Sensory Processing Sensitivity: A Review in the Light of the Evolution of Biological Responsivity

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Abstract

This article reviews the literature on sensory processing sensitivity (SPS) in light of growing evidence from evolutionary biology that many personality differences in nonhuman species involve being more or less responsive, reactive, flexible, or sensitive to the environment. After briefly defining SPS, it first discusses how biologists studying animal personality have conceptualized this general environmental sensitivity. Second, it reviews relevant previous human personality/temperament work, focusing on crossover interactions (where a trait generates positive or negative outcomes depending on the environment), and traits relevant to specific hypothesized aspects of SPS: inhibition of behavior, sensitivity to stimuli, depth of processing, and emotional/physiological reactivity. Third, it reviews support for the overall SPS model, focusing on development of the Highly Sensitive Person (HSP) Scale as a measure of SPS then on neuroimaging and genetic studies using the scale, all of which bears on the extent to which SPS in humans corresponds to biological responsivity.

Keywords

personality, sensory processing sensitivity, biological responsivity, highly sensitive person, temperament, animal personality

Psychologists (e.g., Gosling, 2001) have looked at personality differences within animal species to confirm in an independent context some of the personality differences found in humans, finding extraversion and neuroticism particularly easy to observe reliably in mammals and to explain in humans from an evolutionary perspective. This article looks at the reverse by seeking in humans somewhat different basic traits that evolutionary biologists studying animal personality have delineated, as well as applying the thinking of these biologists to the evolution of human personality traits. Specifically, this article reviews the research on the trait of sensory processing sensitivity (SPS; E. Aron & Aron, 1997) in the light of the evidence from evolutionary biology that many personality differences in nonhuman species (e.g., goats, Lyons, Price, & Moberg, 1988; great tits, Verbeek, Drent, & Wiepkema, 1994; pigs, Hessing, Hagelso, Schouten, Wiepkema, & Vanbeek, 1994) involve being more or less responsive, reactive, flexible, or sensitive to the environment (Dingemanse, Kazem, Reale, & Wright, 2009; Wolf, Van Doorn, & Weissing, 2008).

After briefly defining the SPS trait and model, this article first discusses how biologists studying animal personality have conceptualized this trait of a general sensitivity to the environment; second, reviews research on human personality and temperament differences that, although usually not designed to do so, strongly suggests this general sensitivity; third, reviews support for the SPS model focusing on development of the Highly Sensitive Person (HSP) Scale (E. Aron & Aron, 1997) as a measure of SPS, and neuroimaging (e.g., Jagiellowicz et al., 2011) and genetic (Licht, Mortensen, & Knudsen, 2011) studies using the scale, all of which bears on the extent to which SPS in humans corresponds to biological responsivity.

SPS (unrelated to "Sensory Processing Disorder," e.g., Bundy, Shia, Qi, & Miller, 2007) is proposed to be a genetically determined trait involving a deeper (in the sense of Craik & Lockhart, 1972) cognitive processing of stimuli that is driven by higher emotional reactivity. Direct genetic encoding of depth of processing is not the only possible path to differences in this or any other personality difference. General personality differences can be related to many factors, including of course the physical and social environment, development of specialized skills through experience using them, and as a side effect of other inherited traits such as growth rate in nonhuman animals (Stamps, 2007) and body size and strength in human extraverts (Lukaszewski & Roney, 2011). But from the outset (E. Aron & Aron, 1997) we have seen SPS as the manifestation in our species of one

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of two strategies that have evolved in many other species as well. Although these two strategies may in fact be continuous, they are more easily described in terms of either responding more to the environment or responding less. Responding more to cues in the environment by comparing them (consciously or not) to past experience with similar cues may result in taking more time to observe and reacting less rapidly, and thus *appearing* less "bold" or impulsive and more risk averse, especially in novel situations or when there are conflicting action tendencies (approach–withdraw). After having observed, however, a responsive strategy could result in behaving in an especially bold or at first glance risky (but in fact not risky) manner in the future because in similar situations there would be greater certainty about how to behave. Still, the strategy of greater sensitivity is often named for easily observed behaviors related to pausing to process, such as withdrawing, while missing what may be the underlying cognitive behavior, which we see as a common difficulty for research on this trait in human personality.

We have proposed (E. Aron & Aron, 1997) that in humans the more responsive strategy is partly characterized by being more prone to "pause to check" in a novel situation, being more sensitive to subtle stimuli, and employing deeper or more complex processing strategies for planning effective action and later revising cognitive maps, all of which is driven by stronger emotional reactions, positive and negative. The role of emotional reactivity was not made explicit in 1997, but reflects findings then and later (e.g., E. Aron, Aron, & Davies, 2005), as well as fitting the view that emotionality facilitates learning and memory by providing feedback and retrospective appraisal (Baumeister, Vohs, DeWall, & Zhang, 2007). Similar processes involving the intertwining of reactivity and depth of processing can also be seen in nonhuman animals (e.g., rodents, Koolhaas et al., 1999; fish, Schjolden & Winberg, 2007; and birds, Groothuis & Carere, 2005).

The Possibility of a "Meta-Personality" Trait of Sensitivity or Responsivity to Context

The identification of animal "personalities" that are consistent over time and extend to various contexts (e.g., Gosling & John, 1999; Sih & Bell, 2008; Sih, Bell, & Johnson, 2004; Stamps & Groothuis, 2010) has spurred theorizing about why and how these differences evolve. Some of the first speculation was done in a groundbreaking study by Wilson, Coleman, Clark, and Biederman (1993) in the report of their study of pumpkinseed sunfish, in which individuals from the same pond varied on a continuum from shy to bold behaviors. Behaviorally "bold" fish were initially identified as those caught in a trap, a novel object in their environment. Behaviorally "shy" fish did not enter the traps and were captured by net. The trait continuum was found to be consistent across time and in other contexts, in that compared with the trapped fish, shy (had to be netted) fish were slower to acclimatize to the lab, and in the pond swam closer to other fish and were less likely to approach (or more likely to flee from) a human observer in the water. The two groups also differed in what they ate, the quantity of parasites in or on their bodies, and where in the pond they could be found (bold fish in open water), suggesting a stable difference in genotype. However, as the shy fish acclimatized to the laboratory with time and stopped behaving shyly, it was also speculated that they were evidencing a broader trait of responsiveness to the environment.

Wilson and colleagues (1993) pointed out that two phenotypes for foraging behavior could theoretically emerge whenever a risk-free habitat fills up with fish and some individuals must move to riskier habitats. Hence, shy fish may have been initially aggressive and driven other fish into open water, forcing them to adapt to that environment by behaving boldly. These "shy" fish in other contexts turned out to be more curious, exploring a stick more than other fish, again suggesting there were in fact more responsive (Coleman & Wilson, 1998). Note that a responsive strategy's success is negative-frequency dependent, in that it depends on how many others are using it. When too many use it, it ceases to be adaptive. Individuals capable of responding by taking up another strategy would have an advantage over those inheriting only one behavioral response such as only avoiding open water or only avoiding any new object.

A decade later, responsivity, or sensitivity across time and contexts had been found in enough species to generate theories about a general trait of sensitivity or responsivity to the environment (Gosling, 2001; Korte, Koolhaas, Wingfield, & McEwen, 2005; Sih & Bell, 2008; Wolf et al., 2008; Wolf, Van Doorn, & Weissing, 2011). Personalities had been identified in more than 100 species, from insects to mammals (Sih et al., 2004), and Wolf et al. (2008) noted that "Many researchers believe that a fundamental factor structuring [animal] personality differences is the degree to which individual behavior is guided by environmental stimuli" (p. 15835). For example, Koolhaas and colleagues (1999), in their overview of differences in aggressiveness in several bird and mammal species, observed that in fact, an equally good candidate for being a "fundamental difference seems to be the degree in which behavior is guided by environmental stimuli" (p. 927). As an example, they noted that in certain bird species aggressive males easily develop routines, appearing to be driven and rigid, whereas nonaggressive males "are more flexible and react to environmental stimuli all the time" (p. 927). That is, the easily observed behavior of aggression versus nonaggression might hide a more fundamental difference of responsive versus nonresponsive. By observing aggressive behavior and avoiding it, nonaggressive individuals may be exhibiting one aspect of their broader responsiveness.

In a similar vein, Sih and Bell (2008) wrote that enough examples exist "to suggest that individual difference in environmental and social sensitivity is common, potentially quite important, and worthy of further study" (p. 16). Dingemanse

and colleagues (2009) provided an integrative model for observing personality traits (e.g., shy, bold, aggressive, nonaggressive) that in some species or individuals are inflexible and completely specific to context but in other cases are flexible, occurring in some contexts and not in others, according to its usefulness, so that the underlying trait in these cases would be being sensitive enough to know when to be shy, bold, etc.—suggesting layers of processing.

Stamps and Groothuis (2010) are wary as to whether there is sufficient evidence in animals to demonstrate a "meta-personality" trait of contextual sensitivity but also acknowledge that such a trait

> could lead to major changes in the way we think about the organization of behavior . . . that some consistent individual differences in behavior are so pervasive as to affect the ways that individuals interact with the external world in a wide range of motivational or functional situations. (p. 316)

Noticing and responding to subtle changes in an environment might seem always to be advantageous, but in fact sensitivity to subtle differences can be a costly endeavor. Time and energy must be taken away from foraging, for example, and be used to observe and also to maintain the necessary biological apparatus, especially the "reactive" coping style by which most responsive animals are identified. Moreover, again, the benefits of being responsive depend on how many others in the environment are responsive. Wolf et al. (2008), using computer and mathematical simulations, investigated situations in which individuals in a population are confronted with choices in a changing environment (e.g., can choose between two food patches and the quality of patches changes). Individuals can follow either a responsive or an unresponsive strategy. Responsive individuals take into account cues about their environment (e.g., cues as to which of a number of patches is better). Consequently, responsive individuals can exploit opportunities in their environment better than unresponsive individuals (e.g., the quality of patches may change over time and responsive individuals, as they take into account environmental cues, will be better able to identify which patch is best at a given point in time). However, the value of resources depends not only on their inherent value (e.g., how many resource items are in a patch) but also on the number of competitors for that resource. The more responsive individuals there are around, the lower the value of these opportunities, as more individuals (all responsive) compete for them. This gives rise to negative-frequency dependence, which in turn promotes the coexistence of a minority of responsive individuals along with the majority of non (or less) responsive individuals. That is, the responsive strategy is an advantage only as long as most individuals do not use it, as when a short cut to avoid a traffic jam is useful only as long as most people do not know about it and consistently use the usual route. Negative-frequency dependence, in turn, predicts a polymorphism between responsive and unresponsive individuals. In reality, unlike a simulation, responsiveness might be a much more continuous trait, depending on the exact payoffs, but even minor variations in responsivity produce the same results. (Animal trait variations, including some types of responsivity, occur in other ways, usually due to spatiotemporal variations: One type is better in a particular area or at certain periods in the life span of that species, e.g., years where there are more predators, and the other type is more successful in other places or times.)

Wolf et al. (2011) expanded their work to repeated choices in social interactions, showing that once some individuals in a population are socially responsive, this can have substantial effects on the outcome of the evolution for other traits, creating selection pressures that lead to consistent individual differences in, for example, aggressiveness and cooperativeness (Wolf et al., 2011) and trustworthiness (McNamara, Stephens, Dall, & Houston, 2009). It is only useful to behave consistently in any of these ways when another notices and responds. In these models, consistent individual differences proliferate once some individuals develop a trait of being responsive. These models of how a very broad form of responsivity or sensitivity might evolve are not fully tested in nonhuman species, and Wolf et al. (2008), Sih and Bell (2008), and Stamps and Groothuis (2010) cited research on humans—our work on adults (e.g., E. Aron & Aron, 1997) and that of Boyce and colleagues (1995), Boyce and Ellis (2005), and Belsky, Bakermans-Kranenburg, and Van Ijzendoorn (2007) with children—as a strong indicator that such a "meta-personality trait" could exist in some species.

The Uncovering of Sensitivity in Humans

A trait of broad sensitivity to the environment is indicated by it being observed in a variety of settings or by finding interactions, especially crossover interactions such that some individuals more than others are found to vary their behavior depending on their environment. Both of these, being broadly observed and behavior x environment interactions, have been seen in humans, as discussed below. A third line of support, especially for those studying human personality, would be whether such a trait of general sensitivity has been implied by prior personality research.

Observations

Observation of sensitivity in many environments is, again, one way to identify a consistent personality difference. Thomas and Chess (1977) in their early work on childhood temperament (defined as a behavioral style, or a general way of responding that is stable over time, and assumed to have genetic origins; Kristal, 2005) observed low sensory threshold (LSL) as one of the nine basic traits distinguishing children. It, together with other traits such as social withdrawal,

make up the personality of the slow-to-warm-up child. Rothbart and Bates (2006) described children's temperament with reference to two observable behaviors pointing to sensitivity: Perceptual Sensitivity or awareness of subtle stimuli as part of Effortful Control and Discomfort due to intensity of stimuli as part of Negative Affectivity. We will discuss this separation of sensitivity and affect later, but what matters here is that at least a simple, easily observed form of sensitivity, sensitivity to stimulation, has been observed to occur across contexts and perhaps to underlie groups of traits or consistent behaviors.

Self-reports are another way to obtain observations (albeit self-observations) of behaviors consistent across time and place, and much as we are all aware of the limitations of questionnaires and interviews, these verbal behaviors are unavailable to those studying other species (and ones they probably envy). The first example of a self-report measure of something like sensitivity is probably that of Mehrabian (1976), who identified and developed a measure of low stimulus screening. The second example is the HSP Scale (E. Aron & Aron, 1997), the development of which we will describe later in this article. Here, however, it is important to note briefly that the development of the HSP Scale suggested a much broader responsivity to the environment than simple sensory sensitivity because this development began with a purely exploratory and empirical study of what is meant when the term *sensitive* is used by clinicians and the general public to describe an individual. In the process of first interviewing and then using items from those interviews to create a measure, we found that such varied statements as being highly conscientious, startling easily, having a rich inner life, and being more sensitive to pain were all significantly correlated with each other. If sensitivity was such a broad phenomenon, it seemed to require a broader theory than being bothered by loud noises or itchy clothing and seemed to extend beyond what we noticed at that time, that sensitive persons reporting troubled childhoods were more introverted and shy than those reporting relatively normal childhoods.

A third example of a self-report questionnaire measuring behavior over a range of contexts is Evans and Rothbart's (2007) Adult Temperament Questionnaire, with facets of Sensory Discomfort as part of negative affect and Orienting Sensitivity, defined as attention to mostly subtle sensory events: perceptual sensitivity (awareness of low-intensity stimuli from the body and environment), affective perceptual sensitivity (awareness of subtle emotional valence related to low-intensity stimuli), and associative sensitivity (awareness of other reactive cognitive content).

Interactions

The observation that some people are genetically more vulnerable than others to the effects of stress and a negative life history has been recognized for some time, through observation or self-report in a variety of settings and through interaction studies in particular. This has led to the trait being named and studied as, for example, neuroticism, negative emotionality, vulnerability to depression, or inhibitedness. Any underlying trait of responsivity was largely missed. The pioneering work on a trait approximating a general sensitivity, Kagan's (1994) work on inhibitedness in children, is an example: Although it attempted to describe a neutral trait and was seen to have some evolutionary advantages, it has been mostly viewed as a precursor to various problems and disorders (e.g., shyness and anxiety; Volbrecht & Goldsmith, 2010). Still, research on inhibitedness led to some of the best observations of the processes (Gunnar, 1994; Nachmias, Gunnar, Mangelsdorf, Parritz, & Buss, 1996) that might be behind a crossover interaction—in this case one in which persons carrying a trait thought to lead to vulnerability are, compared with those without the trait, found to show better outcomes in good environments, pointing to a broader trait of responsivity to environments.

Crossover interactions have been essential for pointing to sensitivity as the trait that is behind the vulnerability in many cases, so that in the context of developmental psychology, Belsky (2005) has chosen the term *susceptibility* to indicate a "for better *and* for worse" outcome for children with certain plasticity markers (phenotypic behaviors, endophenotypic attributes, or genotypes), depending on childhood environment. Although, traits seemingly the opposite of responsivity, such as Attention Deficit Hyperactivity Disorder (ADHD), have also been found to yield crossover interactions (Belsky & Pluess, 2009). For example, researchers previously dedicated to uncovering genetic vulnerabilities are now saying, because of the increasing number of crossover interactions being found, that "The most plausible explanation [for traits and genes linked to psychopathology] is that environment shapes the outcome of these fundamentally neutral common genetic factors, leading to negative outcomes, but also holding the potential for positive behavioral manifestations" (Homberg & Lesch, 2011, p. 513).

Early studies finding crossover interactions. Perhaps the first relevant crossover interaction, and one definitely leading to a theory of general sensitivity, was found by Boyce and colleagues (1995) in a study of respiratory illness in children. Children with greater psychobiological reactivity to stress, as measured by cardiovascular and immune reactivity, and who were in a stressful child care (Study 1) or adverse home environment (Study 2) had more illnesses than nonreactive children, but those in low or minimal stress environments had better than average outcomes. Although the measure was stress reactivity, the authors concluded that "one plausible explanation for such a pattern of findings is the possibility that reactive children are more sensitive or more susceptible to the characteristics of the social environment" (p. 419). An earlier study of adolescents (Gannon, Banks, Shelton, & Luchetta, 1989) found similar results but did not discuss the implications of the crossover interaction.

A crossover interaction implicating sensitivity was suggested by studies of the interaction of parenting and temperament in conscience formation. Initially, Kochanska, Casey, and Fukumoto (1995) found that children 2 and 3 years of age who noticed flaws in objects shown to them during a home visit were similarly more upset in a later laboratory situation in which it was contrived that they would feel at fault for breaking an object important to the adult with them in the laboratory. Those who were aware of flaws during the home visit were the most distressed and likely to attempt reparations in the contrived mishap situation in the laboratory. Later Kochanska, Gross, Lin, and Nichols (2002) found that children who were more inhibited in novel situations at age 2 and 3 were also more upset in a situation again contrived to make it seem to them that they had caused a minor mishap. At age 4 to 5 years, these children were less likely to cheat, break rules, or be selfish when they had no fear of being caught and gave more prosocial responses in moral dilemmas. But in studies (Kochanska, 1997; Kochanska, Aksan, & Joy, 2007) including parental child-rearing practices as a variable, inhibited children internalized moral standards only when they had received gentle discipline deemphasizing power, presumably resulting in an optimal, moderate level of anxious arousal. When there was significant power assertion, these children actually evidenced less moral behavior at a later age. (In SPS theory, optimal level of arousal is an important factor in the optimal functioning of the sensitive strategy, as overstimulation can easily lead to overarousal and poorer cognitive functioning.) For the relatively fearless children, however, maternal responsiveness and children's security of attachment, more normative requirements, were associated with internalization.

In sum, for inhibited, and by association presumably sensitive children, the combination of awareness of subtleties, emotional reactivity (or guilt after a mishap and more inhibited behavior in the face of novel, highly stimulating situations), and awareness of consequences of behaviors for self and others, all point to a more general trait of sensitivity involving inhibition of behavior, emotional reactivity, sensitivity to subtle stimuli, and processing of information to a deeper level. However, when there is parental power assertion, emotions and responses are no doubt to parental behavior instead of to the subtler moral lesson to be learned from a transgression.

Looking at adults and using the HSP Scale for the first time in the context of a crossover interaction, E. Aron et al. (2005) found an interaction with childhood experience in three studies, and a nonsignificant tendency toward a crossover interaction in two of these, in spite of only measuring negative affect. That is, among those scoring high on the HSP Scale, those also reporting a troubled childhood on various measures scored especially high on measures of negative affect, but at the same time there was also a tendency for those scoring high on the HSP Scale without such childhoods to score especially low on measures of negative affect. Note that although the measures of parenting were retrospective, the pattern of results is exactly opposite to what might be expected from biased recall or reporting. (In a replication of this study, Liss, Timmel, Baxley, & Killingsworth, 2005, found a similar pattern for parental quality of care and depression, but not for parental overprotection and depression; there was only a main effect for anxiety.) In the first direct experimental exploration of the possible processes behind this interaction, E. Aron et al. (Study 4) set out to evoke in college students an emotional reaction to either good or bad feedback about their academic ability and found that those scoring high on the HSP Scale had far stronger emotional reactions, both for positive and negative feedback, than those scoring low on the scale. Presumably, highly sensitive children are similarly highly reactive to negative and positive events during childhood.

Early experimental studies with nonhuman primates have also yielded crossover interactions. Suomi (1997) cross-fostered rhesus monkeys selectively bred to be high or low in their reactivity. Reactive infants raised by average mothers had the poorest outcomes, whereas those with low reactivity showed little effect from being raised by either type of mother. But the highly reactive infants raised from birth by skilled, nurturing mothers had the best outcomes, in that they showed developmental precocity, behavioral resilience to stress, and ascension within the group's dominance hierarchy, often becoming leaders, all of which suggests a greater responsivity to social cues. Rhesus monkeys and humans are the only primates with variations in the serotonin transporter gene, which in both correlates with reactivity and yields this same parenting × trait crossover interaction (Jedema et al., 2009; SPS is also related to variations in the serotonin transporter gene, Licht et al., 2011). They are also the most adaptive of all primates, suggesting it may in fact be an important gene governing responsivity.

Theoretical developments arising from crossover interactions. A special section of *Development and Psychopathology* (Vol. *23*, 2011) was devoted to crossover interactions and theories regarding them. Belsky and Pluess (2009) were able to identify 56 such studies, providing tables of those measuring phenotypes (e.g., anxiety, social fear, high SPS), endophenotypic attributes (e.g., cardiovascular reactivity), and genotype (e.g., 5-HTTLPR, s-allele). Many of these studies began with the hypothesis that a certain trait led only to vulnerability but reported results (sometimes failing to comment on them) of a crossover interaction—positive environments or interventions leading to positive outcomes—suggesting an underlying sensitivity to the environment. For example, Gilissen, Bakermans-Kranenburg, van Ijzendoorn, and Van der Veer (2008) found that "temperamentally fearful" children in a low-quality mother-child relationship were more distressed by watching a fear-inducing film clip than were nonfearful children in such a relationship. However, they also found that "fearful" children in a high-quality relationship were *less* physiologically distressed in the same situation than less

fearful children with the same high-quality relationship. This result suggests that terms such as *temperamentally fearful* may be misleading in describing the trait under observation.

"Reactive" children have also been found to benefit more from interventions. For example, Velderman, Bakermans-Kranenburg, Juffer, and van Ijzendodorn (2006) found that reactive infants, as rated by their parents, benefited more (became more securely attached) than nonreactive infants from an intervention designed to increase the responsiveness of mothers, whereas in the control group, highly reactive children were worse off than nonreactive children. Similarly, Pluess and Belsky (2009) found that infants evidencing more negative emotion (possibly a common response in sensitive infants to overstimulation) were positively affected more than other children by high-quality child care and more often affected negatively by poor child care.

These results and others have spurred developmental psychologists to look for evolutionary explanations for these crossover interactions from life history theory (Kaplan & Gangestad, 2005), which views each individual as faced with the task of deciding (not necessarily consciously) how to allocate energy resources across the life span so as to maximize successful reproduction. For example, if an individual is living under dangerous conditions, the individual should reproduce early in life so as not to lose the opportunity by early death, and reproduce often in case some offspring are lost because of these dangerous conditions. If living under optimal conditions, however, the individual should wait until full maturity so that offspring are maximally fit, and have fewer offspring so that they are healthier and can make full use of opportunities. Applying life history theory to humans, Belsky, Steinberg, and Draper (1991) posited that the first years of life provide a child with the opportunity to learn through family and community experiences how stressful the rest of the life will be and to time their reproduction accordingly, a prediction borne out by studies of the timing of puberty in girls living under adverse versus supportive conditions (e.g., Ellis, 2004). Although the effect size is small, it appears to be slightly stronger in hypothalamic-pituitary-adrenal (HPA) reactive girls (Ellis, Shirtcliff, Boyce, Deardorff, & Essex, 2011).Two theories have arisen regarding how children vary in their responsiveness to environmental cues that help with decisions regarding allocation of energy resources. A theory of biological sensitivity to context (Boyce & Ellis, 2005; Ellis, Essex, & Boyce, 2005) posits that very early in life a high degree of HPA arousability will be triggered in any child and be present throughout life if the child detects either a highly stressful or highly supportive environment. This heightened reactivity helps individuals avoid danger in the stressful environment and make optimal use of a supportive environment. Other children, standing to benefit less from heightened awareness of their environment, do not develop this reactivity. A theory of differential susceptibility (Belsky, 1997) argues that variations in responsiveness to childhood environment are innate and due to the fact that parents who give birth to children with a range of personalities, some sensitive and some not, are more likely, to have some live to reproduce themselves than parents with children having more uniform personalities. When childhood conditions are good predictors of the future, children sensitive to those conditions are better adapted in adulthood; when childhood conditions fail to predict later conditions, nonsensitive children are better adapted. Both theories predict a crossover interaction, but being focused on childhood, have less to say about responsivity in adulthood or the processes underlying it, beyond heightened HPA reactivity. Indeed, the importance of infancy and early childhood, HPA reactivity, and puberty timing suggests that hormones are as important as neurons, and information processing, whether thorough or superficial, according to individual responsivity, is not only cognitive but also occurs throughout the body.

Prior Research on Aspects of a General Trait of Sensitivity

We have now considered observation of a consistent trait of responsiveness across time and situations and trait × environment crossover interactions as suggesting that a general trait of sensitivity may exist in humans. We would also expect that even though almost no thought had been given to a general trait of sensitivity prior to 1997, it would be present in some way within the vast amount of high-quality research on human personality and temperament that has accumulated for decades. This section reviews research on traits that overlap with sensitivity in some way, in that in some individuals these traits appear to act as an aspect of sensitivity or as a result of it. One can imagine dozens of ways that human personality might be designed to accomplish a general strategy of being more responsive or sensitive that would be reflected in traits already under study. We will discuss four of these: (a) inhibition of behavior, at least in novel situations or in those generating conflicting responses, in order to attend to potentially useful cues; (b) greater awareness of sensory stimulation, so that more subtleties are noted, but overstimulation is also possible; (c) deeper processing of this sensory information, relating it to the past and projecting its consequences into the future; and (d) stronger emotional reactions, extending the elaboration of associative processes, stimulating retrospective appraisal of actions, promoting learning from and memory of important experiences, and thus altering automatic guidelines for future behavior, including more rapid automatic affective responses (Baumeister et al., 2007).

This list is not complete. Sensitive persons might also have more rapid and efficient unconscious processing, commonly called intuition; more useful dreams; or heightened suggestibility. A genetically determined sensitivity would not need to be restricted to the central nervous system either. Persons who describe having the above four sensitivities also

tend to describe themselves as startling more easily than others and being more affected by caffeine, pain, and medications (E. Aron & Aron, 1997). Biological sensitivity to context is correlated with timing of puberty (Ellis et al., 2011) and immune system reactivity (Boyce et al., 1995). Children identified as inhibited in laboratory situations evidence more allergic symptoms (Bell, 1992; Kagan, Snidman, Julia-Sellers, & Johnson, 1991). But for the purposes of reviewing a large body of personality research briefly, we will focus on the above mentioned four. These four might in theory represent separate ways of being responsive. However, our research suggests that increased responsivity to the environment involves most or all of these, while one of these in isolation often does not signal a general sensitivity or responsivity, and in fact may signal an impairment without evolutionary advantage. For example, extreme sensitivity to stimulation can by itself be a sign of Autism Spectrum Disorders and suggest that something is interfering with the type of higher processing required to sort through experiences for their meaning.

The four listed above also are oversimplifications, at least as behavioral indicators of SPS. For example, we cannot expect inhibition of behavior in all or even most situations involving responsivity because the current situation may already be so familiar that there is no need to pause to check. In this case, sensitivity might lead to a faster than average response. This aspect also might better be termed *inhibited/planned behavior*, in that responses already decided upon can also inhibit behavior—sometimes prior experience dictates that there is no need to act. Thus, the meaning of inhibition and even its presence is questionable unless a sensitive person is faced with a completely novel or unusually conflictual situation, as when the relative costs of the usual choices are higher than normal (e.g., situations when one has special reason to fear judgment, leading to shyness; Aron, 2000).

Another example in which an aspect of SPS, emotional reactivity, might vanish from view would be an individual whose prior negative experiences with the expression of intense emotions (e.g., sensitive boys crying on their 1st day of school) has led to a precocious ability to under react emotionally.

Inhibition of behavior. Again, this discussion of the inhibition of behavior is focused on whether sensitivity might be the underlying reason for inhibited behavior in some individuals (and that inhibited behavior is not the best or only underlying explanation of sensitivity). The evolutionary function of the inhibition of behavior was of great interest to Gray (1981), who initially described a Behavioral Inhibition System (BIS) and a Behavioral Activation System (BAS), the former being especially reactive to anxiolytics (anxiety medications) and so equated with being more anxious, fearful, and threat oriented. However, Gray (1985) quickly began questioning the logic of equating the BIS with anxiety in that it would mean that an individual would be more sensitive to threat only. Even in 1981, he said such a function for the BIS would "be tortuous, assuming it to be viable at all" (Gray, 1981, p. 270) because, if the task of the BIS were to compare the present moment with the past (Gray's [1985] formulation) only to detect signs of threat or punishment, would it not still have to examine all stimuli, not just threatening ones? Furthermore, high BIS activity, if it were associated only with anxiety, ought to be generally disorganizing, interfering with the comparison process, but it does not.

Not surprisingly, Gray revised his theory (McNaughton & Gray, 2000), and Amodio, Master, Yee, and Taylor (2008), in describing more current thinking about the BIS, note that unfortunately the conceptualization of the two as traits and the measurement of BIS and BAS (e.g., Carver & White, 1994), developed earlier, have not reflected that change. In brief, the BIS is now thought to produce alert interest and a pause in activity that allows for the processing of conflicting information, a balancing of or negotiation between the urge to approach and satisfy needs (BAS) and the urge to stop and consider risks, costs, or how best to make use of an opportunity. In the case of threat, a third strategy of fight, flight, or freeze is suggested. The greater the relative strength of the BIS system as an individual difference, the more thorough would be the processing of stimuli. A strong BIS would seem to be a good candidate for supporting a trait of increased sensitivity to the environment.

Zuckerman (1994), arguing from the side of impulsive sensation seeking, suggested that in early evolution, organisms could only approach (BAS) or withdraw (fight, flight, or freeze), but the addition of an inhibition system added flexibility and allowed for "further information processing in organisms capable of such activity" (p. 241).

Building on Gray's original theory, Kagan (1989), as already noted, developed the term "behavioral inhibition to the unfamiliar" (p. 1). Some of the standardized laboratory settings and interactions for identifying inhibitedness include a room with unusual objects such as novel toys or a strange adult dressed in unusual clothing, spontaneous talking with stranger peers, and speaking with an adult examiner (Kagan, Reznick, & Snidman, 1988). Inhibited children are defined as those who are slower to play, speak, or interact. Understandably, given Gray's early theory, Kagan related the trait to fearfulness and the amygdala. The usual assumption in this work is that this is an indication of fearfulness. Indeed, studies of inhibited children have found that they all tend to have an initial increase in adrenaline compared with other children when they enter the standard laboratory setting; however, Gunnar (1994) found that their elevated adrenaline was followed by elevated cortisol levels, presumably as a reaction to threat, only for those inhibited children who before entering the stimulating setting had first been left for a half hour with an unresponsive adult. The same effect was also found comparing inhibited children with secure versus insecure attachments to their mothers (Nachmias et al., 1996). However, sometimes inhibiting behavior could also be a part of being responsive—taking the time to observe environmental

cues rather than ignoring them—but these reasons for pausing would not be as easily identified. The observed initial response in inhibited children of adrenaline in the face of novelty may well facilitate processing of information, only leading to fearfulness when there is an actual threat or in children where there is a lack of social support. In these studies, there is no true crossover interaction because there is no indication of a "better than" outcome, in that inhibited children did not have less initial adrenaline than others or behave in a more uninhibited way than others when secure. (An appropriate measure might have been their greater ability under secure conditions to spot a specific toy with some subtle desirable reward attached to it.) The point here is that an important difference has been identified by the Kagan research on inhibitedness, but if the underlying process was nothing more than inhibition to avoid threat, there would be no possibility of a "better than" outcome when the environment provides support for a child who is initially behaviorally inhibited in these settings.

Furthermore, recent neuroimaging studies (e.g., Bar-Haim et al., 2009) have found that reward areas of the brain in "inhibited" adolescents are more easily activated as well as fear areas. That is, these individuals seem to be more responsive to all situations, as if, again, their inhibited behavior is best described as pausing to observe a new situation, and depending on what they find, they are either more excited than others by potential rewards or more threatened than others by danger.

The question remains as to whether a trait defined as a strong BIS is the same as SPS or the only important aspect of SPS. A strong BIS does seem to include noticing subtle stimuli, perhaps motivated by stronger emotional reactivity, but the answer lies in the future, as neuroscience sorts out better the range of the proposed BIS system and whether its function of "pausing to check" to mediate conflicts between approach and flee would extend to a general sensitivity to the environment.

Continuing with the aspect we have called inhibition of behavior, introversion can be seen as another, mostly social form of it. Carl Jung (1921/1961) actually seemed to have come the closest to describing a central role of sensitivity in introversion, which he saw as a preference to observe and reflect on an object, person, or situation, discovering its relation to one's own past experiences and other subjective factors, versus the extraverted attitude of preferring to gain such knowledge through direct, immediate contact. Indeed, his initial descriptor of this basic distinction was sensitiveness versus its lack, describing what amounts to a crossover interaction, in that this sensitiveness as he described it interacts with experience to produce neuroticism, on one hand, and a certain depth of character on the other (Jung, 1913/1961). Indeed, he may have later preferred the term *introversion* because it was a more neutral term for this sensitivity (E. Aron, 2004).

The problem is that separating an introverted attitude that is due to depth of processing from one due to aversive social experiences is not easily accomplished from observing an outward behavior of doing less than others. The Five Factor Model has based the definitions of introversion and extraversion almost exclusively on what people can observe about each other, and not being able to observe what introverts are doing, a variety of lay theories result. For example, this type of analysis of lay terms for generally observable behaviors led Goldberg (1990) to label introversion as *lethargy* and added the descriptors of *aloofness, silence, modesty, pessimism*, and *unfriendliness*. Except for silence, these are all inner states that could only represent guesses as to the reason for inhibited behavior. Goldberg's Surgency (extraversion), however, is associated with easily observed behaviors: spirit, talkativeness, sociability, spontaneity, boisterousness, adventure, energy, conceit, vanity, indiscretion, and sensuality. McRae and John (1993) provided similar adjectives: active, assertive, energetic, enthusiastic, outgoing, and talkative, now summarized as positive affect, and that introversion is simply a lack of these.

In short, introversion does appear to overlap with some inhibition of behavior in the service of sensitivity, but it seems to be too broadly inclusive to understand how it does this.

Sensitivity to stimuli. Early research on children's temperament traits identified individual differences in sensitivity threshold. As already mentioned, Thomas and Chess (1977) made it one of the nine basic traits distinguishing children. It, together with other traits such as social withdrawal, makes up the personality of what they called the slow-to-warm-up child. Building on that work, Rothbart and Bates (2006) described children's temperament with reference to two observable behaviors pointing to sensitivity: Perceptual Sensitivity or awareness of subtle stimuli as part of Effortful Control and Discomfort due to intensity of stimuli as part of Negative Affectivity.

As said before, Evans and Rothbart (2007), in developing the Adult Temperament Questionnaire, kept Effortful Control and Negative Affectivity as scales with separate conceptual and definitional specificity. Sensory discomfort was again incorporated as a part of their scale of negative affect. Orienting Sensitivity was elevated out of Effortful Control, becoming a separate factor described as automatic attention given to mostly subtle sensory events that are perceptual, affective, or associative, a very good description of responsivity/sensitivity as described by SPS and the scale may be a good measure of it. Because as far as we know the Adult Temperament Questionnaire has not been used in crossover interaction studies, it is not clear whether their temperament trait of Negative Affect, and specifically that of Sensory Discomfort, could be partly or totally the result of exposure to a stressful environment, in childhood or recently. When environmental contributions are accounted for, Sensory Discomfort may correlate with Orienting Sensitivity as part of the inevitable biological cost of a sensitive strategy (and what would be expected in those with stronger emotional reactivity when receiving stimuli that is too intense to ignore

or process). If Sensory Discomfort does not correlate with Orienting Sensitivity after controlling for environmentally caused negative affect, that would seem to support a distinction between the extreme sensory sensitivity that is due to processing difficulties (e.g., Sensory Integration Disorders, Autism) and that of a type of sensitivity related to more effective processing of environmental stimuli.

Other interesting early descriptions of individuals with sensitivity to subtle stimuli have called them "augmenters" of stimulation (Petrie, 1967) or "reducers" (Buchsbaum, Haier, & Johnson, 1983) of evoked potentials. Fine (1972) argued for differences in sensitivity to stimuli as the best explanation for field dependence–independence, finding support for his view in the better performance of field independent individuals on color and weight discrimination tasks. Mehrabian (1976; Mehrabian & O'Reilly, 1980) developed a measure of low stimulus screening that assumed arousability to be an effect, not a cause, of having a greater sensitivity to stimulation. That is, the research and measure sought to demonstrate that there are persons who are more sensitive than others to stimulation, and the best explanation for that is a trait of sensitivity, not a trait of general arousability or anxiety giving rise to sensitivity.

At one time, research on introversion came close to turning that trait into one of general sensitivity: For two decades or more, introversion was studied mainly as a physiological difference in sensitivity. (Indeed, the results of this vein of introversion research partly gave rise to our concept of SPS.) Introverts were found to be more sensitive to low auditory frequencies (Stelmack & Campbell, 1974; Stelmack & Michaud-Achorn, 1985), to pain (e.g., Barnes, 1975; Haier, Robinson, Braden, & Williams, 1984; Schalling, 1971), and to electrocutaneous (e.g., Edman, Schalling, & Rissler, 1979), olfactory (e.g., Herbener, Kagan, & Cohen, 1989), and visual thresholds (e.g., Siddle, Morrish, White, & Mangan, 1969). After numerous such studies over a decade or more, Koelega's (1992) meta-analysis and Stelmack and Geen's (1992) review of the literature argued that the hallmark of introversion is sensitivity. As Stelmack wrote in 1997, "In my view, there is a substantial body of evidence in research on the extraversion trait that converges on one general effect, namely the greater sensitivity (or reactivity) of introverts than extraverts to punctate, physical stimulation" (p. 1239). He added, "What is striking about the sensory reactivity effect is that it is evident for such a broad range of psychological methods" (p. 1240). Interestingly, the study of the relationship between introversion and sensitivity to stimuli had largely ended by the turn of the millennium, perhaps because the Five Factor Model has emphasized a different perspective on the concept of introversion/extraversion.

Still, central as sensitivity to "puntate, physical" stimuli is to a general sensitivity to the environment, it does not seem to be identical with SPS. Indeed, without other aspects of SPS, sensitivity to stimuli would seem to lack evolutionary advantage, as is seen in sensory integration impairments and Autism Spectrum Disorders.

Depth of processing. Individual differences in depth of processing have been the slowest to be recognized as a potential personality or temperament trait, and then it was almost by accident. Patterson and Newman (1993) set out to study the problem of impulsive behavior by using rewards and punishments (winning or losing money) for performance on a task with feedback after each attempt. They equated impulsivity with extraversion, and found that introverts consistently used more time to reflect on feedback about the nature of their mistakes before proceeding to the next trial, and as a result were more successful. Patterson and Newman suggested that taking time to reflect "promotes semantic depth and differentiation by means of reflection" (p. 724). As a result of their study, Patterson and Newman reconceptualized "introversion" as reflectivity, perhaps an equally good term for SPS, although the idea has not been expanded and does not appear to include nonconscious, automatic processing or the role of emotion.

Robinson, Moeller, and Fetterman (2010) approached responsiveness to error feedback from the direction of neuroticism rather than introversion, noting that too much responsiveness to negative feedback has been long associated with pathology, on one hand, but too little is associated with the inability to recognize and regulate problematic behaviors on the other hand. As predicted, they found that on various cognitive tasks, the behavioral characteristic of slowing down in response to error feedback was associated with lower-than-average accuracy for individuals high in neuroticism and to greater-than-average accuracy for those low in neuroticism. That is, first, there is individual variation in the degree to which individuals slow themselves down in response to negative feedback, and the reasons for this differ. In neurotics, it is probably due to anxiety and reduces accuracy. Nonneurotics who are highly sensitive may slow down to notice and correct what they have been doing wrong and this increases accuracy. All that is missing perhaps is the appreciation of whatever unnamed trait is behind this slower, more accurate style. They suggest that it is a lack of emotional reactivity, obviously meaning a lack of negative emotional reactivity, but do not consider that a greater-than-average positive feeling following being accurate or a different type of negative affect (perhaps not affecting self-esteem) might be assisting the nonneurotics who slowed down.

These two studies that we suggest amount to a study of depth of processing may come closest to capturing the phenomenon of general sensitivity. However, what we hypothesize to be the roots of these behaviors (e.g., emotional motivation driving processing) are not explored in these studies and the emphasis on conscious decision making misses a large portion of how we argue SPS probably affects behavior.

Finally, we should note that in a quite different study that may be related to depth of processing, Kjellgren, Lindahl, and Norlander (2009a) found that high scorers on the HSP Scale were more likely to report mystical experiences and

altered state of consciousness when placed in sensory isolation in flotation tanks for stress release.

Emotional/physiological reactivity. The final theorized aspect of SPS that we will consider in our review of relevant personality research is greater emotional reactivity, physiological stress reactivity, or arousability. It is this behavior that has been most often equated with SPS. However, we would argue that emotional reactivity to the environment is only an aspect of general sensitivity. It may be highly correlated with SPS, but emotional reactivity can occur for other reasons and on its own does not explain SPS as we conceptualize it. For example, negative emotionality can be the result of Posttraumatic Stress Disorder (PTSD) and have nothing to do with sensitivity. Although the reactions to PTSD are usually focused on stimuli related to the trauma, it can generalize, especially when the trauma is multiple, severe, or occurring in early childhood, in which case we speak of those with negative life histories and learning. The same is true of strong positive-emotional reactivity on its own. Although conceptualized as a part of SPS, it may be expressed more selectively by those high in the trait. At least the stereotype of strong positive emotion is of the nonsensitive, more impulsive extravert as defined by the Five Factor Model (Goldberg, 1990).

As said before, stronger emotional reactivity might seem to be an obstacle to an accurate response to the environment as well as a source of unstable or labile self-esteem and depression (Kernis, 2003). However, as Baumeister et al. (2007) have argued, most emotion occurs after an event, suggesting that its function is to promote a thorough processing of information in order to have a more effective and rapid response to similar situations in the future. In that case, increased emotional reactivity as a trait would be an advantage, in that it would motivate deeper processing and general learning from or responsiveness to experience after it has occurred. There is still the question, however, of being too emotionally reactive prior to or during a response to the environment. But there too emotional reactivity has its advantages, provided it does not lead to overarousal. For example, at the other extreme of arousal, patients with damage to the amygdala and emotionally handicapped are impaired in their ability to learn because they have no felt reason to do so (Adophs, Tranel, & Buchanan, 2005).

The real culprit may be overarousal, as in the above study by Robinson et al. (2010), in which those who were slow to respond but accurate were viewed as using cognition rather than emotion. In fact, perhaps they were simply staying within an optimal level of emotional and general arousal for the task. However, neurotics generally have a history of negative learning experiences that have led to an expectation of feeling punished, shamed, or defeated if an error is made, and this may have led to a level of arousal far beyond what would be optimal for a cognitive task. Sensitive persons, while emotionally reactive, have lifelong experience with their stronger emotional reactions, and if raised in a supportive environment would surely develop methods of affect regulation such that their emotional reactions would remain at a level that mainly enhances decision-making processes. The real issue is accuracy, as emotional reactivity that evaluates a situation correctly without conscious thought is the most quick and efficient form of decision making. The emotional reactions of neurotics, whether highly sensitive or not, are more likely to be inaccurate, being based on a history of dealing with threatening situations that will be overgeneralized to present ones. It may be that the common assumption that emotion interferes with cognition has been particularly fueled by observing the uncontrolled emotional reactivity of sensitive persons with negative histories, as it leads to overarousal when conscious decision making is required and inaccurate decisions when faster responses are needed.

We would argue that a great deal of temperament, personality, and clinical research has understandably focused on negative affect as a heritable trait, thereby overlooking what we suggest is the high likelihood that negative affect as a personality variable is often the result of an interaction of something like sensitivity (our hypothesized source of the heritability) with a negative environment. The confusion is understandable because the greatest need has been to understand the sources of negative affect—chronic anxiety, depression, and anger. In attempting to identify early in life the contributing temperament traits, the presence or absence of negative affect is one of the most easily observed individual differences (Fox, Henderson, Rubin, Caldins, & Schmidt, 2001), and the search for the genetic correlates of neuroticism/negative affect has been reasonably successful (Canli, 2006). Meanwhile, self-reports of stressful events, in childhood in particular, are frequently disqualified as biased by innate traits, and a longitudinal study measuring all types of extreme stressors is difficult. Still, one of the strongest arguments against genetically based neuroticism would seem to be that evolution should have eliminated such a disadvantageous trait. It seems more likely that when an individual's negative emotionality is genetically determined, again, the genes are related to general emotional reactivity, so that negative emotionality is the result of emotional reactivity, as a part of general responsivity, interacting with exposure to a negative environment—that is, it is the negative side of a crossover interaction, and the genes to date most associated with neuroticism, 5-HTTLPR, do indeed yield crossover interactions (Belsky & Pluess, 2009; Taylor et al., 2006). This suggests that greater positive emotionality is being promoted by the same genes and that this general emotional reactivity, we would argue, is one important aspect of a greater sensitivity to the environment. For example, especially in positive, enriched environments, the greater reactivity of a sensitive child might increase sensitivity to the environment by promoting curiosity and an excitement about learning, or lead to deeper positive feelings for a teacher, coach, or mentor that might in turn lead to greater focus on subtle ways to improve responses compared with a less emotional child.

As for general arousability, it has also been a long-standing personality difference (e.g., Duffy, 1962; Eysenck, 1981; Strelau, 1983, 1994). Being more generally arousable or autonomically reactive is then seen as an explanation for other behaviors, such as being more cautious, introverted, or shy, whereas those with low arousability would be extraverts, sensation seekers, reward dominant, and so forth. However, evolutionary advantages were not emphasized nor its relation to a general sensitivity. Ellis, Jackson, and Boyce (2006), speaking of behavioral sensitivity to context, suggested that it operates mainly through greater stress reactivity via the HPA, in response to being born into or sensitive only at birth to those environments (very stressful or very supportive) in which greater stress reactivity is an advantage. It would seem HPA stress reactivity is very similar to the SPS concept of emotional reactivity.

Research on SPS

Sensitivity as responsivity to the environment would seem to mean that from birth those with the trait are noticing and changing their behavior, not necessarily consciously of course, according to their experiences. In that sense, from a very young age they are more than others a product of their environment, more affected by "nurture," because of their genetics, their "nature." (This adds an interesting twist to the personality-situation debate in personality theory, in that an important trait might be how much persons change their behavior from one situation to another, behavioral inconsistency, which is easily studied in that people do vary in behavior between Time 1 and Time 2 laboratory visits; see Funder, 2006; Funder and Colvin, 1991. An interesting topic for future research would be whether a large portion of the variance on many self-report measures and in many laboratory experiments is contributed by highly sensitive participants.) This makes it difficult to identify them solely thorough phenotypical behaviors, or even endophenotypes such as biological reactivity, because environment can contribute to these as well. Still, we can use a range of methods, as has been done, for example, to study neuroticism, which as noted, partially overlaps with sensitivity. At the outset, however, a questionnaire measure is valuable, in order both to focus behavior observation, as well as enable experimental, genetic, and neurophysiological methods such as functional magnetic resonance imaging (fMRI) and evoked potential.

Development of the HSP Scale

The details of the development of the HSP Scale are available elsewhere (E. Aron & Aron, 1997), but the process of its development was one of uncovering a possible trait of general responsivity in humans, which we only gradually realized as we read the animal personality literature as one source of understanding our results. In the 1990s, the first author became curious about the meaning of the common personality descriptor "sensitive," which is also used without definition in clinical literature (e.g., referring to persons more affected by trauma as "extremely bright, sensitive people"; Kalsched, 1996, p. 11) with the implication that it is innate. Curiosity led to interviews with persons self-identified as highly sensitive (E. Aron & Aron, 1997, Study 1) through advertisements for persons who were especially introverted or "easily overwhelmed by stimuli (such as noisy places or evocative or shocking entertainment)," indicating our initial thinking. From the many who responded, we selected for an equal distribution of genders and across decades of age and a variety of vocations (although 12 of the 39 were students). The first author interviewed each person for 3 to 4 hr on a wide range of personal topics, from childhood history to current attitudes and life problems, and it was these interviews that greatly expanded our conceptualization. For example, we intended to ask more personal questions at the end of the interviews, but persons across all categories volunteered early that their particular form of spirituality (e.g., "seeing God in everything," long meditation retreats, a religious vocation) was central to their lives. Most had a strong connection to the arts and nature, and unusual sympathy for the helpless (animals, "victims of injustice," etc.). Furthermore, in spite of the initial advertisement, of the 35 interviewees who completed the Myers–Briggs Type Indicator (Myers, 1962), 7 were extraverted.

When we created a 60-item questionnaire based on the characteristics of those we had interviewed, it ranged far beyond being easily overwhelmed by overstimulation, our initial expectation. We narrowed the 60 to a 27-item scale with alphas ranging from .64 to .75 over six samples (involving 604 undergraduate psychology students at different universities and a community sample of 301 obtained using random digit dialing). Subsequent studies by others (e.g., Benham, 2006; Hofmann & Bitran, 2007; Meyer, Ajchenbrenner, & Bowles, 2005; Meyer & Carver, 2000; Neal, Edelmann, & Glachan, 2002) using the HSP Scale have found alphas of .85 or higher. This is in spite of the items varying from having a rich and complex inner life, and being conscientious and deeply moved by the arts and music, to being more shaken than others by changes in one's life, having more difficulty performing a task when being observed, startling easily, and being more sensitive to pain, hunger, and caffeine. An item discarded from the original 60 due to a difference in response rate between genders, "would you be willing to sit at the bedside of a dying stranger and comfort them," hardly reflected a simple wish to avoid overstimulating situations or to be in ones with subtle stimuli. Yet all of these varied items still correlated with items such as being bothered by loud noises or chaotic scenes. We concluded that being easily overstimulated might be inevitable, given that perceiving subtle cues and processing information so thoroughly has costs in terms of neurobiological energy (Korte et al., 2005; Wolf et al., 2008), so that when a novel or intense stimulus is unrelenting, the drive to process it ought to lead

to depletion and eventually exhaustion as well as a motivation to avoid severe depletion from this cause in the future.

The breadth of the trait that we were exploring empirically led to our model of SPS as a more sensitive *processing* of sensory data rather than simply more sensitive sensory organs. However, we did not yet fully appreciate the role of heightened emotional reactivity, even though it was present in the interviews and in the items in the original 60 (e.g., do you cry easily; fall in love hard). In the final scale, it was only reflected in negative reactions to harsh or unrelenting stimulation (e.g., Do you make it a point to avoid violent movies and TV shows; . . . to arrange your life to avoid upsetting or overwhelming situations). The original 60 also included positive-emotion items that correlated well with the overall scale (e.g., When you are feeling happy, is the feeling sometimes really strong?). Unfortunately these were left out of the final scale, like other well correlated items (e.g., being bothered by heat, cold, films affecting you the next day), for the sake of brevity. Inhibition of behavior was also not represented in the scale, except in the only item about childhood, "Did parents or teachers seem to see you as shy or sensitive?"

That we were studying a single trait in spite of its breadth was also reflected in there being for each of the six samples (Studies 2-7) a clear single-factor solution for this diverse set of items, with a dramatic drop in eigenvalues (overall variance accounted for) from the first to second unrotated factor, with the remaining factors as "scree" (low values tapering off without any sudden drop). Thus, based on the standard scree-test approach, the factor analyses also supported the notion that the measure taps a single construct.

Interestingly, the distributions of scores on the HSP Scale in all of our samples analyzed to date (total $N > 2{,}000$) also mirror Kagan's experience with the temperament construct "inhibitedness" that he studies in young children. Using formal taxometric methods, Woodward, Lenzenweger, Kagan, Snidman, and Arcus (2000) found that the trait is distributed more like an approximately dichotomous category variable rather than as a continuum with a normal distribution. In practice, this means that we usually find a break point somewhere in our sample distributions and the "curve" is flattened, rather than most individuals grouped around a single central mean. In our samples, typically between 10% and 35% fell into the highly sensitive category, depending on the sample—for example, psychology classes tend to attract more sensitive students than other classes. (For a discussion of typological conceptions of personality, see Robins, John, & Caspi, 1998; for a discussion of the related idea of global traits, see Funder, 1991.)

Possible Facets of Sensitivity as Subscales Within the HSP Scale

Some studies (Evans & Rothbart, 2008; Meyer et al., 2005; Smolewska, McCafe, & Woody, 2006) have reported subfactors within the HSP Scale that possibly measure different facets of sensitivity, or at least point to subfactors in the scale. In the studies that have reported the eigenvalues for the first several factors, results have all been very similar, with a very large first eigenvalue (e.g., 26% of variance in the 27 items accounted for by a single factor of around 12 items) and the second factor, substantially lower (e.g., 8% or less), the rest dropping gradually to 0. However, in some studies, the second and third were interpreted as indicating that there may be three (Ease of Excitation [EOE], Aesthetic Sensitivity [AES], and LSL; Smolewska et al., 2006) or even four (Meyer et al., 2005) subfactors of the overall HSP Scale. Still, as Smolewska et al. (2006) noted, "The positive intercorrelations among these factors, however, are consistent with a general, higher-order construct of SPS" (p. 1276).

Evans and Rothbart (2008), using a different method of identifying the number of factors (a version of parallel analysis), found support for both two- and three-factor solutions (the latter similar in content to Smolewska et al., 2006) but argued for a two-factor solution based on the match of the content of these two factors to aspects of temperament measured in their Adult Temperament Questionnaire (Evans & Rothbart, 2007). Specifically, Evans and Rothbart's first HSP-Scale subfactor corresponded to (and correlated with) their Questionnaire's "Sensory Discomfort" subscale, a trait of negative affect. Their second HSP-Scale subfactor correlated with their Questionnaire's "Orienting Sensitivity" subscale, which has items reflecting what we would call noticing subtleties and depth of processing.

In two recently collected large data sets (A. Aron & Aron, 2010), when we forced two- and three-factor solutions, we obtained quite similar patterns to those of Smolewska et al. (2006) and Evans and Rothbart (2008). The first of the three factors Smolewska et al. termed *Ease of Excitation*, but in both theirs and our own first factor, the four strongest items are about disliking being rushed (e.g., "Do you get rattled when you have a lot to do in a short amount of time?" and "Are you annoyed when people try to get you to do too many things at once?"), suggesting the factor comes closer to a negative version of preferring to observe and reflect before acting. However, it also might be the result of there happening to be four items in the HSP Scale that asked almost the same question, which for mathematical reasons could create a strong factor without necessarily reflecting its unique importance to the overall trait.

More generally, as noted, results of factor analyses have been somewhat inconsistent. Indeed, Liss, Mailloux, and Erchull's (2008) confirmatory factor analysis found that two- and three-factor solutions comparable with previous studies had only marginal fits (e.g., respectively, root mean square errors of approximation [RMSEAs] of .08 and .07; comparative fit indexes [CFIs] of .78 and .81).

If there are different facets to an overall trait of sensitivity, this would not be surprising. Indeed, we think there are at least the four we described in the previous main section (inhibition of behavior, sensitivity to stimuli, etc.). However,

the scale was not designed to tap facets having theoretical construct validity, and we are cautious about drawing strong conclusions from the factor analysis procedures because results have been inconsistent across samples and methods as to whether there are one or more factors. In addition, the straightforward application of standard factor analysis methods to the HSP Scale is problematic for several technical reasons: (a) As noted earlier, the distribution of HSP Scale scores appears to be nonnormal (perhaps due to negative frequency, Wolf et al., 2008, and possibly dichotomous in humans, Kagan, 1994), so that factor analyses may be mostly based on the 80% or so of the population who are probably not at all highly sensitive; (b) the apparent two or more facets in some studies may actually be artifacts of gender differences in preference for some of the items in Smoleska et al.'s (2006) AES and Evan and Rothbart's (2008) similar Orienting Sensitivity factors (e.g., "enjoying fine scents, tastes, etc."; "other people's moods affect you"); (c) there may be differential correlations of items with negative affectivity (due to the robust interaction with childhood experience described above and the question of why a trait of negative affect by itself would be supported by evolution); and (d) there is a likely differential susceptibility of items in the apparent facets to self-report response biases (e.g., being conscientious and having a "rich, complex inner life" in Smoleska et al.'s AES and Evan & Rothbart's Orienting Sensitivity seem especially vulnerable to social desirability). Future research will help sort out this issue, perhaps with factor analyses specifically addressing some of these technical issues.

It should be noted that all of this research has relied solely on classical test theory, so that a valuable focus of future research would be an analysis based on item-response theory.

Relation of the HSP Scale to Other Personality Measures

We have already discussed personality traits that could theoretically, in some cases, be aspects of a general sensitivity and therefore not measured in a way that would adequately capture that overall trait. If SPS indeed represents such an overall trait, to the extent the HSP Scale assesses SPS, scores would have to be at least partially distinct from measures of personality traits based on other understandings of behaviors that focus only on what are aspects of it such as the inhibition of social behaviors (introversion) and the reporting of intense negative emotion (neuroticism).

Hence, we undertook (E. Aron & Aron, 1997) systematic statistical comparisons of the sensitivity measure and several measures of traditional personality traits of introversion and neuroticism or negative affect. Regarding introversion, the simple correlation of introversion with sensitivity varied according to the introversion measure and the sample, from .14 to .29. Using John, Donahue, and Kentle's (1992) introversion measure from the Five Factor Model, the correlation was .12 (not significant). Although some of the correlations with introversion measures were significant, none were high. Using four measures of neuroticism, the correlations ranged from .41 to .62 (all significant), but far from perfect. Neuroticism was the only one scale of the Five Factor Model that correlated significantly or near significantly. (The multiple correlation of all five scales with the HSP Scale was .54, $p < .01$, mostly due to Extraversion and Neuroticism scales, so that 71% of the variance was not accounted for by the Five Factor scales.)

Smolewska et al. (2006) also compared the HSP Scale with the Five Factor Model using the Neuroticism-Extraversion-Openness Five Factor Inventory (NEO-FFI) and found a correlation (.45) with Neuroticism, similar to what we had found, plus a .31 correlation with Openness (which we had expected to find but did not in our sample). They replicated our own finding of a lack of a significant relationship with the Five Factor Model's other three scales, most notably extraversion–introversion. Perhaps this should not be surprising, given that the Five Factor Model largely describes introversion as lack of positive affect, while sensitivity seems also to correlate with greater positive affect (see discussion below).

We are particularly interested in the moderately strong correlation of the HSP Scale with negative affect of various kinds. Indeed, a number of studies, none of which unfortunately investigated early childhood experiences that might have created crossover interactions, have found correlations of the HSP Scale or one of its facets with a variety of negative affect, stress, or subclinical negative variables, mostly in college samples (Benham, 2006; Evers, Rasche, & Schabracq, 2008; Hofmann & Bitran, 2007; Kemler, 2006; Kjellgren, Lindahl, & Norlander, 2009b; Liss et al., 2008; Meyer & Carver, 2000; Meyer et al., 2005; Neal et al., 2002). Interestingly these are mainly with various forms of anxiety, perhaps tapping a combination of depth of processing and emotional reactivity. However, correlations with depression have only been found through an interaction with negative childhood environment.

We now view SPS as involving greater general emotional reactivity, yet the original HSP Scale reflects mostly negative affect in response to overstimulation. Thus, we have sought other ways to assess whether this reactivity is to both negative- and positive-emotional stimuli and is present independent of neuroticism. For example, after partialling out neuroticism measures, the HSP scale still correlates with general (not specifically negative) emotion questions—for example, in one of our samples (E. Aron & Aron, 1997, Study 6), with crying easily (.54 before partialling out neuroticism, .33 after), feeling love intensely (.31, .24), and "when you are happy, is the feeling sometimes very strong?" (.50, .30). This general emotional reactivity was further corroborated by an experimental induction of positive and negative emotions (E. Aron et al., 2005, Study 4) already described and has since been found using neuroimaging (Acevedo, Aron, & Aron, 2010, described below). Hence, we think that

emotional reactivity in the context of sensitivity can be viewed as separate from other traits or conceptualizations of intense emotional reactions.

Finally, as expected, the HSP Scale was correlated .62 with Mehrabian's (1976) measure of low sensory screening, which we consider one aspect of SPS.

Biologically Related Research Using the HSP Scale

The SPS model (and the extent to which the construct is assessed by the HSP Scale) suggests a clear link with neural response and genotypes, endophenotypes, and new phenotypical behaviors, all reflecting a broader sensitivity.

Neural response. Two fMRI studies have suggested sensitivity to subtle stimuli through deeper levels of processing. In the first (Jagiellowicz et al., 2011), 18 individuals who varied in their scores on the HSP Scale carried out a change detection task in the scanner, in which they rated each of a series of landscape scenes for whether they were similar or different from the previous one. The presentations were in blocks, in which the variations (when there were variations) were either gross or subtle. Those scoring higher on the HSP Scale showed dramatically more activation in predicted areas, compared with low HSP scorers, when doing subtle (vs. easier) discrimination tasks. This greater activation during subtle tasks appeared in a variety of regions, especially those associated with visual attention and visual processing (as opposed to simple visual perception). Some of these were the right claustrum, left occipitotemporal, bilateral temporal, and medial and posterior parietal regions as well as the right cerebellum, all used for making connections between incoming visual stimuli and information already in the brain. The results held even after partialling out neuroticism and introversion, supporting the idea that it is specifically SPS that is responsible for more elaborate processing. Overall it appears that sensitive persons take more care when having to make fine distinctions between stimuli.

Another result focusing on sensitivity to subtle cues was found as part of a study (Hedden, Ketay, Aron, Markus, & Gabrieli, 2008) designed to test neural response to a known cultural difference in perception. In this study, 10 Americans of European descent and 10 East Asians recently in the United States underwent fMRI while doing simple visuospatial tasks emphasizing judgments that were either context independent (typically easier for Americans) or context dependent (typically easier for Asians). Each group exhibited greater activation for the culturally nonpreferred task in frontal and parietal regions associated with greater effort in attention and working memory.

However, the participants had also been administered the HSP Scale, and in a subsequent analysis (A. Aron, Ketay, et al., 2010), this overall effect of culture was found to be dramatically and significantly moderated by individual differences in SPS. Specifically, consistent with the theory that highly sensitive individuals are more responsive to subtle cues when making choices, they showed little difference as a function of culture, whereas low sensitives showed strong culture differences. That is, those scoring high on the HSP Scale appeared to need less or no effort to overcome a culturally biased perception found in nonsensitive persons. This interaction remained strong and clearly significant controlling for negative affectivity (neuroticism), social introversion, gender, and individual differences in strength of cultural identity, suggesting that a general sensitivity to subtle cues overrides, in those with this trait, a more general tendency as found in the rest of the population to struggle with these cues when they oppose their own cultural bias.

A third fMRI study (Acevedo et al., 2010) found that the HSP Scale correlated with a greater reaction to photos of both happy and sad faces compared with neutral faces, and to photos of a spouse's happy or sad facial expressions compared with strangers with the same expressions. The areas of greater activation were not in areas associated with specific or pure emotion (e.g., only with spouse sad, or mostly amygdala activation) as much as they were in sensorimotor areas and areas associated with empathy (e.g., ventral medial prefrontal cortex, precuneus; Lamm, Decety, & Singer, 2011). Perhaps most striking was the significant activation across all comparisons in areas of general awareness, notably the insula. The insula seems to play so many roles, not only integrating interoceptive stimuli (thirst, need for air, sensual touch, exercise, temperature, wine-tasting in sommeliers, music, perceptual decision making, and so much more) but also integrating these with moment to moment emotional states to create subjective feelings in such a way that Craig (2009) has argued persuasively that the insula is "a potential neural correlate of consciousness" (p. 59). If this is the case, greater insula activation might well represent greater awareness of or sensitivity to the inner and outer environment in general—that is, SPS.

Genotype. Thus far, SPS has been tentatively associated with the serotonin (Licht et al., 2011) and dopamine (C. Chen et al., 2011) systems. Based on preliminary results from a Danish community sample (Licht et al., 2011), high scores on the HSP Scale are associated, not surprisingly, with the short(s), low-expressing variant of the repeat length polymorphism 5-HTTLPR (serotonin transporter, 5-HTT, Linked Polymorphic Region). Specifically, the strongest association was with the EOE facet, the first and largest. (Again, the correlation with the 12-item first factor may simply be due to its internal consistency, having four similar items.)

If this finding is replicated, it may clarify why findings of a relationship between depression and the s-allele in the human serotonin transporter gene have been so inconsistent. If the s-allele serves a different function, one with advantages in some circumstances, such as promoting a general sensitivity, it would lead to depression only when there are

precipitating environmental factors as well, as found by Taylor et al. (2006) and reviewed by Belsky and Pluess (2009). In reviewing this interaction, authors have hypothesized that the s-allele leads to stress reactivity (Caspi, Hariri, Holmes, Uher, & Moffitt, 2010; Pluess, Belsky, Way, & Taylor, 2010). However, again, we think that an alternative likely explanation is a general sensitivity that is dependent on stronger emotional response that motivate the depth of processing necessary for this sensitivity to be effective in promoting learning from past experiences.

Research on humans and other primates focusing on the "bright side" of this s-allele, reviewed by Homberg and Lesch (2011), definitely point to more than stress reactivity. Specifically, findings for superior performance on an array of cognitive tasks point to the s-allele being linked to greater sensitivity to emotionally salient environmental cues. For example, Roiser, Muller, Clark, and Sahakian (2007) compared the effects of acute tryptophan depletion on ss and ll genotype (there are actually three alleles: short, short-long, and long-long) groups on tests of episodic memory and attention. Contrary to predictions, the ss genotype group did not respond more specifically to negative-emotion valenced words; rather, both groups responded more to all emotionally valenced words than to neutral words. In a study (Roiser, Rogers, Cook, & Sahakian, 2006) of how the effects of the drug ecstasy on serotonin depletion differs according to the allele carried, surprising differences were found in the non-ecstasy controls. On a gambling-based decision-making task, ss volunteers outperformed ll participants, showing risk aversion when there was a low probability of winning but risk seeking when there was a high probability, plus substantially longer reflection before making difficult choices. The ss carriers also performed better on a delayed pattern recognition task and a task requiring recognizing letters in mirrored versus normal form. Similar "broadly superior performance" (Jedema, et al., 2009, p. 7) on a variety of decision-making tasks has been found in nonhuman primates carrying the s-allele (rhesus macaques have only two alleles, short and long).

The s-allele is also associated in humans and nonhuman primates with greater sensitivity to social stimuli (e.g., benefiting more from social support, Taylor et al., 2006)—and is even associated with creative social dancing (Bachner-Melman et al., 2005), which Homberg and Lesch (2011) described as "mankind's most ancient and universal trait, reflecting a complex phenotype comprising courtship, social communication, and spirituality" (p. 2). Interestingly, Kim and colleagues (2010) found the same differential effect of this gene on the perceptual bias due to culture in Koreans and European Americans as was found for the HSP Scale looking at brain activation during these tasks in those high and low on the trait in the two cultures (A. Aron, Ketay, et al., 2010).

C. Chen et al. (2011), seeking to find something closer to the strong associations between genes and traits predicted by twin studies but not being found with single gene research, considered essentially all the genes (98) with polymorphisms that affect the dopamine system, and chose a trait, SPS, "deeply rooted in the nervous system," (p. 1). Employing a multistep approach (ANOVA followed by multiple regression and permutation), they found a set of 10 loci on 7 genes that predicted 15% of the variance of HSP Scale scores. An additional 2% of the variance was contributed by stressful life events (effects of earlier stressful life events and parental warmth were absorbed by their covariance with recent life events), a relatively small environmental contribution. Dividing the genes by the subsystems of dopamine synthesis, degradation/transport, receptor, and modulation, the last two made the strongest contribution, but interestingly, only interactions among subsystem genes made unique contributions to SPS.

Most of the newly identified foci have unknown function according to C. Chen et al. (2011), but one, DRD2, was one of the three polymorphisms associated with behavioral susceptibility (Belsky, 2005) in a meta-analysis by Bakermans-Kranenburg and van Ijzendoorn (2011).

Summary and Future Directions

This article has reviewed SPS in the light of the model within evolutionary biology of a negative-frequency dependent trait of general responsivity or sensitivity in many or most species, in that when a minority of individuals are responsive, they gain advantages that are worth the biological costs of this responsiveness, but if all individuals were more responsive, there would be no advantage for any of them. How this responsive strategy manifests in genotype or phenotype would vary with the species. We have proposed that in humans it has thus far been most directly and comprehensively explored as SPS using the empirically derived 27-item HSP Scale (although evidence from other measures and approaches to related constructs—e.g., Boyce & Ellis, 2005; Evans & Rothbart, 2007—have pointed importantly in the same direction). SPS is conceptualized as involving deeper processing of stimuli across a very wide variety of situations, supported by a greater response to both positive and negative stimuli that motivates learning and thus leads to more successful responses in future similar situations. This depth of processing is mainly a cognitive (although not necessarily conscious) activity, but also appears as a heightened response by the immune system (Boyce et al., 1995) and to, for example, pain, caffeine, and hunger (E. Aron & Aron, 1997). The HSP Scale may not capture all of these facets, given how it was created empirically, but those who score high on it also evidence fMRI results, for example, that fit quite directly with the formal definition of SPS.

Again, all forms of sensitivity, whether to hunger, lighting, or others' emotions serve the general evolutionary purpose of noticing more aspects of Situation A to make better choices in later Situation B, with the assumption that A is enough like B to have been worth learning from. (This is assumed to have particular benefits for social animals,

including humans, by being able to gratify others by making their needs more accessible, conform to others when that is adaptive, or sense untrustworthiness in others.) However, in some situations it is more beneficial to be less responsive—for example, if Situation B, although appearing similar, has little to do with Situation A. Furthermore, less sensitive individuals are able to avoid the biological costs of being sensitive, which may include being easily overwhelmed when stimuli are too intense, frequent, or novel.

SPS is similar to a number of previously studied human traits based on more observable behaviors, such as inhibition or social introversion, that we have argued here may in some cases be understood as facets of this underlying overall evolutionary trait of responsivity or sensitivity modeled in humans as SPS. At least four such aspects captured by previous personality research are (a) inhibited behavior, either as a pausing to notice and respond accordingly or as a previously planned nonresponsive behavior (avoiding what is already known to be noxious, threatening, or lacking worth); (b) sensitivity to subtle cues; (c) depth of processing (whether conscious or automatic); and (d) heightened emotional, biological, or stress reactivity, including being easily distressed by too much stimuli. We have also emphasized that in combination with a poor childhood environment, this last aspect (greater emotional reactivity) can result in predominately negative affect or neuroticism, but otherwise the emotional reactivity can be equally intense for positive reactions, and sensitive persons with positive childhood experiences (or participating in a mental health or educational intervention) appear to have better outcomes on many measures.

In addition, if SPS continues to be found to correlate with the s-allele of the 5-HTTPLPR polymorphism, as suggested by preliminary findings (Licht et al., 2011), the apparent interaction with childhood environment noted earlier would help explain the inconsistency in findings regarding the s-allele being a predictor of depression, as well as being in keeping with recent findings that there are advantages to possessing this allele that are very similar to being especially sensitive. An interesting question is whether and how much the s-allele of the 5-HTTLPR polymorphism serves an evolutionary strategy of responsivity that has succeeded because the majority of the population carries one or two of the long sequences (and what role the sl combination plays in such a strategy). Research on genes associated with SPS will need to look for other polymorphisms as well.

Directions for future research suggested by this review also include finding other non-self-report methods, besides genotyping, of identifying SPS. For example, it would be helpful to identify endophenotypes such as predictable patterns of brain activation in specific situations or differences in brain morphology.

Furthermore, as our understanding of the apparent biological roots of and neural processes associated with SPS become increasingly delineated, it may be valuable to refine or elaborate the sturdy HSP Scale, which has served to predict so much of the SPS model, including the neuroscience results. Indeed, it was not formulated taking into account the potential effect of a negative childhood on the response to some of its items, particularly those with negative wordings, so that for now we strongly recommend in most cases partialling out neuroticism when using the scale (as has been done in a number of the recent studies cited here). The scale also may not capture enough behaviors directly reflecting depth of processing, which might be assessed by questions such as being slow to make decisions or behaviors reflecting heightened positive-emotional reactions. Hence, a revision of the HSP Scale may be valuable. Future research might also benefit from including measures that appear to tap specific aspects of SPS, such as the Orienting Sensitivity Scale of Evans and Rothbart's (2007) Adult Temperament Questionnaire. We also think that future work would benefit from the inclusion of a measure of social desirability to ascertain its role on various items or facets and from further studies of the HSP Scale's factorial structure, focusing especially on whether these factors do in fact indicate aspects of SPS that may each serve the general evolutionary purpose of greater responsivity but that have evolved in different ways.

More generally, we think the ultimate determination of whether a trait or consistent individual behavior difference such as SPS truly serves the responsive strategy is whether there are enough situations in which it consistently results in "outsmarting" enough others, making more successful bets, noticing another's behavior in a way that leads to cooperation, and so on. For example, does noticing and responding to one's own hunger (an item on the HSP Scale) relatively early in a cycle of eating and resting encourage an individual to search for food sooner than others, before a shortage, or does being affected more by another's mood (also an item) lead to greater empathy and more successful mating and child-rearing strategies in comparison with those who generally are less in tune with a mate's or child's moods?

Trait × environment interactions, because of their role in demonstrating a general trait of sensitivity across environments, also would seem to deserve much more exploration in the ways Belsky and Pluess (2009) have suggested. For example, those studying trait × environment or gene × environment interactions should be sure to check for crossover interactions and include measures of potential positive outcomes that might produce such a crossover. In terms of SPS, some example directions might be studies of whether under conditions of being given negative feedback, do sensitive individuals perform less well due to their emotional reactivity than others, and conversely under conditions of positive feedback do they perform better than others.

Indeed, knowing a person's level of SPS would seem to have potential application in a wide variety of areas of human life (e.g., education, vocational choice, assignment of roles in organizations, medical treatment, etc.), as well as affecting

other important personality variables, such as self-esteem. (Interestingly, cultures appear to differ in whether a trait like SPS is viewed as attractive or not; X. Chen, Rubin, & Sun, 1992. This might have a particularly profound effect on the self-esteem of those high in SPS given that they are likely to be especially careful readers of the sociometer; Leary & Baumeister, 2000.) More generally, the research on sensitivity in children, already begun by Boyce, Pluess, and others, could have particular importance for society, in that it may identify those children not only most susceptible to damaging stress but also most likely to benefit from interventions and to perform unusually well in the world with the right start in life.

In addition, it would seem especially valuable to be able to assess when a person deemed high in more well-known traits such as neuroticism or shyness is in fact only or mainly high in SPS. We would argue that a name for a trait represents a theory—implicit or explicit, folk or scientific—for explaining an observable behavior. When observable behavior is minimal, as when a person is quiet or not acting in a situation, our theories are less likely to be correct. Especially for the majority who are less sensitive, the theory will probably not be that the person is observing and planning a future response. (The authors have several times witnessed quiet children on the 1st day of preschool being addressed as shy or afraid.) For example, Paulhus and Morgan (1997) gave an intelligence test before placing students in a leaderless group for seven weekly meetings, after each of which members rated one another. At the outset, group members rated quiet persons as less intelligent (in effect gave the trait of quietness a name, less intelligent, based on a theory). By the end, the ratings were more accurate—the less intelligent were rated less intelligent, regardless of how much they talked. More disturbing is that mental health professionals can make the same mistake. A study by Gough and Thorne (1986) used similar leaderless groups as part of a 3-day personality assessment and found that quiet persons, especially men, were rated by mental health professionals as significantly lower on likeability, intelligence, and mental health. Yet these clinicians' assumptions about these men were utterly wrong, given other assessments (SAT, grade point average [GPA], Minnesota Multiphasic Personality Inventory [MMPI], etc.) and the ratings provided by those who actually knew them (their spouses or peers in their sorority/fraternity). Misattributions by clinicians are not a small matter, given the benefits our society might enjoy from a well-raised, well-supported, confident minority who are especially alert to opportunities and dangers in spheres of life affecting us all. Any misattribution about the terms/theories for traits also significantly affects personality research.

Finally, and most generally, we hope this article will serve to encourage deeper thinking about the potential application to humans of work derived from animal personality research on a theory of general responsivity, and the potential of the SPS trait (and the HSP Scale) as a human marker of this responsivity. Even more generally (see also Nettle, 2006), we hope this article will illustrate the potential for those of us studying all aspects of human personality to refine our theories and terms by making use of the growing body of seemingly highly relevant work by evolutionary biologists studying personality differences within diverse species.

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