

# The Biology of Shyness and Adapting to Threat



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## Introduction

Shyness is both a common colloquial term and a ubiquitous biobehavioral phenomenon that can be seen at all points along the developmental timeline. Shy individuals may be hypersensitive to signals of threat, particularly when the perceived threat is social in nature (Tang et al., 2016). In response to social threat, shy individuals show a distinct behavioral profile compared to non-shy individuals, marked by sensitivity and reticence to engage with social cues and concern with social evaluation (Coplan & Rubin, 2010). These responses are often accompanied by a preoccupation with self-well-being within these social contexts (Schmidt & Poole, 2019). These distinctive behaviors are associated with, and potentially driven by, underlying biological factors.

Markers of shyness, such as enhanced attention to social threat, differences in approach and avoidance behaviors, and preservation of childlike traits both behaviorally and neurally (i.e., neoteny), reflect processes that are evolutionarily conserved, early appearing, and primed to help individuals navigate their social environments. Shyness-linked overt behavioral responses to perceived social threat may be coupled with distinct responses at the physiological level, including hypervigilance to threat stimuli, increased brain activity in fear circuitry, and other fear-related behaviors such as freezing or avoidance. These responses may in part make up the etiology of shyness. Depending on environmental context, these mechanistic responses may also prove adaptive or maladaptive for an individual.

In the current literature, the construct of shyness is often associated with maladaptive developmental outcomes (Heiser, Turner, & Beidel, 2003; Nelson et al., 2007; Page, 1989; Rubin, Coplan, & Bowker, 2009; Van Ameringen, Mancini, & Oakman, 1998).

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For example, there is a large overlap between shyness and the temperament trait behavioral inhibition (BI) (Rubin et al., 2009; Schmidt, Fox, Schulkin, & Gold, 1999; Wolfe & Bell, 2014). BI is characterized by wariness and reactivity in the face of novel stimuli in early childhood (Kagan, Reznick, & Snidman, 1988), which often is most prominent in social situations (Kagan et al., 1988; Rubin, Burgess, & Hastings, 2002). By middle childhood, BI is often associated with heightened social withdrawal (Pérez-Edgar et al., 2010, 2011) and increased risk for social anxiety in adolescence (Chronis-Tuscano et al., 2009; Clauss & Blackford, 2012; Hirshfeld et al., 1992; Van Ameringen et al., 1998). Although there are evident similarities between BI and shyness, they are not one in the same—this distinction will be more thoroughly discussed subsequently.

That being said, shyness, like BI, is also a risk factor for anxiety (Van Ameringen et al., 1998), as well as other internalizing disorders (Nelson et al., 2007). Shyness also has been associated with social withdrawal (Rubin et al., 2009), social anxiety disorder (Heiser et al., 2003), poorer quality of interpersonal relationships (Nelson et al., 2007), and higher rates of substance abuse (Page, 1989). However, despite these previous associations with maladaptive outcomes, emerging research suggests that shyness is a multidimensional characteristic rather than a static label for a homogenous group. As such, emerging work is aimed at distinguishing subtypes of shyness, some of which are indeed developmentally adaptive.

In order to delve into the biological underpinnings of adaptive shyness and the way in which responses to threat may be adaptive, it is important to consider previous studies that have used a variety of neuroimaging methods to examine neural correlates of shyness, including magnetic resonance imaging (MRI), electroencephalography (EEG), event-related potentials (ERP), eye tracking, and respiratory sinus arrhythmia (RSA). These common techniques provide insight into both baseline and task-relevant structural and functional connectivity, the physiological differences between shyness and sociability, cognitive factors that interact with shyness, and the relations between shyness and regulation in emotional and social situations. Evidence of a biological basis of shyness is also seen in hormonal measures, particularly cortisol (Tang, Beaton, Schulkin, Hall, & Schmidt, 2014).

The current review focuses on threat sensitivity, approach/withdrawal tendencies, and neoteny as possible biological mechanisms that may be particularly helpful in teasing apart the broad term of “shyness” into multiple dimensions and further understand where on these dimensions specific forms of shy behavior may be adaptive. In addition, environmental context and individual patterns of attention may also interact to moderate the relations between shyness and adaptive development, helping to determine the specific processes that help support positive outcomes. Borrowing from the attention and executive functioning (EF) literature, both shyness and adaptation to threat allow individuals to flexibly respond to their environment to maintain positive goal-oriented behavior. More specifically, individual differences in goal-directed attention interact with trait-level attention biases to threat as either risk or protective factors for maladaptive developmental outcomes. A better understanding of the underlying mechanisms behind shyness and adaptation to threat across multiple contexts will help provide a more multidimensional and nuanced view of shyness across development.

## Subtypes of Shyness: The Case of Adaptive Shyness

Shyness can be organized into several different subtypes. These subtypes are associated with adaptive and maladaptive outcomes depending on an individual's environment, as well as individual differences in temperament, EF, and biological processes. We will refer to several of these shyness subtypes throughout this chapter. Most readers are likely more familiar with maladaptive shyness, as shyness has been typically linked with negative outcomes such as social anxiety. In contrast, adaptive shyness refers to forms of shyness that are linked to adaptive outcomes and positive well-being (see also Poole and Schmidt; Chapter "Adaptive Shyness: A Developmental Perspective" this volume). It is important to note that because the display of shyness itself can change developmentally over an individual's lifespan, there is variability in the contexts in which shyness can be adaptive. Moreover, as an individual's social milieu changes with development, their behavioral presentation of shyness may also change over time. While the shy 5-year-old may hide behind the parent at the prospect of a social interaction, the equally shy 15-year-old may proclaim that they are not interested in a specific social invitation. The 25-year-old, now enjoying greater autonomy over the social world, can structure his or her environment such that distressing social bids simply rarely occur.

A wide assortment of terminology has been used in the literature in attempting to differentiate among different types of shyness and their level of adaptability, but there is little consensus on the boundaries of these divisions. Agreement emerges in the idea that some subtypes of shyness are early-emerging and other are later-emerging. Earlier-emerging forms of shyness are more apt to predict maladaptive developmental outcomes, and later-emerging shyness is *generally* more adaptive. Colonnesi, Bögels, de Vente, and Majdandžić (2013) and Colonnesi, Napoleone, and Bögels (2014) as well as Nikolić, Colonnesi, de Vente, and Bögels (2016) suggest a distinction between positive and negative shyness. Behaviorally, positive shyness is identified by a gaze, head, or body aversion away from threat accompanied by a "coy smile" (Colonnesi et al., 2013), while negative shyness is marked by the same aversion but in the absence of a smile (Colonnesi et al., 2013, 2014; Nikolić et al., 2016). In this formulation, positive shyness is typically later emerging than negative shyness.

Buss (1986) posed a differentiation between a fearful shyness, an early-emerging form of shyness, and a self-conscious shyness, which appears later in development. Fearful shyness is characterized by early-appearing discomfort that is most focused on wariness in the face of social novelty, while self-conscious shyness emerges later and is focused on social evaluations (Eggum-Wilkens, Lemery-Chalfant, Aksan, & Goldsmith, 2014; Schmidt & Poole, 2019). Conceptualizations of shyness subtypes also include conflicted shyness, which is operationalized as a later-emerging shyness marked by temperamental factors, such as fearful reactions to social stimuli, in combination with a desire for social belongingness (Schmidt & Poole, 2019; Tang, Santesso, Segalowitz, & Schmidt, 2016). Thus, the individual displays both heightened motivation to avoid social interactions (shyness) and increased motivation to engage in social interactions (sociability).

Finally, another label for an early-emerging shyness is temperamental shyness (see Schmidt et al., 1999; Schmidt & Miskovic, 2013). Consistent with the broad definitional umbrella for temperament traits (Fu & Pérez-Edgar, 2015), temperamental shyness may be characterized by having an identifiable biological basis as well as stability across development and is also conceptually similar to operationalizations of the BI temperament (Rubin et al., 2009; Schmidt et al., 1999).

## Sensitivity and Attention to Threat

### *External Threat*

Shyness, as an observable behavior, often emerges in response to a social interaction. Shyness, as a cognitive and emotional response, often results when the social interaction is perceived as a potential threat. This threat bias, in turn, may be a prototypical marker of shy children, as they often also display a hypervigilance to threat across contexts, reflected on both a behavioral and neural level. Attentional biases to threat are a common area of study in socioemotional development, as they may act as a mechanism or marker of anxiety (Tang, Beaton, et al., 2016). In this literature, there are two levels of analysis frequently used in examining threat biases. These levels include a microlevel of processing, collecting temporally sensitive measures in highly controlled tasks, and a more macro-level of processing, emphasizing larger-scale behaviors in more ecologically valid tasks.

Microlevel processing is evident in classic task-based measures. These paradigms include the dot probe tasks, emotional Stroop tasks, emotional visual search tasks, and emotional spatial cueing (e.g., Posner) tasks, in which participants must respond to a cognitive demand in light of emotionally valenced stimuli, often faces (Burris, Buss, LoBue, Pérez-Edgar, & Field, 2019; Fu & Pérez-Edgar, 2019). Because of the nature of these tasks, which often present stimuli on computer screens, they assess attention and responses to threat mostly within the scope of visual attention. Responses to the task may vary as a function of where visual attention is deployed in relation to an emotional stimulus, thus assessing biases in attention to salient cues.

It is important to note that most of these tasks have been used extensively in the context of BI and less so in the context of shyness. Generally, these studies have found that children high in BI show an attentional bias to threat on paradigms such as the Posner task (Morales, Taber-Thomas, & Pérez-Edgar, 2017) but less reliably on the dot probe paradigm (Morales et al., 2017; Pérez-Edgar et al., 2010, 2011). Where performance on the dot probe task may not directly characterize BI children, an attention bias to threat as measured by this task moderates the relation between BI and maladaptive developmental outcomes such that a greater attentional bias to threat is related to higher report of behaviors such as social withdrawal (Pérez-Edgar et al., 2010, 2011). Among the few studies that have specifically examined

shy children, findings suggest that children high in shyness may display an attentional bias to threatening stimuli (LoBue & Pérez-Edgar, 2014; Pérez-Edgar & Fox, 2005). Broadly, patterns of attention biases to threat in shy children mirror those seen in BI children. These task-based assessments are able to provide high levels of precision in measurement, collecting data such as button-press latency and metrics of visual attention using eye tracking technology. However, these same tasks may be criticized as lacking in ecological validity.

In addition to preferentially attending to threatening cues in computer tasks assessing threat biases as a function of visual attention or reaction time, shy individuals may also display a hypersensitivity and hypervigilance to perceived threat on a neural level. Previous work has suggested that shyness may be associated with differential arousal and regulation of the fear system, implicating hypersensitivity of the amygdala in response to threat cues (Jetha, Zheng, Schmidt, & Segalowitz, 2012). Shy adults also show a memory bias toward negatively valenced social stimuli, as well as greater neural activation of brain areas associated with affect-based processing in response to negative stimuli (Tatham, Schmidt, Beaton, Schulkin, & Hall, 2013). More specifically, research suggests increased activation of both the inferior frontal cortex and the middle temporal cortex while viewing negative social stimuli (Tatham et al., 2013). Additionally, shy adults show a greater response in the rostral anterior cingulate cortex (ACC) while viewing faces with moderate levels of emotion intensity. The same shy adults also show increased activation in areas of the brain traditionally associated with face processing, such as the superior temporal sulcus and inferior parietal cortices, in response to pairs of faces showing incongruent affect. These patterns of increased neural activation are thought to reflect both increased salience and emotion regulation in the face of social cues, suggesting that shy individuals are more receptive to facial stimuli and have higher vigilance for emotional threat detection as compared to non-shy counterparts (Tatham et al., 2013).

Other work, more frequently used in relation to the construct of shyness, examines on a macrolevel how an individual may respond to broader sources of threat, focusing less on moment-to-moment attention to threat and instead measuring how these responses may unfold more globally in paradigms emphasizing ecological validity. These paradigms often focus on social threat and are more interactive for the individual, directly targeting the centrality of social interaction in the conceptualization of shyness. As with the computer-based tasks, the interactive tasks are designed to be age-appropriate for the participant, since the form and function of shyness may change over time. For example, paradigms have been used as young as infancy, where 4-month-olds in a study by Colonnese et al. (2013) viewed either themselves, another individual (parent or stranger), or both themselves and the other individual in a mirror, tapping into more “self-conscious” aspects of shyness at this early age. Toddlers in Colonnese et al. (2014) were asked to name and imitate animal noises to an experimenter. Similarly, Nikolić et al. (2016) asked the same children at 4.5 years of age to perform a song in front of an audience, including their father, the experimenter, and a stranger. These different paradigms capture age-appropriate situations of social discomfort or threat in a more true-to-life scenario for the child. Metrics acquired may include behavioral measures such as aversion from the threat

or smiling behavior (Colonnesi et al., 2013, 2014; Nikolić et al., 2016), as well as physiological measures like blushing (Nikolić et al., 2016).

Peer tasks also represent a more naturalistic form of social threat among shy children. Fox, Schmidt, Calkins, Rubin, and Coplan (1996) utilized quartets of age- and gender-matched 4-year-olds to assess variations in sociability as a risk factor for internalizing problems, as children participated in free play, a cleanup task, a ticket-sorting task, and a speech task. Similarly, Walker, Degnan, Fox, and Henderson (2013) paired shy children with age- and gender-matched peers in longitudinal dyadic visits, assessing how shyness related to social problem-solving over time. These studies found that shyness in these social scenarios interacted with physiological profiles, specifically right frontal EEG asymmetry, to relate to heightened internalizing and externalizing problems (Fox et al., 1996). Behavior in these social scenarios was also related to developmental trajectories of social competence over time, such that shyness with a peer at 24 months predicted a shallower increase in social problem-solving over time, as compared to children with non-shy peer dyad interactions (Walker et al., 2013). Negative peer relations for shy children may be particularly problematic as negative social feedback may mediate the relations between early shyness and later patterns of self-conscious emotions and withdrawal (Howarth, Guyer, & Pérez-Edgar, 2013; Sette, Baldwin, Zava, Baumgartner, & Coplan, 2019).

Biased attention to threat, measured both by behavioral metrics and neural processing, is commonly noted as a maladaptive behavior. Broadly speaking, attention biases to threat are considered a characteristic of both pediatric and adult anxiety disorders (Roy et al., 2008) and may be part of the etiology of anxiety disorders (Lonigan, Vasey, Phillips, & Hazen, 2004). However, a threat bias may act as a protective factor in higher risk environments. Vigilance to threatening cues may prepare an individual to combat potential hazards to one's well-being. Children living in contexts marked by high levels early-life stress, such as low socioeconomic status (Dufford, Bianco, & Kim, 2018) or institutionalized care (Troller-Renfree, McDermott, Nelson, Zenah, & Fox, 2014) may display heightened threat biases.

While the literature frequently refers to threat biases as maladaptive (Roy et al., 2008), it may also be the case that threat biases emerge in truly threatening environments as a protective mechanism (Dufford et al., 2018; Troller-Renfree et al., 2014), minimizing exposure to early-life stressors embedded in the social environment (Hicks, South, DiRago, Iacono, & McGue, 2009; Ronald, Pennell, & Whitehouse, 2011). This idea again emphasizes the importance of considering environmental context in evaluating any adaptive value of shyness, as the imminence of actual threat may vary by environment. For example, children in high-quality neighborhoods show a negative association between resting RSA and shyness (Zhang & Spinrad, 2018). In this sample, lower RSA suggests a lower emotion regulation capacity among shy children in low-threat contexts (Zhang & Spinrad, 2018). In safe and cohesive contexts, RSA also predicts trajectories of children's shyness over time.

In particular, children's shyness upon entering elementary school can be predicted by RSA regulation when their environment is supportive and enriching. The opposite is true of children in lower-quality neighborhoods, where RSA is positively related to shyness. This association suggests that RSA may indicate an adaptive

regulatory capacity for these shy children. The modulation of the relation between physiological markers of regulation and shyness as a function of environmental threat shows the flexible and adaptive quality of shyness (Zhang & Spinrad, 2018). Shyness in high-threat environments may work to protect children from environmental forces that may constitute sources of stress and harm (Zhang & Spinrad, 2018). As such, shyness and its biological correlates may be protective to promote less deleterious outcomes.

### ***Internal Threat***

Threat may be in the form of an external, tangible detriment to an individual's well-being, but for a shy individual threat may also take the form of a more abstract worry. Shy individuals may display increased "internal focus" and a general self-preoccupation, which could be to the detriment of performance on external tasks (Sylvester et al., 2018). This behavior may be associated with higher resting state functional connectivity in the default mode network (DMN) found in shy individuals as compared to non-shy individuals (Sylvester et al., 2018). Broadly, the DMN is thought to reflect an absence of focus on external stimuli and is engaged during tasks such as retrieving autobiographical memories, planning, and perspective-taking (Buckner, Andrews-Hanna, & Schacter, 2008). Typically, there is a negative slope in DMN connectivity over time, associated with normative adolescent pruning (Sylvester et al., 2018). However, in shy individuals, this slope is flattened (Sylvester et al., 2018). In addition, behaviorally inhibited children show an increase in connectivity to default network hubs, coupled with alterations in salience network connectivity (Taber-Thomas, Morales, Hillary, & Pérez-Edgar, 2016). This combination may bias processing toward personally relevant information during development, heightening the impact of social encounters.

### ***Top-Down Control Over Threat Attention***

The preoccupation with both egocentric well-being and external sources of threat seen in shy individuals may also operate to the detriment of cognitive task performance. Henderson and Wilson (2017) suggest a dissociation between stimulus-driven attention and goal-directed attention, where heightened levels of stimulus-driven attention, like biased attention to both internal and external threat, may detract from goal-directed attention, reflected in EF. Based on accuracy metrics, shy individuals often perform comparably to non-shy counterparts on cognitive tasks, like EF paradigms (Eysenck, Derakshan, Santos, & Calvo, 2007; Wolfe & Bell, 2014). However, group differences may emerge on a neural level in metrics of task efficiency (Eysenck et al., 2007). For example, Wolfe and Bell (2014) found that in a sample of preschoolers, high performers on EF tasks show increases in medial frontal EEG



power, regardless of shyness level. However, among children who score low on these same EF measures, shy children show a similar increase in medial frontal power but without corresponding high cognitive task performance. Wolfe and Bell (2014) refer to this phenomenon as “cognitive busyness.” This busyness reflects the fact that a shy child may be balancing intrusive or anxious thoughts concurrent with a task, so they must exert greater cognitive effort to overcome these extraneous thoughts. As such, they show enhanced activation but still underperform on the task. The power increase without associated task performance is thought to capture neural inefficiency (Wolfe & Bell, 2014).

Differences in levels of goal-directed attention may also interact with shyness-related differences in the processing of threat-related information, modulating behaviors in response to these perceived threats. Typically, high cognitive control and regulation is broadly considered advantageous, supporting adaptive socioemotional functioning. However, these regulatory processes may act differently in shy children, instead operating as a risk factor for maladaptive developmental outcomes. In work with BI children, higher levels of attention shifting may act protectively against developing anxiety disorders, helping children flexibly navigate their social environments even in the face of attention-capturing threat (Henderson & Wilson, 2017). However, in these same children, higher levels of inhibitory control may act as a risk factor for anxiety disorders (Henderson & Wilson, 2017).

Similarly, the ability to engage higher levels of EF or proactive control may differentially lead to adaptive or maladaptive outcomes for shy children. The P300 event-related potential component is broadly associated with attentional processes and working memory (Tang, Santesso, et al., 2016). Tang, Santesso, et al. (2016) found that children high in conflicted shyness showed heightened P300 amplitude in response to an “auditory oddball” task, suggesting greater cognitive effort during the task. Moreover, frontal P300 amplitude mediated the relation between conflicted shyness and neuroticism, such that greater frontal P300 amplitude explained exacerbated risk for neuroticism among children displaying high levels of conflicted shyness.

Differences in response inhibition and attention shifting in shy and non-shy individuals may constitute another controlled aspect of attention associated with broad developmental outcomes. Shyness has been associated with poor outcomes particularly among children with enhanced N2 responses during a Flanker task, again suggesting that cognitive and attentional control can be “too good” in shy children (Henderson, 2010). Differences in the N2, as well as the error-related negativity (ERN) ERP, may reflect increased sensitivity of the ACC to anticipate conflict and uncertainty in some shy children, which may in turn reflect high levels of behavioral rigidity for the individual and moderate the relation between shyness and socioemotional development (Henderson, 2010).

This work suggests that individual differences in elements of cognitive control may further identify shy children who may or may not display adaptive developmental outcomes. Whereas shy children may show a hypersensitivity to threat across multiple processing contexts, elements of top-down control may help to modulate these attentional biases. Potentiating attention biases to threat may encourage negative cognitions characteristic of anxiety disorders like rumination and



apprehension, which may prolong feelings of social malaise and impede social interactions (Henderson, Pine, & Fox, 2015; Henderson & Wilson, 2017). On the other hand, attention shifting may assist a child in directing attention away from distressing cues, thus reducing levels of arousal and distress (Henderson et al., 2015; Henderson & Wilson, 2017). Collectively, both neural and behavioral measures of cognitive control are essential in understanding how shy children may adapt to a hypersensitivity to threat, helping capture patterns of rigidity and flexibility as the child confronts shifting environments and associated developmental challenges.

## Approach/Avoidance Behavior

Studies using a variety of neuroimaging techniques may distinguish shyness and sociability as distinct phenomena, even early in development (Schmidt, 1999; Tang, Santesso, et al., 2016). These differences are important contributing factors for social and cognitive performance and have implications for the different subtypes of shyness. Dimensions of shyness and sociability, reflected on a biological level, suggest again that shyness is not a homogenous construct, but rather a broad term encompassing a subset of behaviors along a number of continuums.

It is important to clearly identify shyness and sociability as two biologically separate traits. Since shyness and sociability may colloquially be considered foils of the same construct, parsing them apart with biological markers can clarify subtypes of shyness as well as help to understand when each of these behaviors may have adaptive value. Distinguishing these two dimensions allows for a more specific focus on the mechanisms specifically underlying shyness, to determine how it manifests as a unique and potentially adaptive trait, and to explicitly examine any influencing effects of sociability on the understanding of shyness. For example, high levels of approach and withdrawal (or sociability and shyness, respectively) suggest the presence of conflicted shyness, which is present in individuals high on both shyness and sociability. This lays the groundwork for understanding conflicted shyness (Schmidt & Poole, 2019), one of several subtypes of shyness that vary in adaptive outcomes across contexts.

Traditional theoretical models of frontal brain activation suggest that left frontal asymmetry, traditionally measured by EEG power in the alpha band, is consistent with higher levels of “approach” behaviors, while right frontal asymmetry is consistent with higher levels of “avoidance” behaviors (Coan & Allen, 2003). Moreover, higher levels of right frontal asymmetry are frequently associated with higher levels of maladaptive outcomes such as anxiety and depression (Coan & Allen, 2003). In the context of shy individuals, higher levels of shyness are associated with higher resting right frontal cortical brain activity, while measures of sociability are associated with the left frontal activity (Schmidt, 1999).

As previously noted, a body of research suggests that shyness is not necessarily synonymous with unsociability and may be associated with distinct neural mechanisms (Tang, Santesso, et al., 2016). Individuals with positive shyness are distinguished

by a concurrent experience of positive affect while also demonstrating some degree of withdrawal behavior, compared to other subtypes of shyness that may be primarily marked by negative affect and withdrawal (Schmidt & Poole, 2019). Despite a lack of exact consistency in terminology, potentially adaptive forms of shyness are unified in that they display greater levels of approach behavior allowing for environmental engagement and learning (Pérez-Edgar, 2018), whereas less adaptive forms of shyness are higher in avoidance behaviors.

There are also identifiable physiological differences for individuals varying along the dimensions of shyness and sociability, further suggesting the importance of distinguishing between these constructs in operationalizing and understanding shyness. Schmidt and Fox (1994) found differences in resting frontal EEG asymmetry as a function of levels of sociability, but not shyness. Low-sociable young adults showed right frontal asymmetry, while high-sociable participants showed left frontal asymmetry. These patterns suggest that young adults displaying conflicted shyness show higher neural sensitivity to stress and lower emotional and attentional control overall. In the same sample, adults who self-reported high on both shyness and sociability showed a higher, less variable heart rate than individuals high in shyness and low in sociability, as well as individuals low on shyness and high on sociability (Schmidt & Fox, 1994). These patterns suggest higher sensitivity to stress and lower emotional and attentional control overall for individuals conflicted shy adults.

Further differentiating biological correlates of shyness and sociability, variations in morning cortisol may relate to different patterns of brain activation during social threat processing, suggesting an adaptation of the neuroendocrine system for dealing with any associated stress of being shy (Tang et al., 2014). In particular, shy adults with relatively lower resting cortisol and higher activation of areas of the brain associated with social behavior (left amygdala, right posterior cingulate gyrus, insula, bilateral inferior, medial, and middle frontal gyri) reported lower levels of sociability (Tang et al., 2014).

These data suggest that, perhaps in evaluating shyness, sociability is equally critical to evaluating adaptive capabilities in shy individuals. Differences seen in heart rate and heart rate variability relate to socioemotional regulation, suggesting a possible mechanism underlying discomfort and/or anxiety for shy individuals during social situations (Schmidt & Fox, 1994). Measures like cortisol, while perhaps less widely used, also facilitate understanding of social approach and withdrawal related behavior (Tang et al., 2014). Prior research has found that shy individuals may display both relatively high and relatively low levels of waking morning salivary cortisol, such that individuals with high waking morning salivary cortisol are more likely to be more sociable. Thus, cortisol levels may be a driving force for some high shy individuals to navigate the socioemotional world in addition to managing their own emotional experience during social challenges (Tang et al., 2014). These hormonal differences represent slower-acting manifestations of the physiological background of shyness and may help to supplement more temporally sensitive measures, such as EEG, in better understanding adaptive shyness.

Behaviors like coy smiles, a definitional characteristic of positive shyness, reflect approach behaviors that often relate to more adaptive behavioral and psychological outcomes (see also Colonnesi et al., Chapter “Development and Psychophysiological Correlates of Positive Shyness from Infancy to Childhood” this volume). Colonnesi et al. (2013, 2014), as well as Nikolić et al. (2016), suggest that a smile accompanying a physical aversion to a social threat leaves the individual able to still engage with the environment and less closed-off than negative shyness, marked as a physical aversion without a smile (Colonnesi et al., 2013). Children displaying positive shyness to social threat often display fewer maladaptive outcomes than children displaying negative shyness. This includes lower levels of anxiety and increased levels of sociability, relative to children displaying more negative reactions (Colonnesi et al., 2014; Poole & Schmidt, 2019).

Additionally, the adaptive value of approach and avoidance behavior may vary as a function of environmental context and risk. Broadly, children reared in adversity such as instances of institutionalized care display greater levels of right EEG asymmetry at baseline over time, reflecting greater avoidance tendencies (McLaughlin, Fox, Zenah, & Nelson, 2011). As noted, greater relative left frontal asymmetry and higher avoidance behaviors may relate to psychopathology such as internalizing disorders (Coan & Allen, 2003; McLaughlin et al., 2011). However, in situations of adversity, such as unreliable caregiving, higher levels of avoidance behaviors and accompanying neural correlates may arise as an adaptation to an environment in which general avoidance may be more apt to preserve well-being in the short term (McLaughlin et al., 2011).

Although early internalizing symptoms are often associated with negative outcomes, such as anxiety (Roy et al., 2008), it may also act as a protective factor against other maladaptive sets of behaviors, such as externalizing problems (Willner, Gatzke-Kopp, & Bray, 2016) which may be associated with stressful early life contexts (Hicks et al., 2009; Ronald et al., 2011). Willner et al. (2016) found that while we typically see comorbidity between internalizing and externalizing behaviors in early childhood, kindergarteners who only display internalizing behaviors were less prone to the emergence of externalizing behaviors. They were also most likely to see a normalization of internalizing problems as well over time. This pattern is in line with adult studies demonstrating that reported shyness lowers the probability of experiencing externalizing behaviors (Nelson et al., 2007). This buffering effect may be particularly beneficial in environments marked by adversity.

Overall, there is differential adaptability in shyness and sociability based on individual differences in approach and avoidance characteristics, and as a function of environment. High levels of both approach and avoidance may be adaptive in certain circumstances to aid shy social individuals in cautiously navigating their social world while still adaptively engaging with social stimuli (Pérez-Edgar, 2018). Borrowing from the ethology literature (Reader, 2015), children who can move from shyness to sociability with relative ease may be able to engage in “low-cost sampling” of the environment, which provides them needed information without overtaxing emotional and cognitive resources.

## Neoteny

Individual differences in shyness are seen from early on in development (see Schmidt & Buss, 2010, for a review). One theory suggests that structural and functional differences in the psychophysiology of shy individuals are explained by their relatively protracted development of “social” brain structures (Schmidt & Poole, 2018, 2019; see also Schmidt et al., Chapter “The Study of Behavioral Inhibition and Temperamental Shyness Across Four Academic Generations” this volume). Evolutionarily, a more protracted developmental timeline is unique to humans compared to other species. Brain development into the postnatal years is associated with larger brain volumes which allow for additional learning while the brain is most highly plastic, which in turn supports the development of higher-order cognitive processes (Schmidt & Poole, 2019). Schmidt and Poole (2019) argue that conflicted shyness may enable an individual to have more time to learn about complicated social environments in the human world. In both familiar and unfamiliar social environments that may be perceived as threatening, a higher level of reticence allows a shy child buffer time to process and infer other’s intentions and motives before responding (Schmidt & Poole, 2019). They posit that conflicted shyness, where an individual may display childlike expressions such as coy smiles, in part retains a more youth-like appearance past sexual maturity, thus extending the amount of time that an individual has available to learn about their social environment before being fully independent. The buffering provided by positive signals coupled with reticence serves as a contrast to children who display indiscriminate friendliness, often as a result of early deprivation (Gleason et al., 2013).

Childlike features associated with forms of shyness may be noted behaviorally, as in coy smiles, as well as neurally. Delayed frontal brain maturation underlies some emotional and behavioral profiles associated with social inhibition and anxiety (Schmidt & Poole, 2018). Recent work suggests that children high in shyness display consistently smaller frontal alpha power/delta power ratios over time, as measured by EEG, suggesting delayed frontal brain maturation as compared to children low in shyness (Schmidt & Poole, 2018). On the other hand, children low in shyness also show a significant increase in the ratio of overall frontal alpha power to delta power longitudinally (Schmidt & Poole, 2018). Thus, neotenus traits sometimes noted in shy children may be associated with a less steep maturational trajectory of the prefrontal cortex which may, in turn, indicate a wider window for plasticity in development. Early plasticity may provide for an increased window of time during which a child can learn to appropriately react to challenging elements of environmental threat.

It is also critical to consider environmental context in assessing the adaptability of neoteny in shyness. Whereas protracted development of brain areas such as the frontal lobe may be advantageous for cognitive development and social learning in the general population, this may not be the case in circumstances of early-life stress. Regions of the frontal lobe, such as the medial prefrontal cortex (mPFC), play a large role in emotion regulation, with projections to the limbic system (Gee et al., 2013).

Negative connectivity in adulthood between the amygdala and mPFC suggests that, over development, the mPFC may downregulate the amygdala in situations of non-threat (Gee et al., 2013).

However, in instances of early-life stress, like maternal deprivation among previously institutionalized children, individuals may display accelerated maturation of connectivity between the mPFC and the amygdala (Gee et al., 2013). In rodent work, rat pups exposed to forms of early-life stress generally will show faster threat conditioning than nonstressed pups (Callaghan & Tottenham, 2016). This suggests the possibility of an early adaptive role of more mature brain structure and function in high-risk, high-stress scenarios, but perhaps at the expense of later-life psychopathology (Callaghan & Tottenham, 2016). Thus, it may be the case that neotenus features of shyness are adaptive in low-risk environments in that they prolong periods of learning and development but may act in a deleterious nature in high-risk environments where more adultlike brain function and rapid learning are initially to the benefit of one's survival.

## Conclusion

A diverse body of work at multiple levels of analysis suggests that shyness is a multifaceted construct, with a great deal of heterogeneity among children described as “shy.” These subtypes of shyness may be differentiated on both behavioral and neural levels, giving rise to different profiles that may vary in adaptability. Multiple methods can inform the structural and functional mechanisms involved in adaptive forms of shyness, giving insight into how different profiles of shy individuals may differentially process information relative to non-shy individuals. These differences, in turn, allow for the identification of social and emotional differences that can lead to adaptive or maladaptive outcomes. As reviewed, using neuroimaging and physiological measures may help note differences in attention to threat between shy and non-shy children, distinguish shyness as a construct independent of sociability, and understand the potential evolutionary value in the elements of neoteny associated with shyness.

Multimodal assessments of biological underpinnings of shyness also allow for a more in-depth understanding of cognitive factors that play a role in protecting shy individuals from maladaptive outcomes, as well as the role of environmental context in how these traits may operate adaptively. The level of perceived and actual threat in an individual's environment may influence how adaptive shy behaviors may be, such that forms of early-life adversity are also critical to consider in examining adaptability.

Traditionally, shyness is regarded as a negative trait-like behavior. However, taking a biological and multimethod approach redefines shyness as a multidimensional trait with multiple biologically influenced subtypes that may act adaptively in a number of developmental contexts. Future work will need to integrate longitudinal studies examining patterns of shyness subtypes, across environments, to better delineate the developmental consequences of early individual variation in the biological, social, emotional, cognitive, and behavioral response to social interactions.

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