).

strength of adaptation to happy faces in HSA individuals. As in Experiment 1, we calculated the PSE before and after adaptation in order to quantify the change in perception post-adaptation, or the strength in adaptation. As expected, we found no difference between the adapt sad and adapt happy condition, further supporting the view that HSA individuals are particularly sensitive to anger but not to other negative emotions such as sadness. This is also in line with other studies showing that socially anxious individuals tend to interpret and misclassify neutral faces as being negative, and in addition they are more likely to pick anger and not other negative emotions during the process of classification (e.g. Bell et al., 2011; Gutiérrez-García & Calvo, 2017; Heuer et al., 2010; Joormann & Gotlib, 2006; Peschard & Philippot, 2016; Yoon et al., 2014; Yoon & Zinbarg, 2007, 2008).

General discussion

In the current study, we investigated if adaptation to emotional information was altered in individuals high in social anxiety, a mechanism that could serve to maintain negative perceptual biases. We proposed that altered adaptation could maintain enhanced sensitivity to negative information or enhance negative perceptual biases by reducing the strength of adaptation to negative and threatening emotions, as conveyed by angry faces, or by enhancing the strength of adaptation to positive emotions, as conveyed by happy faces. We quantified the strength of adaptation to negative versus positive emotional information by measuring the PSE for a perceptual aftereffect. In Experiment 1 we considered a negative threatening emotion, angry faces, and in Experiment 2, a negative non-threatening emotion, sad faces. We predicted a significant difference in adaptation strength to angry versus happy faces in individuals high in social anxiety, but only for threatening negative emotions, with no expected difference between adapting to happy versus sad faces. Furthermore, we predicted no significant difference in adaptation strength to angry versus happy faces in individuals low in social anxiety.

As expected, we found weaker adaptation to angry faces relative to stronger adaptation to happy faces in individuals high in social anxiety (Experiment 1), with no significant difference in individuals low in social anxiety, and no significant difference in adaptation to happy versus sad faces in individuals high in social anxiety (Experiment 2). These results are consistent with previous studies showing that socially anxious individuals tend to attribute threat to anger but not to other negative emotions, such as sadness, and demonstrate increased sensitivity to anger, detecting anger at lower intensities of emotion and misclassifying neutral expressions as angry (Bell et al., 2011; Gutiérrez-García & Calvo, 2017; Joormann & Gotlib, 2006).

Although we find differences in adaptation to happy versus angry faces in individuals high in social anxiety, our results cannot differentiate between (1) decreased adaptation to angry faces [relative to a control condition], (2) increased adaptation to happy faces [relative to a control condition], or (3) both mechanisms occurring within the same individual. To address the underlying perceptual mechanism, one would need to run a control condition of adapting to neutral faces, ideally using a within-subject design which might require short-term adaptation, unlike the long-term adaptation used here (3 min) in a between-subjects design.

Considering emotion along a continuum

Given that HSA individuals can correctly identify emotions but are particularly biased in perceiving ambiguous facial expressions (e.g. Bell et al., 2011; Gutiérrez-García & Calvo, 2017; Joormann & Gotlib, 2006) studying responses to fully affective facial expressions could yield a ceiling effect and not reflect the true sensitivity of emotional perception in socially anxious individuals. This is one main benefit of presenting faces along an emotional continuum, such as the emotional morphs used in our study. Another benefit is minimising the likelihood of a motor response bias, such as participants only selecting the angry option for all ambiguous faces. Instead, if 100%, fully affective, happy faces are also included, it is easier to uncover a motor bias since the angry option should not be selected for 100% happy faces. Finally, our face morph scale was non-linear, a logarithmic scale (80, 40, 20 and 10% of a given emotion) to maximise sensitivity for detecting bias near the ambiguous emotional range while not presenting solely ambiguous faces.

Threatening emotions

Our results highlight the special status of *threatening* negative emotions for individuals high in social anxiety. We found maintained responsiveness, weakened adaptation, for angry relative to happy faces in HSA individuals, with no such maintained responsiveness for sad relative to happy faces. Thus, not all negative emotions are processed, or adapted, the same way. Previous studies have found perceptual biases in processing negative emotions conveying rejection and hostility, such as anger (e.g. Bell et al., 2011; Yoon et al., 2014), and enhanced detection for threatening negative expressions, anger and disgust. Furthermore, when socially anxious individuals interpret neutral faces as negative they more likely to choose a threatening emotion such as anger, whereas non-anxious individuals choose a non-threatening emotion such as sadness (Gutiérrez-García & Calvo, 2017). Our results add to this literature, suggesting that underlying mechanisms of adaptation, which could perpetuate perceptual biases, are selectively altered for threatening, but not non-threatening, negative emotions.

Mechanisms of adaptation

Our results contribute to a growing body of evidence finding altered mechanisms of adaptation in various clinical conditions, including social anxiety, autism spectrum disorder, and schizophrenia (e.g. Andrade et al., 2016). Attenuated adaptation can maintain heightened responsiveness to sensory stimuli, failing to adjust the gain or sensitivity to sensory inputs if adaptation is too weak, a mechanism proposed for sensory over responsivity (reviewed in Soto et al., 2018). A failure of adaptation can also maintain decreased responsiveness to sensory stimuli, over adjusting the gain or sensitivity to sensory inputs, if adaptation is too strong. Overall, a suboptimal adaptation mechanism prevents the nervous system from remaining most sensitive and responsive to novel, non-redundant, information and prevents the re-allocation of limited attentional capacity and processing resources to the most behaviourally relevant information.

Altered adaptation in processing social information has been found in clinical conditions with select impairments in social interactions, such as autism. Adults on the spectrum show altered adaptation to emotional faces (Rutherford et al., 2012). Children on the spectrum (8.5–13.5 year olds) show reduced adaptation to face identity (Pellicano et al., 2007) and toddlers at high risk for autism (18–30 months of age) show slower and reduced habituation to faces but not houses, with slower habituation, or slower learning rate, correlated with poorer social skills and verbal ability (Webb et al., 2010).

In terms of the neural correlates of emotional processing, research has focused on brain areas, such as the amygdala, a model system for understanding fear conditioning (e.g. LeDoux, 2003) and a brain area known to be particularly responsive to valenced emotional content and to habituate rapidly to valenced emotions (e.g. Breiter et al., 1996). Neural evidence reveals impaired adaptation, or habituation. Habituation is *slowed* in response to neutral faces in the amygdala, a mechanism linked to inhibited temperament (e.g. Avery & Blackford, 2016; Blackford et al., 2011; Blackford et al., 2013; Schwartz et al., 2003; Schwartz et al., 2012), which is a risk factor for social anxiety (Clauss et al., 2015; Clauss & Blackford, 2012). In 9–60 year olds, habituation is also *decreased in magnitud*e in the amygdala, maintaining heightened neural responsiveness, when reading text depicting social situations that violated norms and induced shame compared to reading neutral text (Bas-Hoogendam et al., 2020). Highlighting the importance of such a mechanism, these authors propose altered adaptation as a heritable endophenotype for social anxiety.

Despite neural evidence for altered habituation to the social information in neutral faces, there seems to be a dearth of evidence in terms of the perceptual correlates of such altered neural habituation. Our study is the first, to our knowledge, to consider the perceptual effects of adaptation to emotional faces, for which adaptation to neutral faces would serve as an important control condition. Future studies should consider neural mechanisms of adaptation for other facial expressions and adaptation to non-visual emotional stimuli.

Limitations

As with any research, our study has several limitations. One important limitation is that we did not quantify or control how overt or covert attention was allocated to different stimuli. Compared to controls, individuals high in social anxiety attend less to emotional faces over time, especially faces displaying positive emotions, such as happiness (Schofield et al., 2013). Given that attention is known to alter the strength of adaptation to visual stimuli in general (e.g. Carrasco et al., 2006; Rezec et al., 2004) and to faces in particular (Izen & Ciaramitaro, 2020; Rhodes et al., 2011), this is an important consideration. Of note, however, attending to a stimulus tends to enhance the strength of adaptation. If HSA individuals attended less to happy faces, this would be expected to weaken, not enhance, adaptation, contrary to our results. Additionally, it is intriguing to consider our findings in light of the Approach-Avoidance Task (AAT), which is closely related to attention in that it reflects how attention influences automatic behavioural reactions to emotional or socially relevant stimuli. For instance, Heuer et al. (2007) investigated avoidance reactions to stimuli of potential social threat among HSA individuals and non-anxious controls (NACs). HSA individuals displayed stronger avoidance tendencies for both smiling and angry faces in the AAT, despite positively evaluating smiling faces (Heuer et al., 2007). However, if in our study we were to consider these attentional findings, then we wouldn't expect a difference in adaptation between happy and angry faces, because HSA individuals seem to demonstrate avoidance to both happy and angry faces, which would have impacted the process of adaptation. Thus, underlying differences in attention to happy faces are unlikely to explain the differences we observed.

Moreover, individuals high in social anxiety show eye gaze patterns of hypervigilance-avoidance, especially for negative emotions such as anger. They show initial fixation of an angry stimulus followed by avoidance of the stimuli (for a review see Claudino et al., 2019). Such differences in eye gaze patterns could contribute to differences in adaptation: if HSA individuals avert their gaze from angry faces this could weaken adaptation to angry faces.

Another important limitation is that we considered a student sample along the continuum of social anxiety. While BFNE cut-off scores are suggestive of clinically significant social anxiety (e.g. Carleton et al., 2011), it is not clear how our results apply to clinical cohorts. Future studies will need to replicate our results in a clinical sample. However, given that social anxiety exists along a continuum (Rapee & Heimberg, 1997), our results provide valuable information regarding underlying cognitive mechanisms of the disorder even if not specifically targeted for clinically diagnosed groups. Furthermore, we excluded participants scoring high in depression. This may give insight into only a small subset of individuals who are socially anxious since there is a high degree of comorbidity between social anxiety disorders and depression (e.g. Koyuncu et al., 2019).

A third consideration is that mood was not controlled in our study. Previous studies have found that perceptual biases may be stronger or more likely to be observed if socially anxious individuals are stressed via mood induction prior to the experiment (Leber et al., 2009; Mohlman et al., 2007; Mullins & Duke, 2004; Richards et al., 2002). Thus, we might have observed stronger adaptation effects if we had used mood induction.

Conclusions

We observed significantly weaker adaptation to angry vs happy faces in individuals high in social anxiety, with no significant difference when adapting to happy versus sad faces in individuals high in social anxiety. This aligns with prior studies suggesting that not all negative emotions are equal, and the unique importance of threatening negative emotions in social anxiety. More importantly, our findings reveal a potential mechanism through which social anxiety may be maintained – either attenuated adaptation to angry faces and/or exaggerated adaptation to happy faces would perpetuate increased sensitivity to negative information. Importantly, no differences in adaptation strength were observed in individuals low in social anxiety. Future work should explore how these mechanisms may be altered in clinical populations and as a function of clinical severity. There is also a need to understand pharmacological and nonpharmacological therapies for social anxiety disorder, such as cognitive behavioural therapy, that may narrow the observed asymmetry in adaptation aftereffects. Understanding the altered perceptual biases present in social anxiety disorder may ultimately help to improve the clinical assessment, treatment, and quality of life of individuals living with the disorder.

In summary, our results add to a growing body of evidence suggesting that basic mechanisms of emotional adaptation may be altered in conditions affecting social interactions, where the processing and interpretation of emotional information conveyed by faces may be particularly relevant. Future studies should consider other ways in which emotions may be conveyed, not simply by faces, but by tone of voice, or body posture.

Acknowledgements

The authors thank a wonderful team of lab managers, Annalisa Groth Valadez and Daniel Paulus, as well as undergraduate research assistants, especially Justine Crowley, Rebecca

Caruso, Anh Phan, Alexia Williams, Terrence Cook, and graduate student, Sarah Izen, for help with data collection and analysis. Finally, much of this work would not have been possible without support from the UMass Boston Dean's Research Fund and the UMass Boston Department of Psychology Research Fund to vmc and sah-s and undergraduate student research funds to dah, jc, ap, aw, and tc. All authors declare that they have no conflict of interest and that this work has not been published previously.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by UMass Boston undergraduate research awards; UMass Boston Dean's Research Fund.

ORCID

Vivian M. Ciaramitaro http://orcid.org/0000-0001-6767-6441

References

American Psychiatric Association. (2013). *Diagnostic and statistical manual of mental disorders* (Fifth ed.). https://doi.org/10.1176/appi.books.9780890425596

Amin, N., Foa, E. B., & Coles, M. E. (1998). Negative interpretation bias in social phobia. *Behaviour Research and Therapy*, *36*(10), 945–957. https://doi.org/10.1016/S0005-7967(98)00060-6

Amir, N., Elias, J., Klumpp, H., & Przeworski, A. (2003). Attentional bias to threat in social phobia: Facilitated processing of threat or difficulty disengaging attention from threat? *Behaviour Research and Therapy*, *41*(11), 1325–1335. https://doi.org/10.1016/S0005-7967(03)00039-1

Andrade, G. N., Butler, J. S., Peters, G. A., Molholm, S., & Foxe, J. J. (2016). Atypical visual and somatosensory adaptation in schizophrenia-spectrum disorders. *Translational Psychiatry*, *6*(5), e804. https://doi.org/10.1038/tp.2016.63

Antony, M. M., Bieling, P. J., Cox, B. J., Enns, M. W., & Swinson, R. P. (1998). Psychometric properties of the 42-item and 21-item versions of the Depression Anxiety Stress Scales in clinical groups and a community sample. *Psychological Assessment*, *10*(2), 176. https://doi.org/10.1037/1040-3590.10.2.176

Anzures, G., Mondloch, C. J., & Lackner, C. (2009). Face Adaptation and Attractiveness Aftereffects in 8-Year-Olds and Adults. *Child Development*, *80*(1), 178–191. https://doi.org/10.1111/j.1467-8624.2008.01253.x

Avery, S. N., & Blackford, J. U. (2016). Slow to warm up: The role of habituation in social fear. *Social Cognitive and Affective Neuroscience*, *11*(11), 1832–1840. https://doi.org/10.1093/scan/nsw095

Bas-Hoogendam, J. M., van Steenbergen, H., Tissier, R. L. M., van der Wee, N. J. A., & Westenberg, P. M. (2020). Altered neurobiological processing of unintentional social norm violations: A multiplex, multigenerational functional magnetic resonance imaging study on social anxiety endophenotypes. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, *5*(10), 981–990. https://doi.org/10.1016/j.bpsc.2019.03.003

Bell, C., Bourke, C., Colhoun, H., Carter, F., Frampton, C., & Porter, R. (2011). The misclassification of facial expressions in generalised social phobia. *Journal of Anxiety Disorders*, *25*(2), 278–283. https://doi.org/10.1016/j.janxdis.2010.10.001

Blackford, J. U., Allen, A. H., Cowan, R. L., & Avery, S. N. (2013). Amygdala and hippocampus fail to habituate to faces in individuals with an inhibited temperament. *Social Cognitive and Affective Neuroscience*, *8*(2), 143–150. https://doi.org/10.1093/scan/nsr078

Blackford, J. U., Avery, S. N., Cowan, R. L., Shelton, R. C., & Zald, D. H. (2011). Sustained amygdala response to both novel and newly familiar faces characterizes inhibited temperament. *Social Cognitive and Affective Neuroscience*, *6*(5), 621–629. https://doi.org/10.1093/scan/nsq073

Bottesi, G., Ghisi, M., Altoè, G., Conforti, E., Melli, G., & Sica, C. (2015). The Italian version of the Depression Anxiety Stress Scales-21: Factor structure and psychometric properties on community and clinical samples. *Comprehensive Psychiatry*, *60*, 170–181. https://doi.org/10.1016/j.comppsych.2015.04.005

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., Strauss, M. M., Hyman, S. E., & Rosen, B. R. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, *17*(5), 875–887. https://doi.org/10.1016/S0896-6273(00)80219-6

Button, K., Lewis, G., Penton-Voak, I., & Munafò, M. (2013). Social anxiety is associated with general but not specific biases in emotion recognition. *Psychiatry Research*, *210*(1), 199–207. https://doi.org/10.1016/j.psychres.2013.06.005

Carleton, R. N., Collimore, K. C., McCabe, R. E., & Antony, M. M. (2011). Addressing revisions to the Brief Fear of Negative Evaluation scale: Measuring fear of negative evaluation across anxiety and mood disorders. *Journal of Anxiety Disorders*, *25*(6), 822–828. https://doi.org/10.1016/j.janxdis.2011.04.002

Carrasco, M., Loula, F., & Ho, Y.-X. (2006). How attention enhances spatial resolution: Evidence from selective adaptation to spatial frequency. *Perception & Psychophysics*, *68*(6), 1004–1012. https://doi.org/10.3758/BF03193361

Clark, D. M. (2001) A cognitive perspective on social phobia. In W. R. Crozier & L. E. Alden (Eds.), *International handbook of social anxiety: Concepts, research and interventions relating to the self and shyness* (pp. 405–430). John Wiley & Sons Ltd.

Clark, D. M., & Wells, A. (1995). A cognitive model of social phobia. *Social Phobia: Diagnosis, Assessment, and Treatment*, *41*(68), 00022–00023.

Claudino, R. G. e., de Lima, L. K. S., de Assis, E. D. B., & Torro, N. (2019). Facial expressions and eye tracking in individuals with social anxiety disorder: A systematic review. *Psicologia: Reflexão e Crítica*, *32*(1), 9. https://doi.org/10.1186/s41155-019-0121-8

Clauss, J. A., Avery, S. N., & Blackford, J. U. (2015). The nature of individual differences in inhibited temperament and risk for psychiatric disease: A review and meta-analysis. *Progress in Neurobiology*, *127–128*, 23–45. https://doi.org/10.1016/j.pneurobio.2015.03.001

Clauss, J. A., & Blackford, J. U. (2012). Behavioral inhibition and risk for developing social anxiety disorder: A meta-analytic study. *Journal of the American Academy of Child & Adolescent Psychiatry*, *51*(10), 1066–1075. https://doi.org/10.1016/j.jaac.2012.08.002

Ewing, L., Pellicano, E., & Rhodes, G. (2013). Atypical updating of face representations with experience in children with autism. *Developmental Science*, *16*(1), 116–123. https://doi.org/10.1111/desc.12007

Fox, E., Russo, R., & Dutton, K. (2002). Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cognition & Emotion*, *16*(3), 355–379. https://doi.org/10.1080/02699930143000527

Frenkel, T. I., & Bar-Haim, Y. (2011). Neural activation during the processing of ambiguous fearful facial expressions: An ERP study in anxious and nonanxious individuals. *Biological Psychology*, *88*(2), 188–195. https://doi.org/10.1016/j.biopsycho.2011.08.001

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, *24*(1), 187–203. https://doi.org/10.1016/S0896-6273(00)80832-6

Gutiérrez-García, A., & Calvo, M. G. (2014). Social anxiety and interpretation of ambiguous smiles. *Anxiety, Stress, & Coping*, *27*(1), 74–89. https://doi.org/10.1080/10615806.2013.794941

Gutiérrez-García, A., & Calvo, M. G. (2016). Social anxiety and trustworthiness judgments of dynamic facial expressions of emotion. *Journal of Behavior Therapy and Experimental Psychiatry*, *52*, 119–127. https://doi.org/10.1016/j.jbtep.2016.04.003

Gutiérrez-García, A., & Calvo, M. G. (2017). Social anxiety and threat-related interpretation of dynamic facial expressions: Sensitivity and response bias. *Personality and Individual Differences*, *107*, 10–16. https://doi.org/10.1016/j.paid.2016.11.025

Harris, D. A., & Ciaramitaro, V. M. (2016). Interdependent mechanisms for processing gender and emotion: The special status of angry male faces. *Frontiers in Psychology*, *7*, 1046. https://doi.org/10.3389/fpsyg.2016.01046

Henry, J. D., & Crawford, J. R. (2005). The short-form version of the Depression Anxiety Stress Scales (DASS-21): Construct validity and normative data in a large non-clinical sample. *British Journal of Clinical Psychology*, *44*(2), 227–239. https://doi.org/10.1348/014466505X29657

Heuer, K., Lange, W.-G., Isaac, L., Rinck, M., & Becker, E. S. (2010). Morphed emotional faces: Emotion detection and misinterpretation in social anxiety. *Journal of Behavior Therapy and Experimental Psychiatry*, *41*(4), 418–425. https://doi.org/10.1016/j.jbtep.2010.04.005

Heuer, K., Rinck, M., & Becker, E. S. (2007). Avoidance of emotional facial expressions in social anxiety: The Approach–Avoidance Task. *Behaviour Research and Therapy*, *45*(12), 2990–3001. https://doi.org/10.1016/j.brat.2007.08.010

Hirsch, C. R., & Clark, D. M. (2004). Information-processing bias in social phobia. *Clinical Psychology Review*, *24*(7), 799–825. https://doi.org/10.1016/j.cpr.2004.07.005

Hope, D. A., Heimberg, R. G., & Klein, J. F. (1990). Social anxiety and the recall of interpersonal information. *Journal of Cognitive Psychotherapy*, *4*(2), 185–195. https://doi.org/10.1891/0889-8391.4.2.185

Hsu, S.-M., & Young, A. (2004). Adaptation effects in facial expression recognition. *Visual Cognition*, *11*(7), 871–899. https://doi.org/10.1080/13506280444000030

Huppert, J. D., Pasupuleti, R. V., Foa, E. B., & Mathews, A. (2007). Interpretation biases in social anxiety: Response generation, response selection, and self-appraisals. *Behaviour Research and Therapy*, *45*(7), 1505–1515. https://doi.org/10.1016/j.brat.2007.01.006

Itier, R. J., Latinus, M., & Taylor, M. J. (2006). Face, eye and object early processing: What is the face specificity? *Neuroimage*, *29*(2), 667–676. https://doi.org/10.1016/j.neuroimage.2005.07.041

Izen, S. C., & Ciaramitaro, V. M. (2020). A crowd of emotional voices influences the perception of emotional faces: Using adaptation, stimulus salience, and attention to probe audio-visual interactions for emotional stimuli. *Attention, Perception & Psychophysics*, *82*(8), 3973–3992. https://doi.org/10.3758/s13414-020-02104-0

Izen, S. C., Lapp, H. E., Harris, D. A., Hunter, R. G., & Ciaramitaro, V. M. (2019). Seeing a face in a crowd of emotional voices: Changes in cortisol in response to emotional information across the senses. *Brain Sciences*, *9*(8), 176. https://doi.org/10.3390/brainsci9080176

Jaquet, E., Rhodes, G., & Hayward, W. G. (2008). Race-contingent aftereffects suggest distinct perceptual norms for different race faces. *Visual Cognition*, *16*(6), 734–753. https://doi.org/10.1080/13506280701350647

Joormann, J., & Gotlib, I. H. (2006). Is this happiness I see? Biases in the identification of emotional facial expressions in depression and social phobia. *Journal of Abnormal Psychology*, *115*(4), 705. https://doi.org/10.1037/0021-843X.115.4.705

Kessler, R. C., Chiu, W. T., Demler, O., & Walters, E. E. (2005). Prevalence, severity, and comorbidity of 12-month DSM-IV disorders in the national comorbidity survey replication. *Archives of General Psychiatry*, *62*(6), 617. https://doi.org/10.1001/archpsyc.62.6.617

Kleiner, M., Brainard, D., & Pelli, D. (2007). *What's new in Psychtoolbox-3?*

Koyuncu, A., İnce, E., Ertekin, E., & Tükel, R. (2019). Comorbidity in social anxiety disorder: Diagnostic and therapeutic challenges. *Drugs in Context*, *8*, 21257. https://doi.org/10.7573/dic.212573

Leary, M. R. (1983). A brief version of the fear of negative evaluation scale. *Personality and Social Psychology Bulletin*, *9*(3), 371–375. https://doi.org/10.1177/0146167283093007

Leber, S., Heidenreich, T., Stangier, U., & Hofmann, S. G. (2009). Processing of facial affect under social threat in socially anxious adults: Mood matters. *Depression and Anxiety*, *26*(2), 196–206. https://doi.org/10.1002/da.20525

LeDoux, J. (2003). The emotional brain, fear, and the amygdala. *Cellular and Molecular Neurobiology*, *23*, 727–738.

LeMoult, J., & Joormann, J. (2012). Attention and memory biases in social anxiety disorder: The role of comorbid depression. *Cognitive Therapy and Research*, *36*(1), 47–57. https://doi.org/10.1007/s10608-010-9322-2

Little, A. C., DeBruine, L. M., Jones, B. C., & Waitt, C. (2008). Category contingent aftereffects for faces of different races, ages and species. *Cognition*, *106*(3), 1537–1547. https://doi.org/10.1016/j.cognition.2007.06.008

Little, A. C., Feinberg, D. R., DeBruine, L. M., & Jones, B. C. (2013). Adaptation to Faces and Voices: Unimodal, Cross-Modal, and Sex-Specific Effects. *Psychological Science*, *24*(11), 2297–2305. https://doi.org/10.1177/0956797613493293

Lovibond, P. F., & Lovibond, S. H. (1995). The structure of negative emotional states: Comparison of the depression anxiety stress scales (DASS) with the beck depression and anxiety inventories. *Behaviour Research and Therapy*, *33*(3), 335–343. https://doi.org/10.1016/0005-7967(94)00075-U

Luo, W., Feng, W., He, W., Wang, N.-Y., & Luo, Y.-J. (2010). Three stages of facial expression processing: ERP study with rapid serial visual presentation. *NeuroImage*, *49*(2), 1857–1867. https://doi.org/10.1016/j.neuroimage.2009.09.018

Mellings, T. M. B., & Alden, L. E. (2000). Cognitive processes in social anxiety: The effects of self-focus, rumination and anticipatory processing. *Behaviour Research and Therapy*, *38*(3), 243–257. https://doi.org/10.1016/S0005-7967(99)00040-6

Miller, R. S. (1995). On the nature of embarrassablity: Shyness, social evaluation, and social skill. *Journal of Personality*, *63*(2), 315–339. https://doi.org/10.1111/j.1467-6494.1995.tb00812.x

Mobini, S., Reynolds, S., & Mackintosh, B. (2013). Clinical implications of cognitive bias modification for interpretative biases in social anxiety: An integrative literature review. *Cognitive Therapy and Research*, *37*(1), 173–182. https://doi.org/10.1007/s10608-012-9445-8

Mohlman, J., Carmin, C. N., & Price, R. B. (2007). Jumping to interpretations: Social anxiety disorder and the identification of emotional facial expressions. *Behaviour Research and Therapy*, *45*(3), 591–599. https://doi.org/10.1016/j.brat.2006.03.007

Morrison, A. S., & Heimberg, R. G. (2013). Social anxiety and social anxiety disorder. *Annual Review of Clinical Psychology*, *9*(1), 249–274. https://doi.org/10.1146/annurev-clinpsy-050212-185631

Moser, J. S., Huppert, J. D., Foa, E. B., & Simons, R. F. (2012). Interpretation of ambiguous social scenarios in social phobia and depression: Evidence from event-related brain potentials. *Biological Psychology*, *89*(2), 387–397. https://doi.org/10.1016/j.biopsycho.2011.12.001

Mullins, D. T., & Duke, M. P. (2004). Effects of social anxiety on nonverbal accuracy and response time I: Facial expressions. *Journal of Nonverbal Behavior*, *28*, 3–33.

Murphy, R., Hirsch, C. R., Mathews, A., Smith, K., & Clark, D. M. (2007). Facilitating a benign interpretation bias in a high socially anxious population. *Behaviour Research and Therapy*, *45*(7), 1517–1529. https://doi.org/10.1016/j.brat.2007.01.007

Ng, M., Ciaramitaro, V. M., Anstis, S., Boynton, G. M., & Fine, I. (2006). Selectivity for the configural cues that identify the gender, ethnicity, and identity of faces in human cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(51), 19552–19557. https://doi.org/10.1073/pnas.0605358104

Öhman, A. (1986). Face the beast and fear the face: Animal and social fears as prototypes for evolutionary analyses of emotion. *Psychophysiology*, *23*(2), 123–145. https://doi.org/10.1111/j.1469-8986.1986.tb00608.x

Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General*, *130*(3), 466–478. https://doi.org/10.1037/0096-3445.130.3.466

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10* (4), 437–442. https://doi.org/10.1163/156856897X00366

Pellicano, E., Jeffery, L., Burr, D., & Rhodes, G. (2007). Abnormal adaptive face-coding mechanisms in children with autism spectrum disorder. *Current Biology*, *17*(17), 1508–1512. https://doi.org/10.1016/j.cub.2007.07.065

Peschard, V., & Philippot, P. (2016). Social anxiety and information processing biases: An integrated theoretical perspective. *Cognition and Emotion*, *30*(4), 762–777. https://doi.org/10.1080/02699931.2015.1028335

Philippot, P., & Douilliez, C. (2005). Social phobics do not misinterpret facial expression of emotion. *Behaviour Research and Therapy*, *43*(5), 639–652. https://doi.org/10.1016/j.brat.2004.05.005

Ran, G. M., Chen, X., Pan, Y. G., Hu, T. Q., & Ma, J. (2014). Effects of anticipation on perception of facial expressions. *Perceptual and Motor Skills*, *118*(1), 195–209. https://doi.org/10.2466/24.PMS.118k13w4

Rapee, R. M., & Heimberg, R. G. (1997). A cognitive-behavioral model of anxiety in social phobia. *Behaviour Research and Therapy*, *35*(8), 741–756. https://doi.org/10.1016/S0005-7967(97)00022-3

Reiss, S. (1991). Expectancy model of fear, anxiety, and panic. *Clinical Psychology Review*, *11*(2), 141–153. https://doi.org/10.1016/0272-7358(91)90092-9

Rezec, A., Krekelberg, B., & Dobkins, K. R. (2004). Attention enhances adaptability: Evidence from motion adaptation experiments. *Vision Research*, *44*(26), 3035–3044. https://doi.org/10.1016/j.visres.2004.07.020

Rhodes, G. (2017). Adaptive coding and face recognition. *Current Directions in Psychological Science*, *26*(3), 218–224.

Rhodes, G., Jeffery, L., Evangelista, E., Ewing, L., Peters, M., & Taylor, L. (2011). Enhanced attention amplifies face adaptation. *Vision Research*, *51*(16), 1811–1819. https://doi.org/10.1016/j.visres.2011.06.008

Richards, A., French, C. C., Calder, A. J., Webb, B., Fox, R., & Young, A. W. (2002). Anxiety-related bias in the classification of emotionally ambiguous facial expressions. *Emotion*, *2*(3), 273.

Rodebaugh, T. L., Woods, C. M., Thissen, D. M., Heimberg, R. G., Chambless, D. L., & Rapee, R. M. (2004). More information from fewer questions: The factor structure and item properties of the original and brief fear of negative evaluation scale. *Psychological Assessment*, *16*(2), 169–181. https://doi.org/10.1037/1040-3590.16.2.169

Roelofs, K., Putman, P., Schouten, S., Lange, W.-G., Volman, I., & Rinck, M. (2010). Gaze direction differentially affects avoidance tendencies to happy and angry faces in socially anxious individuals. *Behaviour Research and Therapy*, *48*(4), 290–294. https://doi.org/10.1016/j.brat.2009.11.008

Roesch, E. B., Sander, D., Mumenthaler, C., Kerzel, D., & Scherer, K. R. (2010). Psychophysics of emotion: The QUEST for Emotional Attention. *Journal of Vision*, *10*(3), 1–9. https://doi.org/10.1167/10.3.4

Rossignol, M., Anselme, C., Vermeulen, N., Philippot, P., & Campanella, S. (2007). Categorical perception of anger and disgust facial expression is affected by non-clinical social anxiety: An ERP study. *Brain Research*, *1132*(1), 166–176. https://doi.org/10.1016/j.brainres.2006.11.036

Rutherford, M. D., Chattha, H. M., & Krysko, K. M. (2008). The use of aftereffects in the study of relationships among emotion categories. *Journal of Experimental Psychology. Human Perception and Performance*, *34*(1), 27–40. https://doi.org/10.1037/0096-1523.34.1.27

Rutherford, M. D., Troubridge, E. K., & Walsh, J. (2012). Visual afterimages of emotional faces in high functioning autism. *Journal of Autism and Developmental Disorders*, *42*(2), 221–229. https://doi.org/10.1007/s10803-011-1233-x

Schneier, F. R., Kent, J. M., Star, A., & Hirsch, J. (2009). Neural circuitry of submissive behavior in social anxiety disorder: A preliminary study of response to direct eye gaze. *Psychiatry Research: Neuroimaging*, *173*(3), 248–250. https://doi.org/10.1016/j.pscychresns.2008.06.004

Schofield, C. A., Inhoff, A. W., & Coles, M. E. (2013). Time-course of attention biases in social phobia. *Journal of Anxiety Disorders*, *27*(7), 661–669. https://doi.org/10.1016/j.janxdis.2013.07.006

Schwartz, C. E., Kunwar, P. S., Greve, D. N., Kagan, J., Snidman, N. C., & Bloch, R. B. (2012). A phenotype of early infancy predicts reactivity of the amygdala in male adults. *Molecular Psychiatry*, *17*(10), 1042–1050.

Schwartz, C. E., Wright, C. I., Shin, L. M., Kagan, J., Whalen, P. J., McMullin, K. G., & Rauch, S. L. (2003). Differential amygdalar response to novel versus newly familiar neutral faces: A functional MRI probe developed for studying inhibited temperament. *Biological Psychiatry*, *53*(10), 854–862. https://doi.org/10.1016/S0006-3223(02)01906-6

Schweinberger, S. R., Zäske, R., Walther, C., Golle, J., Kovács, G., & Wiese, H. (2010). Young without plastic surgery: Perceptual adaptation to the age of female and male faces. *Vision Research*, *50*(23), 2570–2576. https://doi.org/10.1016/j.visres.2010.08.017

Sinclair, S. J., Siefert, C. J., Slavin-Mulford, J. M., Stein, M. B., Renna, M., & Blais, M. A. (2012). Psychometric evaluation and normative data for the depression, anxiety, and stress scales-21 (DASS-21) in a nonclinical sample of US adults. *Evaluation & the Health Professions*, *35*(3), 259–279. https://doi.org/10.1177/0163278711424282

Soto, T. W., Ciaramitaro, V. M., & Carter, A. S. (2018). Sensory over responsivity. In C. Zeanah (Ed.), *Handbook of infant mental health* (4th ed.). Guilford Press. 330-344.

Staugaard, S. R. (2010). Threatening faces and social anxiety: A literature review. *Clinical Psychology Review*, *30*(6), 669–690. https://doi.org/10.1016/j.cpr.2010.05.001

Stein, D. J., Lim, C. C. W., Roest, A. M., de Jonge, P., Aguilar-Gaxiola, S., Al-Hamzawi, A., Alonso, J., Benjet, C., Bromet, E. J., Bruffaerts, R., de Girolamo, G., Florescu, S., Gureje, O., Haro, J. M., Harris, M. G., He, Y., Hinkov, H., Horiguchi, I., Hu, C., … Scott, K. M. (2017). The cross-national epidemiology of social anxiety disorder: Data from the World Mental Health Survey Initiative. *BMC Medicine*, *15*(1), 1-21. https://doi.org/10.1186/s12916-017-0889-2

Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., Marcus, D. J., Westerlund, A., Casey, B. J., & Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research*, *168*(3), 242–249. https://doi.org/10.1016/j.psychres.2008.05.006

Turi, M., Burr, D. C., Igliozzi, R., Aagten-Murphy, D., Muratori, F., & Pellicano, E. (2015). Children with autism spectrum disorder show reduced adaptation to number. *Proceedings of the National Academy of Sciences*, *112*(25), 7868–7872. https://doi.org/10.1073/pnas.1504099112

Vasconcelos-Raposo, J., Fernandes, H. M., & Teixeira, C. M. (2013). Factor structure and reliability of the depression, anxiety and stress scales in a large Portuguese community sample. *The Spanish Journal of Psychology*, *16*, E10. https://doi.org/10.1017/sjp.2013.15

Watson, D., Clark, L. A., & Carey, G. (1988). Positive and negative affectivity and their relation to anxiety and depressive disorders. *Journal of Abnormal Psychology*, *97*(3), 346. https://doi.org/10.1037/0021-843X.97.3.346

Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality and Social Psychology*, *54*(6), 1063. https://doi.org/10.1037/0022-3514.54.6.1063

Webb, S. J., Jones, E. J. H., Merkle, K., Namkung, J., Toth, K., Greenson, J., Murias, M., & Dawson, G. (2010). Toddlers with elevated autism symptoms show slowed habituation to faces. *Child Neuropsychology*, *16*(3), 255–278. https://doi.org/10.1080/09297041003601454

Webster, M. A. (2015). Visual adaptation. *Annual Review of Vision Science*, *1*, 547–567.

Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1571), 1702–1725. https://doi.org/10.1098/rstb.2010.0360

Weeks, J. W., Heimberg, R. G., Rodebaugh, T. L., Goldin, P. R., & Gross, J. J. (2012). Psychometric evaluation of the Fear of Positive Evaluation Scale in patients with social anxiety disorder. *Psychological Assessment*, *24*(2), 301. https://doi.org/10.1037/a0025723

Wells, A., Clark, D. M., Salkovskis, P., Ludgate, J., Hackmann, A., & Gelder, M. (1995). Social phobia: The role of in-situation safety behaviors in maintaining anxiety and negative beliefs. *Behavior Therapy*, *26*(1), 153–161. https://doi.org/10.1016/S0005-7894(05)80088-7

Wermes, R., Lincoln, T. M., & Helbig-Lang, S. (2018). Attentional biases to threat in social anxiety disorder: time to focus our attention elsewhere?. *Anxiety, Stress, & Coping*, *31*(5), 555–570.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, *63*(8), 1293–1313. https://doi.org/10.3758/BF03194544

Wieser, M., Pauli, P., Grosseibl, M., Molzow, I., & Mühlberger, A. (2010). Virtual Social Interactions in Social Anxiety-The Impact of Sex, Gaze, and Interpersonal Distance. *Cyberpsychology, Behavior and Social Networking*, *13*(5), 547–554. https://doi.org/10.1089/cyber.2009.0432

Yoon, K. L., Yang, J.-W., Chong, S. C., & Oh, K. J. (2014). Perceptual sensitivity and response bias in social anxiety: An application of signal detection theory. *Cognitive Therapy and Research*, *38*(5), 551–558. https://doi.org/10.1007/s10608-014-9619-7

Yoon, K. L., & Zinbarg, R. E. (2007). Threat is in the eye of the beholder: Social anxiety and the interpretation of ambiguous facial expressions. *Behaviour Research and Therapy*, *45*(4), 839–847. https://doi.org/10.1016/j.brat.2006.05.004

Yoon, K. L., & Zinbarg, R. E. (2008). Interpreting neutral faces as threatening is a default mode for socially anxious individuals. *Journal of Abnormal Psychology*, *117*(3), 680. https://doi.org/10.1037/0021-843X.117.3.680