Next Steps: Behavioral Inhibition as a Model System

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Abstract The current volume brings together a complex network of research that stemmed from the initial observation of individual variation in infants and toddlers. Since then, the last three decades of work has morphed the initial definition of behavioral inhibition, the systems associated with the temperamental trait, and the trajectories that we have associated with early profiles. The current chapter first outlines some of the core lessons that can be drawn from the extant literature. We then ask five questions that still puzzle researchers and may point to the "developmental arc" of the studies that will emerge in the decades to come.

In his essay, *Follow the Evidence, Not the Words,* Jerome Kagan (2016) suggests that psychologists should view Charles Darwin, not Albert Einstein, as a role model for the field. This exhortation is fitting as behavioral inhibition (BI) illustrates the triumph of observation and description in identifying, and then carving out, a unique phenomenon for further study. As noted in chapter the "The History and Theory of Behavioral Inhibition" by Kagan, and in other writings, the initial formulation of behavioral inhibition arose from the careful observation of infant reactivity and behavior, which in turn relied on the repeated viewing of videotapes. Keen observation allowed Kagan to extract the signal from the surrounding noise. While not predicted, the signal was nonetheless robust, supporting over three decades of research. This volume represents only a selection of the work that has emerged from the initial discovery (Kagan, 2012) of behavioral inhibition (García Coll, Kagan, & Reznick, 1984; Kagan, Reznick, Clarke, Snidman, & García-Coll, 1984). Even so, the volume illustrates the many ways in which researchers have come to build on, transform, and expand upon the initial observation.

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The different sections of the book were designed to reflect some important areas of inquiry that build on or help us better understand the phenomenon of behavioral inhibition, beginning in childhood and expanding through the life span. This included animal models of behavioral inhibition, biological underpinnings, social relationships, cognitive mechanisms, and psychopathology. The diversity of these topics supports our contention that behavioral inhibition can be seen as a model system for the study of development. Here, we briefly touch on six ways in which behavioral inhibition research reflects and advances important approaches to developmental research.

First, as noted, research began with the initial observation and *description* of the phenomenon of interest. This is crucial, as it allowed researchers to begin their work with a shared understanding of the entity *out in nature* that they wish to better understand through further observation and experimental manipulation (Pérez-Edgar & Hastings, 2018). Behavioral inhibition is observed in toddlers when they are confronted with novel objects, contexts, and people. All of the work builds from this foundation. Of course, this is not to say that the definition that emerges from observation is rigid or immutable. Anyone who has read this literature, or the previous 15 chapters, can quickly see that multiple operationalizations and labels have come to sit under the umbrella of behavioral inhibition. But fundamentally, behavior is the cornerstone for identifying and describing this temperament. We touch on this a bit more later in this chapter.

Second, behavioral inhibition emerges over *time,* as it is an epiphenomenon of a more basic pattern of reactivity, which is itself identified by observing behavior in early infancy. Negative reactivity is a core antecedent of the behaviorally inhibited behavior seen later in the first and second years of life. Indeed, Kagan would argue that high reactive infants exhibit the temperamental type that then manifests as the pattern of behaviors known as behavioral inhibition (Fox, Henderson, Rubin, Calkins, & Schmidt, 2001; Fox, Snidman, Haas, Degnan, & Kagan, 2015). Going forward in time, behavioral inhibition is related to social reticence in early childhood and then, for some adolescents, clinically significant social anxiety (Chronis-Tuscano et al., 2009; Rapee, Kennedy, Ingram, Edwards, & Sweeney, 2005).

Behavioral inhibition is one of the best characterized and most potent individual predictors of social anxiety (Clauss & Blackford, 2012). One of the important advances in the field was the recognition that many of the behaviors and physiological responses of behaviorally inhibited children (freezing, avoidance, elevated heart rate) were similar to those found by neuroscientists studying the origins of anxiety and fear learning in rodents (LeDoux, 1995; Phelps & LeDoux, 2005). Indeed, the reactivity that Kagan first observed (back arching, distress vocalizations, motor movements) was described in the rodent literature examining the neuroscience of fear learning. Specific areas in the brain stem and limbic system (e.g., central gray, etc.) were thought to underlie these responses in both rodents and infants. In addition, child psychiatrists and child clinicians noted that the behaviors of young children who were the offspring of anxious and depressed mothers often looked similar to those described for the behaviorally inhibited child (Rosenbaum et al., 1988, 1992,

2000). Together this work ignited interest in examining patterns of reactivity and behavioral inhibition as potential precursors of anxiety disorders.

Much of the current work linking behavioral inhibition and anxiety focuses on the progression from behavioral inhibition to varying levels of social reticence and inhibition, as outlined by the chapter "The Temperamentally Shy Child as the Social Adult: An Exemplar of Multifinality" by Poole and colleagues. The task is no easier if we are focused on more extreme trajectories that lead to clinical disorder. Indeed the chapter "Behavioral Inhibition as a Precursor to Psychopathology" by Klein and Mumper outline *seven* different models that may account for the documented relation between early behavioral inhibition and the later emergence of anxiety.

Equally important is the fact that while many behaviorally inhibited children go on to exhibit social anxiety, the majority do not (Degnan & Fox, 2007). In addition, not all anxious individuals were previously behaviorally inhibited (Clauss & Blackford, 2012). Shyness and clinical anxiety are not dependent on having had extreme negative reactivity in infancy nor behavioral inhibition as a toddler. In addition, problematic trajectories need not only lead to anxiety as we have data linking behavioral inhibition multiple outcomings, including depression (Gladstone & Parker, 2006) and substance use (Lahat et al., 2012; Williams et al., 2010).

Third, researchers built on the complexity of initial descriptions to examine potential underlying *mechanisms.* The dogged search for processes and mechanisms often set developmental psychologists apart from colleagues in the other subdisciplines. Mechanisms arise from functional influences on a child's current state that can lawfully direct change over time (van der Molen & Molenaar, 1994). Given the central focus on change, it is natural for developmental psychologists to want to capture and explain the causes of this change. To ask this question, we often rely on experimental methods that manipulate a potential mechanism of interest and then carefully track any and all changes in the outcome. This is a mechanistic approach to the developmental question.

Each of the sections in this volume illustrates work that, to varying extents, attempts to isolate and (quasi-) manipulate potential mechanisms of change. The chapters "Behavioral Inhibition in Nonhuman Primates: The Elephant in the Room" by Capitanio and "Behavioral Inhibition in Rodents: A Model to Study Causes and Health Consequences of Temperament" by Cavigelli, for example, use animal models to document and manipulate experiences that influence social and health-related functions. As another example, the chapter "Behavioral Inhibition and the Associative Learning of Fear" by Reynolds and colleagues build on animal models, and our understanding of basic learning processes, to show how behaviorally inhibited children acquire (learn) fears through both direct experience and vicarious observation.

Historically, there has been some concern that an overly mechanistic approach may isolate developmentalists for the very phenomenon that first interested them. Wohlwill (1973), for example, argued that if developmental psychology opened itself up to "the invasion of the experimentalists," the field would lose its place as a distinct contributor to psychology. Rather, it would devolve into a paler branch of general

psychology defined simply by the age of the participants. However, the last few decades of behavioral inhibition research clearly show that you can marry a careful description of children's natural trajectories with systematic study (and manipulation) of potential mechanisms without becoming "mechanistic tinkerers." Indeed, it was careful observation that suggested that behavioral inhibition morphed over time due to the emergence of cognitive and emotional self-evaluation (see the chapter "Relations Between Behavioral Inhibition, Cognitive Control and Anxiety: Novel Insights Provided by Parsing Subdomains of Cognitive Control" by Buzzell et al.), as well as decreased influence from parents and increasing importance of peers (see the chapter "The Social World of Behaviorally Inhibited Children: A Transactional Account" by Henderson et al. and the chapter "Peer Relations and the Behaviorally Inhibited Child" by Rubin et al.).

Fourth, behavioral inhibition research exemplifies the importance of isolating and examining *individual differences*. One core goal of developmental research is to document and understand the expected sequence of change over time, linking antecedent events to subsequent change. This work sets the foundation for more specialized study. However, there are inherent tensions between outlining nomothetic laws that focus on universal sequences and their contexts versus identifying idiographic patterns that are unique to individuals (Scarr, 1992; Scarr & McCartney, 1983).

In studying individual differences, we have to make space for the realization that the environment, and experiences encountered within an environment, does not have the same meaning for all children. Scarr (1992) argued that a child constructs a unique reality for him- or herself. Behavioral inhibition research shines a light on clear differences in how children react to ostensibly identical social contexts. Some children rush to embrace the novelty of the social world, while others pull back from ambiguous and unexpected threats. These variations appear early and shape the child's "experienced environment." In this way, fairly subtle individual differences can impact socioemotional functioning from infancy by creating cascading and self-reinforcing biases in social cognition and behavior (see the chapter "The Social World of Behaviorally Inhibited Children: A Transactional Account" by Henderson et al. and the chapter "Attention Mechanisms in Behavioral Inhibition: Exploring, and Exploiting, the Environment" by Pérez-Edgar).

Taking an individual difference approach can also expand our methodological toolbox. Petrill and Brody (2002) argued that experimental psychology creates variability by manipulating the environment, while researchers interested in individual differences study naturally occurring variation. To do so we use using statistical methods to "partition sources of variance in a measure." We are lucky, as a science, that individual differences are likely to be lawful rather than a random assortment of disconnected and independent traits. As a result, we can shift from a focus on variance across conditions to variance among individuals. This change in focus is then coupled by a shift from a variable-centered analytic approach to a person-centered approach. Thus, the focus is not on how a variable behaves across context or time but on how individuals, or groups of individuals, react in response to maturational forces and the surrounding environment.

Fifth, often more by necessity than desire, research in behavioral inhibition has incorporated *multiple levels of analysis.* As noted, the initial work in behavioral inhibition was rooted in carefully describing behavior in response to standardized experiences. However, this description was also closely tied to a proposed mechanism that suggested that underlying hyper-reactivity in the amygdala generated the behavioral inhibition phenotype (Kagan, Reznick, & Snidman, 1987). So, from the start, there was the challenge of tying together neural functioning with observed behavior, despite the many intervening layers of processing and activity.

This was a particularly tricky proposition in the mid-1980s since there were both developmental and technological barriers to examining the limbic correlates of behavioral inhibition. First, neuroimaging techniques were not readily available to researchers interested in human behavior. Indeed, the initial studies demonstrating the feasibility of capturing the blood oxygen level dependent (BOLD) signal associated with neural functioning were not published until the early 1990s (Kwong et al., 1992; Ogawa et al., 1992). Second, the specific parameters of neuroimaging require participants to remain very still (at the level of millimeters) and require specific task parameters and responses (except in the case of resting state measures). Keeping still and following directions have never been strengths of the toddler population.

As a result, researchers first proceeded by systematically measuring secondary, peripheral, measures that both reflect "deeper" neural structures and can track variation in observed behavior. Creative studies examined electroencephalogram (EEG) activity at rest and in response to challenge, stimulus-locked EEG responses via event-related potentials (ERPs), startle responses to expected and unexpected stimuli, resting and reactive cardiac patterns, and skin conductance responses (Fox, Hane, & Pérez-Edgar, 2006). As the chapter "Psychobiological Processes in the Development of Behavioral Inhibition" by Buss and Qu points out, psychophysiological measures can both help find heterogeneity underlying surface level homogeneity in behavior and track the functional antecedents of observed behaviors. Then, as neuroimaging technology became more widely available, we saw the first functional imaging study directly examining limbic activity in adults with a history of behavioral inhibition (Schwartz, Wright, Shin, Kagan, & Rauch, 2003). This work triggered a rapid succession of studies that worked to capture the normative (see the chapter "The Neural Mechanisms of Behavioral Inhibition" by Jarcho and Guyer), developmental (see the chapter "The Neurobiology of Behavioral Inhibition as a Developmental Mechanism" by Blackford et al.), and clinical (see the chapter "The Biological Bridge Between Behavioral Inhibition and Psychopathology" by Sylvester and Pine) antecedents and consequences of behavioral inhibition.

In doing so, the most comprehensive studies (Fox, Henderson, Marshall, Nichols, & Ghera, 2005; Kagan, 2012; Klein, Dyson, Kujawa, & Kotov, 2012) incorporated observed behavior, cognitive functioning, social interactions, self-report, biological measures, genetic variation, clinical diagnoses, and adult outcomes. Multiple measures, of course, also mean greater complexity—complexity in methodology, analytics,

and interpretation. This is reflected in entire volumes that have attempted to capture the ins and outs of this approach, as in the *Handbook of Multimethod Measurement in Psychology* (Eid & Diener, 2006). When you gather these multiple measures, you are then confronted with the daunting question of how to best aggregate these measures—if at all—and how to interpret the inevitably highly complex relations that will emerge or, worse, how to explain when the relations do not emerge.

Indeed, while we work to choose measures that theoretically reflect a shared underlying construct, our actual results often have correlations that likely could have been achieved by drawing measures out of a hat. For example, Nesse et al. (1985) examined measures of distress during in vivo exposure therapy in phobic individuals. Although they noted increases in subjective anxiety, pulse, blood pressure, plasma norepinephrine, epinephrine, insulin, cortisol, and growth hormone, there was only modest convergence in the "magnitude, consistency, timing, and concordance" (p320) of their measures. And this is with a well-understood, relatively straightforward mechanism. Clearly, more work is needed to better understand the shared and unique information provided across measures of interest.

Sixth, behavioral inhibition helps illustrate how basic research can spur *application*, which looks to intervene for children potentially on a path to negative outcomes. The initial description of behavioral inhibition identified children of interest (e.g., the chapter "The History and Theory of Behavioral Inhibition" by Kagan) and documented the trajectory to social anxiety (e.g., the chapter "The Neurobiology of Behavioral Inhibition as a Developmental Mechanism" by Blackford et al. and the chapter "Behavioral Inhibition as a Precursor to Psychopathology" by Klein and Mumper). Follow-up research then documented the mechanisms that could alter this trajectory for children (e.g., interactions with peers, the chapter "Peer Relations and the Behaviorally Inhibited Child" by Rubin et al.; fear-learning, "Behavioral Inhibition and the Associative Learning of Fear" by Reynolds et al.). The next piece of the chain is then to target, and manipulate, these mechanisms in order to modify risk. In this volume, the chapter "Behavioural Inhibition and the Prevention of Internalising Distress in Early Childhood" by Rapee and Bayer outline a systematic line of research that has worked to ameliorate risk by either targeting parental behaviors (e.g., overprotectiveness) or the child herself (e.g., engendering "bravery" in the face of uncertainty). Additional approaches, such as the Turtle Program (Chronis-Tuscano et al., 2015), are working to divert maladaptive trajectories as early as preschool, leveraging the power of social interaction. Indeed, prior work showed that simply attending a preschool, which exposes children to novel teachers and peers, was enough to lessen shyness and anxiety for many children (Almas et al., 2011; Phillips, Fox, & Gunnar, 2011).

Even with the breadth and depth of research carried out over the last three decades, we continue to face open questions that still puzzle researchers in behavioral inhibition and/or point to potential avenues for future work. Surprisingly, some of the questions are rather basic (what is behavioral inhibition?). Luckily for us, the breadth and depth of the remaining questions should keep researchers busy for the next three decades as well. Here we note only five of the many questions left to debate and solve.

We Say We Study Behavioral Inhibition, But Are We All Studying the Same Thing?

We would argue that the wide range of studies described and discussed in the current volume reflects the strength of behavioral inhibition as a construct of study. This volume suggests that behavioral inhibition is pervasive as a developmental phenomenon and it is prominent in the developmental literature. This may also mean that the term "behavioral inhibition" has come to be used for a number of constructs that are only partially overlapping. Recruiting 5-year-old children assessed through maternal report of behavioral inhibition is not the equivalent of directly assessing behavior at age 2. Initially assessing behavior at age 2 is likely also not the equivalent of constraining the label to children who displayed negative reactivity in infancy. The use of multiple assessment measures under the same label may dilute the collective strength of the knowledge generated across studies.

In addition, there are constructs and behaviors that appear quite similar to "behavioral inhibition" but are labeled as shyness, temperamental shyness, social reticence, social withdrawal, social anxiety, and so on. Indeed, this equifinality and multifinality of labeling, to borrow a term, is evident within and across all of the chapters in the current volume. We present here animal models, direct observation, self- and parent-report, infant antecedents, adult sequelae, and cognitive and biological underpinnings. Then we layer on the correlates of behavioral inhibition.

Thus, the construct and its correlates are reflected in data generated by a rat who did not explore an enclosure, a monkey who became immobile upon seeing a human approach the cage, a college student who showed a potentiated eye blink startle to a loud sound while looking at unpleasant pictures, an adolescent's verbal report of reluctance to attend parties, a rise in salivary cortisol during the Trier Stress Test, less alpha-band power in the right than the left frontal lobe, or a large BOLD signal in the amygdala to social pictures. In all likelihood, were we to repeat these measures in the same individual, we may not see them "hang together" in the way we expect.

As such, there are a number of issues that must be kept in mind when reading the literature. When you move beyond the initial direct observation of behavior in toddlers, can we continue to use the term behavioral inhibition? Even if we do see behaviors that we all agree are "inhibited," how do we determine that these are not simply phenotypic copies of the construct of interest? Is heterogeneity in outcomes linked to behavioral inhibition due to the influence of the environment and maturation, or due to the fact that we have swept up multiple traits (e.g., dysregulated fear, Buss et al., 2013), under the umbrella of behavioral inhibition? Are we examining categorically distinct individuals or individuals that reside at the extreme of a temperamental spectrum?

It seems clear that the emerging strategy of observing children at multiple levels of analysis, across contexts (see point 5, below), over time, will be central to answering these questions. This may help us understand if observed changes reflect changes in underlying temperament, or the manifestation of this trait. We may be able to

better understand if constructs of interest are mechanisms of behavioral inhibition, that is, they generate the behavioral profile we see in the laboratory, or if they are independent moderators of behavioral inhibition.

What Is the "Allostatic Load" of Being Behaviorally Inhibited?

Much of the focus on the long-term outcomes and impact of early behavioral inhibition has been on socioemotional concerns and psychiatric diagnoses. This reflects the profiles that emerged over time with observation. It also reflects the scientific interests and expertise of many of the researchers studying behavioral inhibition. After all, the person doing the science may be just as important as the subject of study as they will be the ones determining which questions go to the front of the line to be asked first, what answers are interesting and worth following up, and which data points should be allowed to influence the ongoing conversation.

Clearly, the socioemotional processes associated with behavioral inhibition are central to how we understand the construct. However, there is growing recognition of the basic health consequences of stable high behavioral inhibition in humans (the chapter "The Temperamentally Shy Child as the Social Adult: An Exemplar of Multifinality" by Poole et al.), nonhuman primates (the chapter "Behavioral Inhibition in Nonhuman Primates: The Elephant in the Room" by Capitanio), and rodents (the chapter "Behavioral Inhibition in Rodents: A Model to Study Causes and Health Consequences of Temperament" by Cavigelli). We see signs of increases in early perinatal risk, asthma and allergies, cardiovascular disease, and, in the case of Cavigelli's rodent model, early mortality.

The wide-ranging health-related outcomes reflect the multitude of systems that have been either linked directly to individual variation in behavioral inhibition or are altered when risk factors are assessed in the context of behavioral inhibition: gene expression, glucocorticoid production and function, hormone levels, and central and peripheral nervous system function. Thus, it may be helpful to base work on the position that behavioral inhibition increases the overall allostatic load an individual carries (the chapter "The Temperamentally Shy Child as the Social Adult: An Exemplar of Multifinality" by Poole et al.). Through allostasis, the body's set points are altered in order to deal with pressing challenges to the child in the moment. High, or repeated, levels of challenge may overwhelm the behaviorally inhibited child's ability to flexibly respond and then downregulate to a point of homeostasis (Susman, Schmeelk, Ponirakis, & Gariepy, 2001). The downstream impact of chronically high allostatic loads is then seen in a cascade of deteriorating neurodevelopmental systems and psychological distress. In the case of behavioral inhibition, a general hypersensitivity to stress and distress may be particularly difficult when embedded in a harsh environment. However, as Chronis-Tuscano and colleagues note (Chronis-Tuscano, Danko, Rubin, Coplan, & Novick, 2018), "there are

virtually no studies of BI/SW [behaviorally inhibited/socially withdrawn] young children who are growing up in stressful, dangerous community and family settings" (p. 9).

How Central Is Self-Referential Processing to Observed Patterns and Trajectories of Behavioral Inhibition?

The initial characterization of behavioral inhibition focused on the outward. That is, children were exposed to novel social and nonsocial experiences, and researchers coded their behavioral responses. Parental measures of behavioral inhibition, such as the Behavioral Inhibition Questionnaire (Bishop, Spence, & McDonald, 2003), have a similar approach.

Although the initial formulation of infant reactivity and behavioral inhibition was not dependent on social context, subsequent studies quickly found that many concerns were most evident in social contexts (Kagan, 2001). The reasons for the shift from sensory novelty to social novelty are still an open question. However, it is clear that the concern with a social environment may be a deep-seated mechanism of behavioral inhibition. For example, both the chapter "Behavioral Inhibition in Rodents: A Model to Study Causes and Health Consequences of Temperament" by Cavigelli and the chapter "Behavioral Inhibition in Nonhuman Primates: The Elephant in the Room" by Capitanio found that behavioral and health outcomes of their animal models were dependent on whether they characterized neophobia (a marker of behavioral inhibition) with or without the presence of conspecifics.

Recent work in children and adolescents also suggests that many of the processes generally linked to behavioral inhibition are specifically amplified when placed in a social—or self-referential—context. At age 7, children with a history of behavioral inhibition showed few behavioral or electrophysiological (EEG and ERP) differences relative to non-inhibited peers when completing a Posner cued attention task (Pérez-Edgar & Fox, 2005). However, when performance was then tied to having to perform an embarrassing task, behaviorally inhibited children showed faster response, greater errors, more difficulty shifting attention, larger ERP components, and more right frontal EEG activity. In adolescence, neuroimaging studies found that the same children unexpectedly showed greater striatal response to monetary reward than non-inhibited peers (Guyer et al., 2006). Follow-up work further refined this observation by noting that the increased striatal response in behavioral inhibition was most pronounced when the reward was tied to the child's performance, rather than simply provided at random (Bar-Haim et al., 2009).

In this volume, the chapter "Relations between Behavioral Inhibition, Cognitive Control and Anxiety: Novel insights provided by Parsing Subdomains of Cognitive Control" by Buzzell and colleagues noted a series of studies suggesting that self-referential monitoring of performance, particularly in the presence of others, is a strong predictor of anxiety outcomes. Previous work (Lahat et al., 2014; McDermott

et al., 2009) found that behaviorally inhibited children and adolescents who show an enhanced error-related negativity (ERN) are at increased risk for anxiety. Follow-up research noted that the relation between monitoring, behavioral inhibition, and anxiety may be most acute when errors are committed in the presence of others (Buzzell et al., 2017).

The neuroimaging and ERN data suggest that many of the trajectories of interest in behavioral inhibition reflect the child's systematic self-monitoring and his subjective evaluation of feedback. Moving beyond task measures, resting-state fMRI studies (Rogers et al., 2017; Roy et al., 2014; Sylvester et al., 2018; Taber-Thomas, Morales, Hillary, & Pérez-Edgar, 2016) suggest that neural networks associated with self-referential processing are "weighted" more heavily than task-centered networks. Future work will further disentangle how the child's sense of self, as an actor, may influence their psychosocial adjustment.

Are Regulatory Processes Necessarily a Good Thing in the Context of Behavioral Inhibition?

Typically, the emergence of regulatory processes is seen as a necessary "good" in a child's developmental trajectory. That is, regulatory processes help the child dampen reactive responses in the moment, shuffle through potential responses, choose and implement the best response, and then interpret subsequent responses (Crick & Dodge, 1994). Indeed, in many cases, maladaptive trajectories are thought to be rooted in poor or fragile regulatory processes, particularly in the case of externalizing difficulties (Eisenberg et al., 2001).

From this perspective, high levels of self-regulation would serve as a resilience factor for children. That is, at risk children would show internalizing problems and anxiety *unless* control mechanisms could come in and disrupt the trajectory (Lonigan & Vasey, 2009; Susa, Pitică, Benga, & Miclea, 2012). However, recent work suggests that high levels of control, much like monitoring, may be detrimental in the context of behavioral inhibition. Henderson and Wilson (2017) note that some regulatory processes can potentiate and sustain behavior that increase risk. In particular, response monitor can maintain a focus on contextual and self-referential cues. The effect may be particularly acute when confronting negative feedback in social realm, which further reinforces withdrawal tendencies and learning. The child is then even slower to return to goal-directed attention, which is already potentially fragile given the resting state and electrophysiology data. Overall, response monitoring works to limit flexibility, rather than allowing the child to marshal attentional and cognitive processes as needed.

Together, these findings suggest that we should treat behavioral inhibition as a unique developmental context in which core cognitive, emotional, and social processes may not respond as we would typically expect. Indeed, it has forced us to examine which aspects of cognitive control are actually activated (monitoring vs. control) and the effects of context on the consequences of deploying control mechanisms.

What Do We Really Know About Behavioral Inhibition Beyond the Laboratory?

The vast majority of behavioral inhibition studies rely on direct observation of behavior with standardized scenarios or present participants with controlled stimuli in order to capture a motor or neural response. Relatively less work has examined behaviorally inhibited children in their daily environments, as they interact with familiar adults and peers. In this volume, the chapter "Peer Relations and the Behaviorally Inhibited Child" by Rubin and colleagues make the argument that we need to better understand how behaviorally inhibited children interact with familiar peers in order to explain how early temperament traits may lead to specific developmental outcomes.

In this vein, we see that patterns of behavioral inhibition/temperamental shyness shift over the course of the school year and impact socioemotional and academic functioning (Rudasill & Rimm-Kaufman, 2009). Indeed, social components of testing, even if not directly related with the subject matter, may impact how well behaviorally inhibited children perform (Crozier & Hostettler, 2003). In addition, the chapter "Psychobiological Processes in the Development of Behavioral Inhibition" by Buss and Qu notes that we cannot assume that behaviorally inhibited children view "positive" social interactions in the same way as parents, teachers, and researchers. The authors point out that popularity may actually be associated with increasing cortisol over time for behaviorally inhibited children (Tarullo, Mliner, & Gunnar, 2011).

While we puzzle through the impact of behavioral inhibition in "traditional" social settings, we now have to layer on new and emerging contexts for social interaction. The explosion of the internet and social media means that children and adolescents now have more ways than ever to interact (or avoid interacting) with the social world. We do not know how these new experiences may interact with social tendencies linked with behavioral inhibition. In some cases, social media may allow behaviorally inhibited adolescents the opportunity to interact in a manner that feels safer and more in control. This could ease their concern with unpredictability and serve as a transition to more direct social contact. However, it could be that the Internet and social media allow the behaviorally inhibited child to retreat even further from the social world, insuring that they never confront, and overcome, their fears (the chapter "Attention Mechanisms in Behavioral Inhibition: Exploring, and Exploiting, the Environment" by Pérez-Edgar).

Ironically, these new modes of communication may actually ease our ability to carry out research. Historically, we have been concerned that the methods we use in the laboratory show poor ecological validity. This criticism is particularly sharp for tasks that are designed to be compatible with electrophysiology and neuroimaging techniques (the chapter "The Neural Mechanisms of Behavioral Inhibition" by Jarcho and Guyer). However, as children and adolescents increasingly videochat, text, and check in on social media, we see that our computer-reliant tasks and the "outside" social world are coming closer and closer together.

Closing Commentary

Two generations of researchers have followed two tracks since the introduction of behavioral inhibition as a construct of study. The first track looks to document developmental trajectories centered on the behavioral inhibition profile, beginning prenatally (DiPietro, Ghera, & Costigan, 2008; DiPietro, Hodgson, Costigan, & Johnson, 1996) through to adulthood (Poole, Van Lieshout, & Schmidt, 2017). The second (sometimes overlapping) track has worked to isolate and experimentally manipulate candidate moderators that shift prototypical developmental trajectories. Here the large portion of attention has been on social factors including parenting behaviors, peer relationships, and cultural expectations. Smaller scale individual mechanisms, such as attention to salient stimuli and interpretive mechanisms, have also been examined. Variations due to these mechanisms are evident as early as the second year of life, suggesting that even by age 2, our observations of "pure" behavioral inhibition are not quite so pure.

So where do we stand? We have identified a striking individual difference factor that is evident early in life, relatively stable, and has a broad impact on multiple levels of functioning well into adulthood. We are still trying to tease apart instances of change over time that reflect the influence of the environment versus the unspooling of somewhat predetermined trajectories. We have described the strongest, and best characterized, individual risk factor for the most common form of psychopathology, anxiety. And yet, the data imply that behavioral inhibition is a better predictor of the traits that *will not* develop rather than the profile that does emerge (see the chapter "The History and Theory of Behavioral Inhibition" by Kagan). Moving forward, the accumulation of knowledge, coupled with new technology and methods, should allow us to better situate the behaviorally inhibited child in context as we recognize the myriad of forces that both impact the child, and are deployed by the child, to shape the life course.

References

Almas, A. N., Phillips, D. A., Henderson, H. A., Hane, A. A., Degnan, K. A., Moas, O. L., & Fox, N. A. (2011). The relations between infant negative reactivity, non-maternal childcare, and children's interactions with familiar and unfamiliar peers. *Social Development, 20*, 718–740. https://doi.org/10.1111/j.1467-9507.2011.00605.x

Bar-Haim, Y., Fox, N. A., Benson, B., Guyer, A. E., Williams, A., Nelson, E. E., … Ernst, M. (2009). Neural correlates of reward processing in adolescents with a history inhibited temperament. *Psychological Science, 20*, 1009–1018. https://doi.org/10.1111/j.1467-9280.2009.02401.x

Bishop, G., Spence, S., & McDonald, C. (2003). Can parents and teachers provide a reliable and valid report of behavioral inhibition? *Child Development, 74*, 1899–1917.

Buss, K. A., Davis, E. L., Kiel, E. J., Brooker, R. J., Beekman, C., & Early, M. C. (2013). Dysregulated fear predicts social wariness and social anxiety symptoms during kindergarten. *Journal of Child Clinical & Adolescent Psychology, 42*(5), 603–616. https://doi.org/10.1080/15374416.2013.769170

Buzzell, G. A., Troller-Renfree, S. V., Barker, T. V., Bowman, L. C., Chronis-Tuscano, A., Henderson, H. A., … Fox, N. A. (2017). A neurobehavioral mechanism linking behaviorally inhibited temperament and later adolescent social anxiety. *Journal of the American Academy of Child & Adolescent Psychiatry, 56*, 1097–1105.

Chronis-Tuscano, A., Danko, C. M., Rubin, K. H., Coplan, R. J., & Novick, D. R. (2018). Future directions for research on early intervention for young children at risk for social anxiety. *Journal of Clinical Child & Adolescent Psychology, 47*, 655.

Chronis-Tuscano, A., Degnan, K. A., Pine, D. S., Pérez-Edgar, K., Henderson, H. A., Diaz, Y., … Fox, N. A. (2009). Stable behavioral inhibition during infancy and early childhood predicts the development of anxiety disorders in adolescence. *Journal of the American Academy of Child & Adolescent Psychiatry, 48*, 928–935. https://doi.org/10.1097/CHI.ob013e3181ae09df

Chronis-Tuscano, A., Rubin, K. H., O'Brien, K. A., Coplan, R. J., Thomas, S. R., Dougherty, L. R., … Menzer, M. (2015). Preliminary evaluation of a multimodal early intervention program for behaviorally inhibited preschoolers. *Journal of Consulting and Clinical Psychology, 83*, 534–540.

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 and Adolescent Psychiatry, 51*, 1066–1075. https://doi.org/10.1016/j.jaac.2012.08.002

Crick, N. R., & Dodge, K. A. (1994). A review and reformulation of social information-processing mechanisms in children's social adjustment. *Psychological Bulletin, 115*, 74–101. https://doi.org/10.1037/0033-2909.115.1.74

Crozier, W. R., & Hostettler, K. (2003). The influence of shyness on children's test performance. *British Journal of Educational Psychology, 73*, 317–328.

Degnan, K. A., & Fox, N. A. (2007). Behavioral inhibition and anxiety disorders: Multiple levels of a resilience process. *Development and Psychopathology, 19*, 729–746. https://doi.org/10.1017/S0954579407000363

DiPietro, J. A., Ghera, M. M., & Costigan, K. A. (2008). Prenatal origins of temperamental reactivity in early infancy. *Early Human Development, 84*, 569–575.

DiPietro, J. A., Hodgson, D. M., Costigan, K. A., & Johnson, T. R. (1996). Fetal antecedents of infant temperament. *Child Development, 67*, 2568–2583.

Eid, M. E., & Diener, E. E. (2006). *Handbook of multimethod measurement in psychology*. Washington, DC: American Psychological Association.

Eisenberg, N., Cumberland, A., Spinrad, T., Fabes, R. A., Shepard, S., Reiser, M., … Guthrie, I. (2001). The relations of regulation and emotionality to children's externalizing and internalizing problem behavior. *Child Development, 72*, 1112–1134.

Fox, N. A., Hane, A. A., & Pérez-Edgar, K. (2006). Psychophysiological methods for the study of developmental psychopathology. In D. Cicchetti & D. J. Cohen (Eds.), *Developmental psychopathology* (Vol. 2, pp. 381–426). Hoboken, NJ: Wiley.

Fox, N. A., Henderson, H. A., Marshall, P. J., Nichols, K. E., & Ghera, M. M. (2005). Behavioral inhibition: Linking biology and behavior within a developmental framework. *Annual Review of Psychology, 56*, 235–262.

Fox, N. A., Henderson, H. A., Rubin, K. H., Calkins, S. D., & Schmidt, L. A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development, 72*, 1–21. https://doi.org/10.1111/1467-8624.00262

Fox, N. A., Snidman, N., Haas, S. A., Degnan, K. A., & Kagan, J. (2015). The relations between reactivity at 4 months and behavioral inhibition in the second year: Replication across three independent samples. *Infancy, 20*(1), 98–114.

García Coll, C., Kagan, J., & Reznick, J. S. (1984). Behavioral inhibition in young children. *Child Development, 55*, 1005–1019. https://doi.org/10.2307/1130152

Gladstone, G. L., & Parker, G. B. (2006). Is behavioral inhibition a risk factor for depression? *Journal of Affective Disorders, 95*, 85–94.

Guyer, A. E., Nelson, E. E., Perez-Edgar, K., Hardin, M. G., Roberson-Nay, R., Monk, C. S., … Ernst, M. (2006). Striatal functional alteration in adolescents characterized by early childhood behavioral inhibition. *Journal of Neuroscience, 26*(24), 6399–6405.

Henderson, H. A., & Wilson, M. J. (2017). Attention processes underlying risk and resilience in behaviorally inhibited children. *Current Behavioral Neuroscience Reports, 4*, 99–106.

Kagan, J. (2001). Temperamental contributions to affective and behavioral profiles in childhood. In S. G. Holman & P. M. DiBartolo (Eds.), *From social anxiety to social phobia: Multiple perspectives* (pp. 216–234). Needham Heights, MA: Allyn & Bacon.

Kagan, J. (2012). The biography of behavioral inhibition. In M. Zentner & R. L. Shiner (Eds.), *Handbook of temperament* (pp. 69–82). New York, NY: Guilford Press.

Kagan, J. (2016). Follow the evidence, ignore the words. In R. J. Sternberg, S. T. Fiske, & D. J. Foss (Eds.), *Scientists making a difference: One hundred eminent behavioral and brain scientists talk about their most important contributions* (pp. 260–263). New York, NY: Cambridge University Press.

Kagan, J., Reznick, J. S., Clarke, C., Snidman, N., & García-Coll, C. (1984). Behavioral inhibition to the unfamiliar. *Child Development, 55*(6), 2212–2225.

Kagan, J., Reznick, J. S., & Snidman, N. (1987). The physiology and psychology of behavioral inhibition in children. *Child Development, 58*, 1459–1473. https://doi.org/10.2307/1130685

Klein, D. N., Dyson, M. W., Kujawa, A., & Kotov, R. (2012). Temperament and internalizing disorders. In M. Zentner & R. L. Shiner (Eds.), *Handbook of temperament*. New York, NY: Guilford.

Kwong, K. K., Belliveau, J. W., Chesler, D. A., Goldberg, I. E., Weisskoff, R. M., Poncelet, B. P., … Turner, R. (1992). Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation. *Proceedings of the National Academy of Sciences, 89*, 5675–5679.

Lahat, A., Lamm, C., Chronis-Tuscano, A., Pine, D. S., Henderson, H. A., & Fox, N. A. (2014). Early behavioral inhibition and increased error monitoring predict later social phobia symptoms in childhood. *Journal of the American Academy of Child and Adolescent Psychiatry, 53*, 447–455.

Lahat, A., Pérez-Edgar, K., Degnan, K. A., Guyer, A. E., Lejuez, C. W., Ernst, M., … Fox, N. A. (2012). Early childhood temperament predicts substance use in young adults. *Translational Psychiatry, 2*, e157.

LeDoux, J. E. (1995). Emotion: Clues from the brain. *Annual Review of Psychology, 46*, 209–235.

Lonigan, C., & Vasey, M. (2009). Negative affectivity, effortful control, and attention to threat-relevant stimuli. *Journal of Abnormal Child Psychology, 37*, 387–399. https://doi.org/10.1007/s10802-008-9284-y

McDermott, J. M., Pérez-Edgar, K., Henderson, H. A., Chronis-Tuscano, A., Pine, D. S., & Fox, N. A. (2009). A history of childhood behavioral inhibition and enhanced response monitoring in adolescence are linked to clinical anxiety. *Biological Psychiatry, 65*, 445–448. https://doi.org/10.1016/j.biopsych.2008.10.043

Nesse, R. M., Curtis, G. C., Thyer, B. A., McCann, D. S., Huber-Smith, M. J., & Knopf, R. F. (1985). Endocrine and cardiovascular responses during phobic anxiety. *Psychosomatic Medicine, 47*, 320–332.

Ogawa, S., Tank, D. W., Menon, R., Ellermann, J. M., Kim, S. G., Merkle, H., & Ugurbil, K. (1992). Intrinsic signal changes accompanying sensory stimulation: Functional brain mapping with magnetic resonance imaging. *Proceedings of the National Academy of Sciences, 89*, 5951–5955.

Pérez-Edgar, K., & Fox, N. A. (2005). A behavioral and electrophysiological study of children's selective attention under neutral and affective conditions. *Journal of Cognition and Development, 6*(1), 89–118.

Pérez-Edgar, K., & Hastings, P. D. (2018). Emotion development from an experimental and individual differences lens. In J. T. Wixted & S. Ghetti (Eds.), *Stevens' handbook of experimental psychology and cognitive neuroscience* (Vol. 4, 4th ed., pp. 289–321). New York, NY: Wiley.

Petrill, S. A., & Brody, N. (2002). Personality and individual differences. In H. Pashler (Ed.), *Stevens' handbook of experimental psychology*. New York, NY: WIley.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron, 48*, 175–187.

Phillips, D. A., Fox, N. A., & Gunnar, M. R. (2011). Same place, different experiences: Bringing individual differences to research in child care. *Child Development Perspectives, 5*, 44–49.

Poole, K. L., Van Lieshout, R. J., & Schmidt, L. A. (2017). Shyness and sociability beyond emerging adulthood: Implications for understanding the developmental sequelae of shyness subtypes. *Journal of Social and Clinical Psychology, 36*, 316–334.

Rapee, R. M., Kennedy, S., Ingram, M., Edwards, S., & Sweeney, L. (2005). Prevention and early intervention of anxiety disorders in inhibited preschool children. *Journal of Consulting and Clinical Psychology, 73*, 488–497.

Rogers, C. E., Sylvester, C. M., Mintz, C., Kenley, J. K., Shimony, J. S., Barch, D. M., & Smyser, C. D. (2017). Neonatal amygdala functional connectivity at rest in healthy and preterm infants and early internalizing symptoms. *Journal of the American Academy of Child & Adolescent Psychiatry, 56*, 157–166.

Rosenbaum, J. F., Biederman, J., Bolduc, E., Hirshfeld, D., Faraone, S., & Kagan, J. (1992). Comorbidity of parental anxiety disorders as risk for childhood-onset anxiety in inhibited children. *American Journal of Psychiatry, 149*, 475–481.

Rosenbaum, J. F., Biederman, J., Gersten, M., Hirshfeld, D. R., Meminger, S. R., Herman, J. B., … Snidman, N. (1988). Behavioral inhibition in children of parents with panic disorder and agoraphobia: A controlled study. *Archives of General Psychiatry, 45*, 463–470.

Rosenbaum, J. F., Biederman, J., Hirshfeld-Becker, D. R., Kagan, J., Snidman, N., Friedman, D., … Faraone, S. V. (2000). A controlled study of behavioral inhibition in children of parents with panic disorder and depression. *American Journal of Psychiatry, 157*, 2002–2010.

Roy, A. K., Benson, B., Degnan, K. A., Perez-Edgar, K., Pine, D. S., Fox, N. A., & Ernst, M. (2014). Alterations in amygdala functional connectivity reflect early temperament. *Biological Psychology, 103*, 248–254.

Rudasill, K. M., & Rimm-Kaufman, S. E. (2009). Teacher–child relationship quality: The roles of child temperament and teacher–child interactions. *Early Childhood Research Quarterly, 24*(2), 107–120.

Scarr, S. (1992). Developmental theories for the 1990s: Development and individual differences. *Child Development, 63*, 1–19.

Scarr, S., & McCartney, K. (1983). How people make their own environments: A theory of genotype-environmental effects. *Child Development, 54*, 424–435.

Schwartz, C. E., Wright, C. I., Shin, L. M., Kagan, J., & Rauch, S. L. (2003). Inhibited and uninhibited infants "grown up": Adult amygdalar response to novelty. *Science, 300*, 1952–1953.

Susa, G., Pitică, I., Benga, O., & Miclea, M. (2012). The self regulatory effect of attentional control in modulating the relationship between attentional biases toward threat and anxiety symptoms in children. *Cognition & Emotion, 26*, 1069–1083. https://doi.org/10.1080/02699931.2011.638910

Susman, E. J., Schmeelk, K. H., Ponirakis, A., & Gariepy, J. L. (2001). Maternal prenatal, postpartum, and concurrent stressors and temperament in 3-year-olds: A person and variable analysis. *Development and Psychopathology, 13*, 629–652.

Sylvester, C. M., Smyser, C. D., Smyser, T., Kenley, J. K., Ackerman, J. J., Shimony, J. S., … Rogers, C. E. (2018). Cortical functional connectivity evident after birth and behavioral inhibition at age 2. *American Journal of Psychiatry, 175*, 180–187.

Taber-Thomas, B., Morales, S., Hillary, F., & Pérez-Edgar, K. (2016). Altered topography of intrinsic functional connectivity in childhood risk for social anxiety. *Depression and Anxiety, 33*, 995–1004.

Tarullo, A. R., Mliner, S., & Gunnar, M. R. (2011). Inhibition and exuberance in preschool classrooms: Associations with peer social experiences and changes in cortisol across the preschool year. *Developmental Psychology, 47*, 1374–1388.

van der Molen, M. W., & Molenaar, P. C. M. (1994). Cognitive psychophysiology: A window to cognitive development and brain maturation. In G. Dawson & K. W. Fischer (Eds.), *Human behavior and the developing brain* (pp. 456–491). New York, NY: Guilford Press.

Williams, L. R., Fox, N. A., Lejuez, C. W., Reynolds, E. K., Henderson, H. A., Pérez-Edgar, K., … Pine, D. S. (2010). Early temperament, propensity for risk-taking and adolescent substance-related problems: A prospective multi-method investigation. *Addictive Behaviors, 35*, 1148–1151.

Wohlwill, J. F. (1973). *The study of behavioral development*. New York, NY: Academic Press.