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A socio-relational framework of sex differences in the expression of emotion

Jacob Miguel Vigil
Department of Psychology, Center for Applied Research in Child and Adolescent Development, University of North Florida, Jacksonville, FL 32224-2673
j.vigil@unf.edu **http://www.unf.edu/~j.vigil/**

Abstract: Despite a staggering body of research demonstrating sex differences in expressed emotion, very few theoretical models (evolutionary or non-evolutionary) offer a critical examination of the adaptive nature of such differences. From the perspective of a socio-relational framework, emotive behaviors evolved to promote the attraction and aversion of different types of relationships by advertising the two most parsimonious properties of *reciprocity potential*, or perceived attractiveness as a prospective social partner. These are the individual's (a) *perceived capacity* or ability to provide expedient resources, or to inflict immediate harm onto others, and their (b) *perceived trustworthiness* or probability of actually reciprocating altruism (Vigil 2007). Depending on the unique social demands and relational constraints that each sex evolved, individuals should be sensitive to advertise "capacity" and "trustworthiness" cues through selective displays of dominant versus submissive and masculine versus feminine emotive behaviors, respectively. In this article, I introduce the basic theoretical assumptions and hypotheses of the framework, and show how the models provide a solid scaffold with which to begin to interpret common sex differences in the emotional development literature. I conclude by describing how the framework can be used to predict condition-based and situation-based variation in affect and other forms of expressive behaviors.

Keywords: emotion; evolutionary psychology; femininity; masculinity; affect; motivation; nonverbal behaviors; sex differences; social behaviors; social cognition

1. Introduction

In *The Expression of Emotion in Man and Animals*, Charles Darwin (1872) made multiple observations of similarities and differences in emotional behaviors of humans and other animals, and stylistic differences in emotional expression between men and women that have yet to be fully understood in an evolutionary context. Integrating such between-species and within-species variations in emotional expression into a single framework of expressive behaviors remains a challenge for scientists today.

From a clinical standpoint, pathologies that tend to affect one sex more than the other, such as low mood in adolescent girls and women, and conduct and autistic spectrum disorders among males, require a better understanding of the causes of normal sex differences in emotional development and emotional expression (e.g., Baron-Cohen et al. 2005; Garber 2000; Rutter et al. 2003). Although males and females may experience these conditions similarly (e.g., felt sadness), they express themselves differently (Bogner & Gallo 2004). Boys are often described as producing more *externalizing* behaviors that act on the external environment (e.g., physical aggression, psychomotor agitation, risk-taking), whereas girls are described as producing more *internalizing* behaviors that are focused on the individual (e.g., worrying, sadness, self-blame [Crick & Zahn-Waxler 2003; Khan et al. 2002; Salokangas et al. 2002]). These patterns beget the questions of whether or not common distress behaviors are associated with adaptive cost-benefit trade-offs, and how and why these trade-offs may differ by sex.

In the first section of the article, I introduce a theoretical framework for understanding phenotypic variation in expressed emotion, which I refer to as a *socio-relational framework of expressive behaviors* (SRFB). The framework integrates and extends traditional non-evolutionary (e.g., Lazarus 1991; Leary 1957) and evolutionary (e.g., Cosmides & Tooby 2000; Nesse 1990) discussions of emotionality by describing the social constraints that

JACOB M. VIGIL is an assistant professor in the Psychology Department and co-founder of the Center for Applied Research in Child and Adolescent Development at the University of North Florida. He received his Ph.D. in 2007 from the University of Missouri–Columbia, and has published more than eighteen scientific articles across various areas of social, developmental, and evolutionary psychology. His research in social neuroscience has also been featured in popular media such as *Scientific American*. Dr. Vigil is currently focused on understanding how the mind adjusts the perception of pain according to social factors, including stochastic life experiences and situational audience effects.

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were likely essential to the evolution of human social and expressive behavioral systems. I reason that sex-typical emotive behaviors would have coevolved with these constraints in order to regulate interpersonal dynamics to enhance social fitness. The framework also attempts to integrate earlier models of emotionality that highlight subjective dimensions of emotional experiences (e.g., valence and arousal; Barrett 1998) with the natural diversity of *expressed* emotion.

In the second section, I discuss new work in the evolution and development of sex-typical social dynamics, relationship demands, and social styles, including the perception and expression of *masculine* versus *feminine* behaviors. I go on to review common sex differences in the emotional development literature and show how the vast majority of findings can be integrated into the broader socio-relational framework.

In the third and final section, I outline how this framework regularizes our understanding of gender variation, relationship variation, and conditional variation in expressive behaviors across the life span. I describe how the quality and quantity of one's relationships can be related to cost-benefit fitness trade-offs, and how distinctive patterns of expression may be functional for the formation and maintenance of specific types of relationships.

2. The evolution of emotional expressivity

The SRFB rests on the assumptions that the adaptive significance of affective responses (e.g., emotions, dispositions, moods) lies in their expression and that affect behaviors function to systematically motivate other people to respond to the signaler in ways that enhance the signaler's fitness (e.g., Darwin 1872; Dunn 2003; McGuire 1993; Snowdon 2003; see also Panksepp 2000; 2003; Patterson 2003). Neither physiological arousal, nor feelings occurring within a person can enhance fitness unless there are actions associated with these internal states (James 1884). I thus operationally define *emotions* as expressive behaviors that are often associated with the conscious awareness of intense, appealing and aversive sensations. Likewise, I define a social expression as *any* behavior that is both observable *and* can be exaggerated or attenuated by the individual's audience or other social context.

Several lines of research support this description. Developmental studies, for example, show that human infants produce their very first emotive gestures, such as smiling, *subsequent* to a social interaction that includes face-to-face contact, and that these behaviors tend to cease *immediately following* the termination of a mutual gaze (Yale et al. 2003). Similarly, people become more expressive (e.g., smile) when they know that others are observing them; when observers have similar descriptive characteristics to the participant; when fellow audience members are perceived to be interacting, such as engaging in mutual eye contact; and even when audience members are not physically present, but are only perceived to be, such as when children are told that another child is viewing the same film in another room (Chapman 1973; 1975; Fridlund 1991; Jakobs et al. 1996; Kraut & Johnston 1979; LaFrance et al. 2003). Fridlund summarized this research by suggesting that emotional expressivity is not only moderated by, but is perhaps mediated by, the imaginary presence of others, and that the expressive components of emotionality should not be assumed to represent felt experiences (see Fridlund et al. 1990). I use these examples not to debate whether the expressive component of emotion is more biologically primary than the cognitive and experiential components (e.g., see Haidt 2001), but simply to justify the relevance of focusing on the types of *social properties* or socially relevant information that may underlie variation in the expression of emotive gestures.

2.1. Basic dimensions of emotive behaviors

The SRFB subsumes many traditional models of emotive behaviors, especially models that highlight the significance of trust and dominant/submissive patterns of interaction behaviors (e.g., Carson 1969; Darwin 1872). For example, Leary (1957) proposed that personality behaviors (e.g., acting nice, weak, aggressive, and confident) can be conceptualized as representing two dimensions: dominance versus submissiveness and love versus hate. He described these behaviors in the context of the reciprocated reactions (e.g., kindness, sympathy, fright, and respect) that they evoke from others. The SRFB extends Leary's and similar models by explicating potential fitness advantages of the motivations to both signal and respond to these traits, as well as by describing how and why these interaction patterns covary with experiential successes versus failures and situational circumstances, such as interpersonal relationship dynamics and audience characteristics.

2.1.1 Approach and withdrawal behaviors. Central to the SRFB is the premise that the most basic dimension of expressed emotion is the universal motivation to respond to external stimuli, and especially to other social agents, with either *approach* or *withdrawal* behaviors (Buck 1999; Davidson 1993; Davidson et al. 2000; see also Cacioppo et al. 1993; Camras et al. 1993; Gray 2002). *Approach* behaviors are actions designed to exploit the environment such as food and mates, whereas withdrawal behaviors are actions designed to avert environmental threats such as toxins and predators. In humans, this system may be especially sensitive to evaluate potential benefits and dangers of interacting with other people and engaging in different types of relationships. Interactions that have the potential to provide reciprocated investment should stimulate *affiliative* behaviors, whereas interactions that are non-reciprocal in nature, and thus potentially exploitive, should stimulate *avoidant* behaviors. When considered from an evolutionary perspective, the basic motivation to respond to other social agents through either affiliative or avoidant behaviors should occur reflexively and heuristically and thus be responsive to ecologically relevant stimuli, and develop and manifest as prototypical facial and bodily gestures in the absence of extensive social modeling (Darwin 1859; see also Cosmides & Tooby 2000; LeDoux 1996; Öhman & Wiens 2003). From this perspective, the types of experiences (e.g., social losses) that elicit a behavioral response (e.g., sadness behaviors) are directly associated with the *form* and *functionality* of the behaviors themselves.

Research on facial expression processing shows that the human amygdala is sensitive to process threatening faces

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(e.g., expressions of *anger* and *fear*) more quickly and accurately than other stimuli, and especially when the signaler is a male (e.g., Fox et al. 2000; Goos & Silverman 2002; Mogg & Bradley 1999). Öhman (2002) summarized this research by suggesting that hypersensitivity to fearful and angry faces does not reflect an emotion-processing system that is specialized to process the physical characteristics of the human face, per se, but rather an evolved cognitive bias to discriminate threatening from non-threatening individuals. This interpretation is supported by research showing parallel sensitivities for processing nonsocial dangers (e.g., snakes and spiders [Öhman et al. 2001]).

A related prediction is that attentive and perceptual biases to detect threatening and non-threatening individuals should have coevolved with expressive behaviors designed to promote affiliative and aversive responses from others. In theory, these behaviors should operate by signaling the opportunity to form reciprocal relationships (e.g., displayed *kindness*) or the ability to protect oneself (e.g., displayed *meanness*), depending on the likelihood of receiving reciprocal investment from others (see also Hamm et al. 2003). In this sense, all expressive gestures, including affect behaviors, should be identifiable along an affiliative/avoidant dimension of behavioral response, depending on whether the behavior typically results in social bonding or in social distancing, across individual relationships. The basic questions that follow are: "What types of social properties should individuals be sensitive to attend to in other people?" and, correspondingly, "What characteristics should individuals express or advertise to others?"

2.1.1.1. Reciprocity potential. The SRFB is based on the thesis that the social properties that influence the motivation to either be attracted to or to avoid other people may be framed in terms of the construct "reciprocity potential" (Vigil 2007). According to this framework, organisms should be sensitive to display or advertise their *reciprocity potential*, or perceived attractiveness as a social partner (e.g., mate, friend, community member), by displaying the types of characteristics that are preferred among conspecifics. In the broadest sense, reciprocity potential represents the individual's cache of resources that are extractable by others through a single or series of social interactions. More specifically, I have previously hypothesized that this potential is contingent on two essential social properties: perceived *capacity* and *trustworthiness* cues. *Capacity cues* demonstrate the individual's ability to provide some sort of resource (genetic material, food, protection, socio-political opportunities, etc.) or to inflict immediate harm on others. In contrast, trustworthiness cues demonstrate the individual's intentions, desires, or otherwise probability of actually reciprocating altruism and hence investing into a relationship (Vigil 2007; for a similar discussion, see Newcomb 1990). These two elementary concepts (capacity and trustworthiness) may be the most parsimonious properties of reciprocity potential, because insufficient levels of either of these constructs, such as having a lot to offer but being unwilling to do so, or being willing but having nothing to offer, result in little impact on others.

2.1.2. Capacity and trustworthiness behaviors. *2.1.2.1. Capacity cues.* Empirical studies show that humans, as do other highly affiliative species, respond to social challenges with either "dominant" or "submissive" behavioral strategies (e.g., happiness vs. sadness, aggression vs. appeasement, disdain vs. shame, confidence vs. worry [Aureli 1997; Bugental & Lewis 1998; Sapolsky 2004; see also Darwin 1872]). These patterns may reflect behavioral advertisements of one's abilities (cues of capacity) and intentions (cues of trustworthiness), respectively. For example, capacity cues may be perceived through personal characteristics, such as physical stature, personal competencies, material resources, and perceived dominance that signal the individual's ability to physically invest in or to otherwise affect the welfare of others, either positively or negatively. Traits that distinguish the individual's personal competencies and healthiness (e.g., physical attractiveness; Scheib et al. 1999) are fundamental components of implicit personality theories (Schneider 1973) and appear to be unrelated to perceptions of integrity and concern for others (Eagly et al. 1991). Likewise, behavioral studies of humans and other socially embedded species (e.g., monkeys and hyenas) show that individuals implicitly attend to, stare at, and mimic peers whom they perceive to be more powerful, dominant, and higher-status, rather than behaving in this manner towards subordinates (Fiske 1993a; Holekamp 2006). These studies suggest that cognitive biases to attend to cues of dominance (e.g., larger size, erect posture, threat stares, assertive speech, expressed confidence) may be corollary features of social processing in primates, in general, and almost certainly in humans (Mazur 1985; Mignault & Chaudhuri 2003; Moors & De Houwer 2005; see also Tiedens & Fragale 2003). The current suggestion is that these perceptual biases may represent a modularized detection system that is primed to evaluate traits and behaviors that signal others' capacity to reciprocate social favors or capacity to inflict physical harm onto the individual.

2.1.2.2. Trustworthiness cues. In contrast to signals of capacity, trustworthiness cues are perceived through interpersonal characteristics such as kindness, sympathy, and integrity in humans, and through submissive behaviors in less social species. The basic reasoning is that explicit demonstrations of prosocial behaviors (e.g., expressed compassion) and displays of vulnerability (e.g., head bow, gaze aversion, slow movement patterns, crying and worrying behaviors, self-degradation) may be adaptive by *reducing the perception of threat* and thus disarming the threat interpretation by others. Through exaggerated displays of benevolence, individuals may be signaling their motivations and intentions, and hence their trustworthiness or probability of reciprocating altruism. Of course, the phenotypic manifestation of submissive behaviors (e.g., crying) may also reflect the individual's *actual* vulnerability and inability to reciprocate resources. However, the current reasoning is that these handicaps would not be displayed so explicitly or in such an exaggerated form unless there was a specific fitness advantage to doing so.

Likewise, several studies have identified a specialized neural circuitry (involving the right superior temporal sulcus) that may be responsible for the detection of trustworthiness in other people (Winston et al. 2002; see also Adolphs et al. 1998). Todorov and colleagues, for instance, showed that people are particularly sensitive to process

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cues of competency and trustworthiness in human faces, and that these evaluations are both automatic and integral to social trait impressions (Todorov 2008; Todorov et al. 2005; Willis & Todorov 2006). More specific analyses show that amygdala activity is positively correlated with perceptions of distrust and with facial expressions (e.g., *anger* and *fear*) that signal threat (Engell et al. 2007; Todorov 2008; Zald 2003).

Other research shows that people elicit specific endocrine responses, involving the release of oxytocin and vasopressin, when they experience increased trustworthiness and bonding toward others (e.g., Bartels & Zeki 2004; Zak et al. 2004). Behavioral studies have similarly uncovered numerous factors (e.g., repeatedly interacting with others; Ben-Ner et al. 2004; Buckingham et al. 2006) and interpersonal behaviors that humans may use to induce perceptions of trustworthiness and compliance, including eye contact, self-disclosure, physical touch, smiling, and simple mimicry (Bayliss & Tipper 2006; Collins & Miller 1994; Crusco & Wetzel 1984; Kurzban 2001; Lakin & Chartrand 2003; van Baaren et al. 2004; Webbink 1986; Willis & Hamm 1980). At least one other study has shown that participants who were administered oxytocin in turn expressed higher levels of eye contact than did controls (Guastella et al. 2008). From a socio-relational perspective, these perceptual, neuroendocrine, and expressive biases may have coevolved to process the trustworthiness component of other peoples' reciprocity potential, as well as the motivation to advertise these cues to others selectively (see also Boone & Buck 2003).

2.2. Unique features of capacity and trustworthiness cues

Collectively, these studies suggest that humans are sensitive to categorizing others according to dominance status and traits that signal altruistic tendencies and vulnerability (e.g., babyish features; Fiske 1993b). From a socio-relational perspective, these sensitivities reflect the basic motivation to process the abilities and intentions and hence reciprocity potential of other people. Related research on social preferences suggests that people may evaluate capacity and trustworthiness attributes in others somewhat differently. People tend to evaluate capacity traits (e.g., physical attractiveness, intelligence, material resources) in others relative to self-evaluations (Lazarsfeld & Merton 1954; see also Kenrick et al. 2003) and prefer peers that have similar, yet slightly higher, levels of these traits over peers with significantly lower or significantly higher capacity attributes than themselves (Vigil 2007). In contrast, people tend to appreciate trustworthiness traits (e.g., kindness, responsibility) in others in a more linear fashion such that the highest levels are most preferred, and preferences are independent of self-evaluations (Li et al. 2002; Vigil 2007).

These findings are important, because they suggest that perceptions of trustworthiness are obligatory for the formation of most reciprocal relationships, whereas the selective increase or decrease of capacity displays may be needed to strengthen individual relationships between people that differ in social status. The importance of trustworthiness for human sociality may be why people tend to report and presumably believe that they are "kinder than the average person" and why people inflate their self-described *kindness* more so than other attributes (Vigil 2007). Increased sensitivity to appreciate kindness in others and to exaggerate expressions of, and perhaps (falsely) believe in, the unique virtue of one's own kindness may ultimately result in stabilizing human relationships at the dyadic, group, and perhaps species levels of sociality.

Other research suggests that humans may be motivated to adjust preference for capacity and trustworthiness traits in others in relation to the expected extent of the relationship. For example, research on human mate preferences shows that both men and women place greater emphasis on preference for high capacity traits (e.g., physical attractiveness, material resources) rather than high trustworthiness traits when seeking short-term relationships. In contrast, people place a greater emphasis on high trustworthiness traits (e.g., kindness, responsibility) when seeking long-term, more committed, or more exclusive relationships (Cottrell et al. 2007; Geary et al. 2004; Li et al. 2002; Vigil et al. 2006). From a socio-relational perspective, capacity cues may be sought and preferred in short-term relationships, because these types of characteristics do not require repeated interactions to be accurately assessed; they are immediately and more generally *observable* in other people. In contrast, the veracity of trustworthiness cues may be less discernable through limited exposure, and instead requires repeated interactions to be evaluated accurately.

A complementary hypothesis is that people perceive capacity and trustworthiness cues as signaling the potential to interchange different types of resources with others. Capacity cues may signal one's *expedient* or immediate resource potential, such as genetic resources in the case of mate preferences. In contrast, trustworthiness cues may signal one's willingness to provide more *continuous* provisioning, such as extensive and reliable social support. In this sense, the selective advantage in evaluating and potentially interchanging capacity and trustworthiness cues with other people may pivot on the cost-benefit trade-offs that may be associated with investing in different types of relationships (e.g., Vigil & Geary 2007).

In any case, sensitivity to subtleties in capacity and trustworthiness cues in others, and the tendency to increase preference for higher levels of these cues in short-term and long-term relationships (respectively), suggest that detection and expression of these attributes may be integral to relationship formation. Finally, it is important to note that not all capacity and trustworthiness attributes are intuitively associated with the perception of dominance and submissiveness, respectively. Consider the case of a diseased person who has the capacity to infect others but who is perceived as vulnerable, or a person who is perceived to be trustworthy because of a high-status job. These cases show that dominance and submissiveness trait impressions, while typically associated with high-capacity and high-trustworthiness attributes, are merely examples of cues that humans may use to interchange reciprocity potential.

2.3. Variation in discrete emotive behaviors

From the perspective of the SRFB, discrete emotive gestures (e.g., facial expressions, body-movement patterns, sustained mood behaviors) are examples of social expressions that have evolved to display capacity and trustworthiness cues in order to promote interpersonal affiliation or distancing from other people. In this sense, the

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following models incorporate both dimensional and discrete aspects of emotionality. According to the SRFB, discrete emotive behaviors (e.g., *sadness* vs. *joy*), while specialized in form and function, may also be conceptualized along broad patterns or dimensions of functionality. This is not to say that discrete emotive behaviors are always manifested within an immediate social context, they are always associated with either the motivation to promote affiliation *or* avoidance, they never overlap, or that they are only targeted at single individuals or types of audiences. On the contrary, just like other forms of communication such as speech, emotions can manifest in the absence of physical audiences. Likewise, many emotive gestures such as sadness and aggressive responses are pleiotropic, emerge in coordination with other emotions (e.g., simultaneous displays of joy and aggression; Hubbard et al. 2002), and can be functional for both social consolidation and social distancing (discussed in more detail in section 3, "Implications for variation in expressive behaviors"). The current suggestion is that discrete emotive behaviors, while variable in context, may operate through systematic processes, each in terms of the types of events that precipitate their expression, the expressive characteristics of the gestures themselves, and the social outcomes or responses they elicit from others.

2.3.1. Responses to events. One prediction from the SRFB is that discrete emotive behaviors covary with conditions that affect the opportunity to advertise the capacity and trustworthiness components of reciprocity potential. A conceptual illustration of how salient life conditions and evaluations of other people may affect the expression of so-described "basic" emotions (see Ortony & Turner 1990) is presented in Figure 1. For convenience, I have separated the emotions into two categories: responses to events (Fig. 1a) and responses to other people (Fig. 1b). Figure 1a shows examples of emotions that people express in response to events and circumstances that affect their own perceived reciprocity potential; I refer to these emotions as *intra-appraisal* emotions. "High" and "Low" levels of capacity and trustworthiness traits represent the individual's state in relation to the event or circumstance, and in relation to one's immediate peers. The corresponding emotions should then be inferred as behavioral responses to the event that operate in part to selectively promote affiliation or avoidance, and as advertising either capacity or trustworthiness cues to others (Fig. 1a).

For example, Figure 1a shows how behavioral expressions of *joy* and *anger* may be conceptualized as distinct forms of high-capacity displays that, under certain conditions, are functional for either attracting or averting interactions with other people. Facial expressions of joy and anger are both associated with the perception of dominance from others, though they differ in that joy is associated with the attendant perception of high affiliation, whereas anger is associated with the perception of low affiliation (e.g., Izard 1993; Marsh et al. 2005; Montepare & Dobish 2003). According to the SRFB, people are predicted to express these emotions when they either *increase* or retain high levels of capacity attributes (e.g., health, material resources, physical prowess, social status), but express these emotions differently according to whether

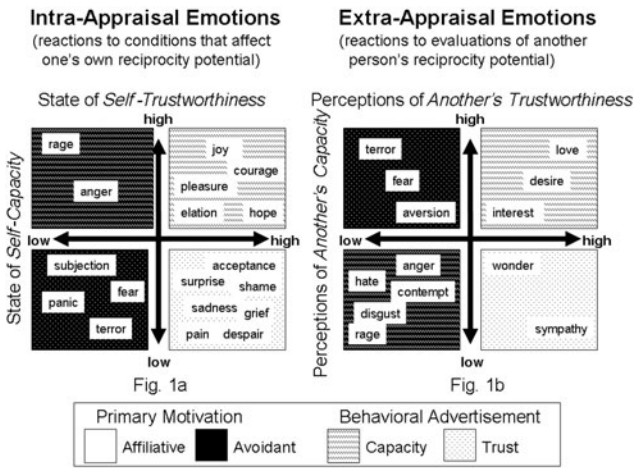


Figure 1. **(a)** *Intra-appraisal emotions* are responses to the impact of an event or set of circumstances on the individual's *own* reciprocity potential. Events that decrease the individual's capacity resources (see the *y*-axis) elicit low-capacity emotions (e.g., *sadness* and *fear*), whereas events that retain or enhance these attributes elicit high-capacity emotions (e.g., *anger* and *joy*). Depending on the individual's perceived trustworthiness status (see the *x*-axis), he or she should express emotions that either avert social interactions (e.g., *anger* and *fear*) when he or she is not trusted or cannot trust others, or solicit affiliation (e.g., *joy* and *sadness*) under more secure social conditions. **(b)** In contrast, *extra-appraisal emotions* are responses to the evaluation of *other people's* reciprocity potential. Individuals should respond to other people who are perceived as "low" in trustworthiness (*x*-axis) with avoidant emotions (e.g., *disgust* and *fear*), and respond to other people who are perceived as "high" in trustworthiness with affiliative emotions (e.g., *love* and *sympathy*). Depending on the simultaneous perception of the other person's capacity attributes (*y*-axis), individuals should produce emotions that advertise their own cues of high-capacity (e.g., *love* and *disgust*) or high-trustworthiness (e.g., *sympathy* and *fear*) to the person being evaluated.

the individual also perceives their immediate relationships to be trustworthy or untrustworthy. Thus, expressions of *joy* and *pride* may be conceptualized as affiliative responses that signal successful experiences and available resources and hence capacity to reciprocate with others under trustworthy social conditions. Instead, expressions of *anger* and *hostility* may be primarily avoidant responses that are used to signal the ability to protect oneself under conditions in which the perception of trust has been breached. People who endure repeated experiences of distrust (e.g., peer rejection, child abuse, adult assault) in their lives show greater sensitivities to recognize and display felt anger and aggression (Hubbard 2001; Pollak & Sinha 2002; Vigil et al., submitted). When individuals experience these feelings, they prefer to avoid other people (Vigil, 2008); when individuals encounter angry peers, they similarly inhibit affiliative gestures (e.g., expressed sympathy; Strayer & Roberts 2004).

In contrast, under conditions in which people experience *decreased* capacity resources, such as financial and social losses (Brown 2000; Salvador 2005), they may instead exaggerate displays of vulnerability and harmlessness in order to signal their intentions and thus the trustworthiness component of reciprocity potential through emotions such as *sadness* and *fear*. However, as shown

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in Figure 1a, the expression of these emotions may differ according to the level of social support available to the individual. People are predicted to express *sadness* under conditions in which the individual can rely on the trustworthiness of others, and instead express *fear* when in untrustworthy, less secure social contexts. Sadness behaviors such as crying and blushing are highly associated with the perception of *trust* and with expressed *sympathy* by others (e.g., de Jong 1999; Van Tilburg et al. 2002; Williams 1982; Zeifman 2001; see also Boone & Buck 2003). From the current perspective, sadness behaviors have evolved to signal trustworthiness cues to others at times when the ability to display high capacity is diminished and in ways that solicit reciprocal advertisements of trustworthiness displays from others, such as increased attention, expressed sympathy, and behavioral and material investment. In contrast, *fear* behaviors (e.g., high-pitched whimpering and alarm screams, worrying, incontinence) may be better suited for exaggerating the display of submissiveness and vulnerability in ways that avert interactions with dangerous people. These behaviors may ultimately operate to subjugate the display of capacity, diffuse the threat interpretation of others, stigmatize the status reward of a confrontational victory by others, and ultimately motivate potential assailants to leave the debilitated individual alone.

2.3.2. Responses to other people. Figure 1b shows that the types of emotions that people express in response to the evaluation of others, referred to as *extra-appraisal* emotions, may also be understood in terms of reciprocity potential and the motivation to affiliate or avert interactions with others. For these emotions, "High" and "Low" trait levels represent perceptions of another person's reciprocity potential relative to self-evaluations. The corresponding emotions should again be inferred as behavioral responses to the evaluations of another person, and as reciprocating displays of capacity or trustworthiness cues in order to promote affiliation or avoidance with the other person. For example, individuals may respond to other people who are perceived as "high" in trustworthiness but having "low" capacity attributes with affiliative responses designed to reciprocate the display of one's own trustworthiness, such as through expressed *compassion* and *sympathy* (see also Miller 2004; Rudolph et al. 2004). Likewise, individuals may respond, when perceiving the other person as both highly trustworthy and highly competent, with behaviors that signal one's own capacity and desire to invest in a reciprocal relationship, through expressions such as *admiration* and *love*.

Other people who are perceived as untrustworthy should instead increase one's threat interpretation and should thus stimulate avoidant responses designed to protect the individual. Depending on whether the other person is also perceived as possessing high or low capacity to inflict harm, individuals may express emotions designed to reciprocate the display of vulnerability (e.g., expressed *fear*) or capacity (e.g., expressed *disgust*), respectively (see Fig. 1b). Humans and other primates express fear and other submissive displays (e.g., apologizing behaviors, allogrooming, lip smacking) for mitigating conflict with more dominant individuals (Aureli 1997; McCullough et al. 1998). In contrast, people may respond to others who are perceived as both untrustworthy and incapable with dominant emotions such as *disgust* and *hatred* in order to intimidate, stigmatize, or otherwise avert future interactions with such persons (see also Kurzban & Leary 2001; Nesse 2005). Thus, while both *fear* and *disgust* responses promote social avoidance, they are predicted to manifest differently depending on the costs and benefits of displaying either lower or higher capacity cues to potential adversaries.

The preceding examples pertain only to a handful of common emotions. However, the overarching thesis – that discrete emotive behaviors are functional for promoting affiliation and avoidance and for selectively advertising capacity and trustworthiness cues to others – may be helpful for understanding more complex emotional experiences. For example, discrete emotions can sometimes occur in the absence of an apparent social context, such as feelings of joy in achieving an insight, anger over a failed hard-drive, fear of incarceration, and sadness over losing a treasured object. These phenomena may be due to the way that the situations simulate experiences that actually influence reciprocity potential, including the loss or gain of capacity resources, and the dependability and threat of relied-upon relationships. Other emotions may similarly be understood in terms of reciprocity potential, such as the relative dissonance between self-perceived and other-perceived reciprocity potential (e.g., guilt, embarrassment, pride, honor), the perceived integrity of other people's reciprocity potential relative to oneself (e.g., disdain, respect), expectations of social affiliations (e.g., feelings of entitlement, remorse, sorrow, jealousy), and lack of control over changes in reciprocity potential (e.g., anxiety). In theory, each of these reactions is systematic in form and function, and is therefore predicted to be associated with the perception of competencies (e.g., dominance) and/or trustworthiness (e.g., submissiveness) and to manifest in ways that either strengthen or diminish relationship formation.

2.4. Summary

The current framework suggests that many, if not all, forms of expressive behaviors, including the momentary and sustained expression of emotion, may be functional for regulating interpersonal relationships. In this sense, even some seemingly problematic behaviors, such as the awareness and self-report of feelings of despair, self-degradation, and somatic disturbances (e.g., loss of appetite and irregular sleep) that constitute depression, may be interpretable from a socio-relational perspective. For example, several theorists have suggested that extreme sadness behaviors may be *adaptive* in several ways that help offset the fitness costs of reduced social standing and risk of being exploited that are associated with negative life-experiences. Such benefits of depressive behaviors may be lowering risk-taking behaviors and reducing conflict with more dominant individuals, sometimes described as an "involuntary defeat strategy" (Allen & Badcock 2003; Fournier et al. 2002; Keller & Nesse 2005; Sloman & Gilbert 2000). The current suggestion, however, is that that these behaviors operate primarily as expressive mechanisms that function to explicate demonstrations of vulnerability and incapacity in order to reduce the perception of

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threat to others. By responding to social adversity through submissiveness behaviors (e.g., Vigil et al., in press), individuals may be advertising the single most important criterion for the ability to solicit high levels of reliable social support in times of stress; that is, trustworthiness cues in the form of displayed vulnerability (see also Hagen 2003).

3. The evolution of sex differences in the expression of emotion

Ironically, even Darwin struggled to understand sex differences in emotionality from the principles of *sexual selection* – selection forces that act on one sex and not the other – that he first described and which presently underlie our understanding of all sexual dimorphisms in nature (e.g., Geary 2009). For instance, in his 1872 monograph on the expression of emotion, Darwin concluded that the prototypical absence of *weeping* in males "may be accounted for by its being thought weak and unmanly by men, both of civilized and barbarous races, to exhibit bodily pain by any outward sign" (Darwin 1872, p. 153). From a contemporary scientific perspective, this explanation is of course insufficient, because it provides no biological rationale for *why* emotive behaviors such as weeping are associated with specific social properties (e.g., perceptions of submissiveness), *why* children implicitly model same-sex behaviors (e.g., Bandura et al. 1961), and *why* the fitness advantage of displaying these behaviors and associated social properties may differ for human males as compared to females.

Despite the universality of observable sex differences in emotion styles (reviewed in detail in section 3.2), some researchers believe that these distinctions are nonexistent or unimportant (e.g., Wester et al. 2002). Such conclusions are usually drawn from research indicating statistically small effect sizes for some elements of emotionality (e.g., sex differences in empathetic behaviors) compared to other elements (e.g., sex differences in self-reported empathy; see Eisenberg & Lennon 1983). In these studies, researchers find as much intra-group variability as is found between the sexes. However, even behaviors such as depressive symptoms with statistically modest effect sizes (e.g., $d = .36$) can result in a multifold risk of suffering from clinically profound distress in one sex (e.g., in this case, females) over the other (e.g., Vigil et al., in press). Findings like these suggest that developing a better understanding of sex differences in emotionality is not only worthy of consideration, but that this focus may be essential for understanding the behavior syndromes themselves.

From the perspective of the SRFB, phenotypic variation in the expression of capacity (e.g., externalizing) and trustworthiness (e.g., internalizing) behaviors is predicted to covary with fundamental characteristics of the individual's relationships, such as the perceived trustworthiness and perhaps the expected extent of interpersonal investment (e.g., short-term vs. long-term) across different types of relationships. A large body of research in the social developmental literature describes related distinctions in the prototypical social networks and relational styles of human males and females. These studies show that girls and women spontaneously form and report a preference for fewer, but more intimate, relationships with their same-sex peers. Boys and men evidence the opposite pattern, forming and reporting a preference for larger, but less intimate, social networks, on average (Geary et al. 2003; Lever 1978; Maccoby 2002; Rose & Rudolph 2006; Vigil 2007). In other words, the corollary distinctions between males' and females' social styles pivot on the quality and quantity of individual relationships that children are sensitive to form and that children and adults engage in their daily lives. In order to ascertain how and why these relationship strategies are manifested psychologically and behaviorally, we must therefore examine the types of social constraints that may have been unique to ancestral males as compared to females (Baumeister & Sommer 1997).

3.1. Male-biased philopatry and male-male coalitional competition

Within the last decade, several theorists have integrated a model that provides a potential evolutionary explanation for sex differences in social styles. Collectively, this model can be framed in terms of a human evolutionary history characterized by *male-biased philopatry* and *male-male coalitional competition*. In this type of social system, males remain in closer proximity to their male kin, thus allowing them to form strong, kin-based coalitions, whereas females tend to emigrate into the social networks of their husbands upon marriage (see Geary 2002; 2009; Geary & Flinn 2002; Geary et al. 2003; Wrangham & Peterson 1996). This system describes the migratory patterns of traditional societies (Murdock 1981; Pasternak et al. 1997) and is consistent with population-genetics studies on extant (Seielstad 2000; Seielstad et al. 1998; Wells et al. 2001; Wilson et al. 2001) and historical societies (Hammer et al. 2001; Semino et al. 2000), which show that males are more likely to remain in closer proximity to their genetic relatives than are females.

Still, while predominant throughout human societies, the extent of male-biased philopatry does vary according to a number of contextual and ecological factors (see Geary 2009). For example, in foraging societies with *bride service*, the prospective husband is expected to reside with his bride's family to provide service to them before the marriage and often for some time afterwards (Marlowe 2004). As would be expected, these patterns are related to the nature of inter-group hostilities (Pasternak et al. 1997), with male philopatry being more common during times of, and among societies that engage in, frequent between-group conflict. Nevertheless, these consistent patterns of social migration and cohesion are important, because they would have resulted in unique sub-ecologies in the day-to-day interactions of males and females throughout human evolutionary history.

Within systems of male-biased philopatry, males would have been exposed to and reliant upon more daily interactions with kin, on average. In contrast, females would have been dependent upon more daily interactions with non-kin or distantly related kin (de Waal 1993; Geary 2002; Geary et al. 2003). According to inclusive fitness theory (Hamilton 1964; Trivers 1971) and based on behavioral research (Daly & Wilson 1988; de Waal 1993; 2000; West et al. 2002), relationships between non-kin require

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more initial investment and maintenance behaviors and are generally more fragile than relationships among genetic relatives. This is because relationships between kin are maintained by inclusive fitness (the sharing of genes; Hamilton 1964), whereas relationships between non-kin are maintained by reciprocal altruism (the sharing of investment behaviors; Trivers 1971). In the context of the SRFB, the tendency for women to solicit more committed and secure relationships among non-kin would have created a heavy reliance on behaviors designed to advertise their trustworthiness through higher levels of submissive displays such as crying behaviors, intimate self-disclosure, self-depreciation, and displayed compassion. At the same time, females may have facilitated reciprocal exchanges of trust cues by forming smaller social networks; fewer daily interactions enable greater allocation of intimate, time-consuming investment behaviors in individual relationships (Geary & Flinn 2001; 2002; Geary et al. 2003; Vigil 2007).

In contrast, as a result of an evolutionary history of male-male, kin-based, coalitional competition, there is predicted to be an overall relaxation of the selection pressures for males to exaggerate the expression of vulnerability (e.g., expressed pain) and intimacy behaviors (e.g., self-disclosure, expressed sympathy). In theory, this would have enabled men to form a greater number of total relationships, and thus larger and more functional coalitions. At the same time, men may have evolved a sensitivity to rely more heavily on the advertisement of externalizing behaviors (e.g., physical aggression), displays of dominance (e.g., inflated self-evaluations), and thus capacity cues in order to attract and maintain more numerous, but less intimate and less exclusive, relationships.

According to this reasoning, intra-sexual selection forces were predominantly responsible for driving the evolution of sex differences in social styles. This general thesis is consistent with studies showing that children are better able to process same-sex, rather than opposite-sex, faces (Goos & Silverman 2002), and report more comfort observing same-sex speech styles and body language (Underwood et al. 2001). This thesis is also consistent with stress-response studies showing that men produce greater hypothalamic pituitary adrenal (HPA) activity from between-group competition than from within-group competition (Wagner et al. 2002), and that these responses are associated with pre-competition preparation and focus. Instead, pre-competition HPA activity in women is less associated with inter-group competition and more associated with interest in bonding and affiliation with fellow team-members (Kivlighan et al. 2005). Other research suggests that men produce greater stress responses in anticipation of events that compare capacity attributes (e.g., public demonstrations of intelligence), whereas women's stress systems are more sensitive to social exclusion (Stroud et al. 2002; Uhart et al. 2006).

Despite this support, some scientists contend that male-biased philopatry is an artifact of modern culture, that these patterns are driven by economic rather than instinctual advantages, and that ancestral males were unlikely to have formed dominance hierarchies and to have engaged in systematic violence (Knauft 1991; Wood & Eagly 2002). Some of these researchers have, in turn, suggested that sex differences in social behaviors may arise from asexual cognitive processes, such as the motivation to conform and to form norms, and that these behaviors are neither functional nor particularly expressive (e.g., Wood & Eagly 2002). This position is counterbalanced by cross-cultural and developmental research (described in the following section) that shows consistent sex differences in emotional development, and by research supporting a major thesis of the SRFB – that *sex differences in emotionality are specific and functional*. In the following sections, I review the literature on sex differences in emotional development, and allow readers to judge for themselves the utility of a socio-relational approach for interpreting this body of work.

3.2. Empirical support from the emotional development literature

3.2.1. Sex differences in nonverbal expressions. *3.2.1.1. Facial expressions.* The central hypotheses from the SRFB are that males have evolved increased sensitivities to process and exaggerate expressions of capacity cues, relative to females, and that females have evolved increased sensitivities to process and exaggerate expressions of trustworthiness cues, relative to males (Vigil 2007). On average, women are more skilled at decoding the emotional disposition of both sexes (Belle 1987; Neff & Karney 2005; Rosip & Hall 2004; see also Hojjat 2000; Kiecolt-Glaser & Newton 2001). Electroencephalographic studies and emotion-discrimination tasks using filtering and merging techniques, for example, show that females are able to process discrete facial expressions (e.g., sadness vs. fear) faster and more accurately than males (Campanella et al. 2004; Cellerino et al. 2004; Hall & Matsumoto 2004; Larkin et al. 2002; see also Hall 1984). This effect size is largest during infancy and smaller, but still constant, as children mature (McClure 2000). The only type of facial expression that boys and men may be more accurate at detecting is *anger*, and especially when the poser is another male (Goos & Silverman 2002).

Other research suggests that males and females may be biased to process facial expressions differently, depending on the sex of the poser. For example, several studies have found that boys and men demonstrate higher accuracy rates and shorter detection times in categorizing neutral or ambiguous facial expressions of male posers as *anger* and *disgust*. In contrast, girls and women are more apt to categorize ambiguities in female faces as *fear* and *sadness* (Goos & Silverman 2002; Larkin et al. 2002; Mignault & Chaudhuri 2003; Widen & Russell 2002). According to the SRFB, because anger/disgust and fear/sadness expressions are associated with the perception of dominance and submissiveness, respectively (e.g., Marsh et al. 2005; Montepare & Dobish 2003), these biases may reflect a differential sensitivity in processing the capacity and trustworthiness components of reciprocity potential in males and females.

In general, however, both sexes are better able to process the facial expressions of female posers (Dimitrovsky et al. 2000; Ramsey et al. 2005), probably because females tend to produce more exaggerated facial expressions than males. Regardless of whether expressions were assessed via electromyography, facial-action coding, or cross-context observational techniques, women produced more exaggerated facial expressions, even when both sexes reported similar levels of felt

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emotion (Eisenberg et al. 1996; Grossman & Wood 1993; Kring & Gordon 1998; LaFrance et al. 2003; Thunberg & Dimberg 2000). Other studies have found greater facial expressivity in female infants (e.g., 28–42 weeks old; Guinsberg et al. 2000) and more rapid development and overall motor movement of the mouths of female fetuses, compared to males (Hepper et al. 1997; Miller et al. 2006). The prenatal differences were found despite no sex differences in overall physical growth. Collectively, these findings suggest that females may develop affective processing and expressive systems, effectively characterizing "women's intuition," that are more specialized for moderating intimate relationships than are developed by males.

3.2.1.2. Vocal expressions. Research on emotional prosody (see Scherer et al. 2003) has yielded similar findings in terms of an overall female advantage in decoding and propensity to express emotion sounds. Women appear to be more accurate at discerning the emotional prosody of others (Besson et al. 2002; see also Sternglanz & DePaulo 2004), although these differences are not always detected (e.g., Morton & Trehub 2001; Wells et al. 2004). Other research on preschoolers' conversation styles shows that girls tend to be more talkative and recite more collaborative, informing, and obliging sentences, and interject their partner's speech with more 'positive' interruption behaviors by using more sympathetic and encouraging utterances and nodding. In contrast, boys tend to produce more controlling and assertive sentences, and provide more 'negative' interruption feedback (e.g., contradictory, analytical) to their partners, especially during unstructured activities with same-sex peers (Anderson & Leaper 1998; Dindia 1987; Leaper & Smith 2004; Leaper et al. 1999; Leman et al. 2005).

Although these behaviors are sometimes described as "behavioral misconduct," recent evidence suggests that assertive speech styles may be particularly functional for group-level problem-solving tasks. Boys who used more assertive and controlling, but less obliging, speech styles tended to do better at group-level competitive tasks than did girls and other boys who used more collaborative conversation tactics (Leman et al. 2005; see also Wood 1987). In contrast, girls are more efficient at sharing tasks, but experience greater conflict than males when they engage in unstructured activities (McElwain & Volling 2002). These conversation styles suggest that boys are more sensitive to accentuate their confidence and dominance, and engage in more instrumental cooperation to achieve goals that involve an extrinsic task. In contrast, girls appear to be more sensitive to accentuate prosocial intentions and other trustworthiness cues (e.g., using inquisitive sentences) and to engage in more affiliative cooperation related to the strength of the relationship rather than to the outcome of an event.

3.2.1.3. Crying and laughing behaviors. Perhaps the best example of a female propensity to advertise trustworthiness cues is females' greater frequency and intensity of crying behaviors as compared to males' (De Fruyt 1997; Lombardo et al. 2001; Van Tilburg et al. 2002; Vingerhoets & Scheirs 2000; Williams 1982; Williams & Morris 1996). In a meta-analysis of crying behaviors across thirty countries and six continents, Becht and Vingerhoets (2002) found that women reported crying an average of $2\frac{1}{2}$ times more often than men. This ratio is also found when researchers experimentally induce crying behaviors, such as when researchers measure tear production in response to emotional films (Martin 1998; Rottenberg et al. 2002).

Other studies suggest that women cry in response to a wider array of experiences compared to men, for instance, following the loss or deterioration of a relationship (e.g., criticism from a coworker or family member), as well as situations involving less conspicuous social relevance (e.g., exhaustion from lack of sleep, personal religious experience; Williams & Morris 1996). Likewise, girls and women report crying and desiring consolation in response to a wider variety of emotions than do males, including experiences of intense anger (Jones et al. 1992) and feelings of frustration, embarrassment, anxiety, fear, and distress. In contrast, men report a greater propensity to respond to these feelings with more aggressive behaviors (e.g., hitting or banging a nearby object) and the desire to avoid peers (Vigil 2008).

Research on laughing behaviors shows women laugh more than men, whereas men are more likely to make other people laugh (Provine 1993). Women are more attracted to men who make them laugh (Grammer & Eibl-Eibesfeldt 1990), and some laughing sounds (e.g., involving clearly voiced phonemes such as "ha") are more attractive than others (e.g., muffled grunts). Overall, however, both sexes rate female-laughter as more "friendly" than male-laughter (Bachorowski & Owren 2001). When people laugh, they raise the pitch of their voice, and some studies have found that higher-pitched and lower-pitched vocal sounds are associated with the perception of submissiveness and dominance, respectively (Puts et al. 2007; see also Cosmides 1983). These findings suggest that laughter and related phenomena, including humor, tickling, and the inhibition of motor activity that occurs during laughter, may be dynamic affiliative gestures (see Provine 2004). Specifically, the comedian may be displaying capacity cues by conveying wit and/or projecting interpersonal derogation (Bonanno & Keltner 2004), whereas the person laughing may be displaying trustworthiness cues by demonstrating appeasement, freezing, and allowing access to vulnerable areas of the body for tickling.

3.2.1.4. Body movement, eye gaze, and touch behaviors. Research on body movement shows sex differences present at birth in the form of increased psychomotor activity in male infants compared to females (e.g., Campbell & Eaton 1999; Eaton & Enns 1986). As boys develop, they tend to adopt more open body postures when sitting or standing and produce greater overall body movements than girls. These movements tend to last longer and consist of more complex behaviors, for instance, involving multiple pivots and greater coordination (Bente et al. 1998; Cashdan 1998; Hall 1984; see also Costa et al. 2001). In addition, as early as infancy, males tend to adopt wider interpersonal distance stances (see Hall 1984) and use their body language to assert dominance differently than females. Males convey dominance through personal space, open and animated body postures, forward-leaning posture, and rapid rate of approach. In contrast, women convey their dominance through downward head tilts and by using "appropriate" approach

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patterns such as interjecting eye contact and smiling behaviors in concordance with their partners' responses (Cashdan 1998; Mast & Hall 2004; Webbink 1986).

Women are also more likely to bow their heads and gaze downward in response to feelings of both sadness and joy, whereas these behaviors are rarely used to convey happiness in men (Mignault & Chaudhuri 2003). In terms of absolute gaze rate, infant girls tend to gaze at human figures for longer durations and more frequently than do infant boys, a trend that remains stable throughout childhood and adulthood (see Hall 1984). Other research has found that women are more likely to gaze at others' faces for longer durations and to punctuate their glances with submissive behaviors such as downward-gaze patterns. In contrast, men tend to engage in more direct, but less frequent, eye contact; for instance, shifting their gaze to and from a target's face more often and terminating a mutual gaze more quickly than do women (Bente et al. 1998).

Similar trends are observed in the absolute rate of nonaggressive touching behaviors, such that young girls (e.g., toddlers) and women tend to engage in more comforting and affiliative touch behaviors than males (e.g., Hall 1984; Kneidinger et al. 2001). Interestingly, similar patterns of earlier onset and more complex patterns of interpersonal touch behaviors have been observed among prenatal female twins (around 100 days post-menstruation), compared to prenatal males and mixed-sex twins (Arabin et al. 1996). Because physical proximity, sustained gaze, and gentle touching have been found to induce interpersonal bonding in humans (e.g., Kurzban 2001; Webbink 1986; Willis & Hamm 1980), it is reasonable to hypothesize that these are examples of trustworthiness cues that females have evolved a sensitivity to display more frequently and overtly than males. These cues may ultimately function to increase perceptions of trustworthiness in order to consolidate the reliability and security of women's relationships.

3.2.2. Sex differences in verbal expressions. *3.2.2.1. Momentary expressions.* In addition to nonverbal behaviors, humans express their emotions through self-report; that is, through the momentary use of emotion terms and descriptions of felt experiences (Brody & Hall 2000). Studies in both natural and artificial settings show that girls and women use emotion terms to describe themselves and others at rates of nearly three times the frequency of boys and men (Goldshmidt & Weller 2000; see also Burke et al. 1976; Girdle et al. 1990). At the same time, females report more exaggerated experiences of felt emotion than males, such as when viewing slides of facial expressions (Grossman & Wood 1993), and especially submissive emotions such as fear, sadness, and embarrassment (Costa et al. 2001; Lewis & Ramsay 2002; Waters et al. 2005).

Greater expression of felt vulnerability is also apparent in the perception and expression of *pain*. Female infants (e.g., 2–12 months old) have been found to produce more overall and higher-pitched crying in response to acute and established pain, compared to male infants, despite no evidence of sex differences in the actual threshold for pain (Fuller 2002). As they grow older, girls report more frequent and intense experiences of pain and are more likely to attribute ailments to non-physical causes such as interpersonal arguments, weather conditions, family relations, and various felt emotions (e.g., anger; Myers et al. 2003; Ramírez-Maestre et al. 2004; Roth-Isigkeit et al. 2005). Related studies show that adolescent girls and women are more likely than same-age males to report having experienced (e.g., during the previous week) and having anticipated experiences of other types of submissive emotions, including feelings of shyness, surprise, shame, guilt, sadness, and self-hostility (Stapley & Haviland 1989; Timmers et al. 1998). In contrast, boys and men tend to deny experiencing these emotions in favor of more feelings of dominant emotions such as *contempt*. Other studies show that girls report a greater propensity to experience surprise and sadness in the company of female peers than when alone, whereas boys report a greater likelihood of experiencing these types of emotions when alone than among male peers (Stapley & Haviland 1989).

3.2.2.2. Self-presentations. The hypothesis that females are more prone to advertise their trustworthiness via displayed vulnerability is also consistent with the breadth of research demonstrating sex differences in self-reported *depressive* and *anxiety* symptoms. Compared to males, girls and women report higher levels of negative life experiences (Davis et al. 1999; Pinquart & Sörensen 2006), lower self-esteem, and exaggerated symptoms of depression following a traumatic experience (e.g., Kling et al. 1999; Marttunen et al. 1995; Parslow et al. 2006; Solomon et al. 2005; Twenge & Nolen-Hoeksema 2002). Other research suggests that activation of the sympathetic nervous system is associated with increased depressive symptoms in traumatized females and with decreased symptoms (e.g., greater confidence) among traumatized males (Vigil et al., in press). Sex differences in depressive symptoms and self-reported distress become pronounced upon puberty, due to rapid increases in symptoms among adolescent girls compared to the relatively constant rates among adolescent boys. These differences peak in early adulthood and then decline slowly but continue to exist throughout middle and late adulthood (e.g., Davis et al. 1999; Ge et al. 2001; 2003; Russac et al. 2007; see also Twenge & Nolen-Hoeksema 2002).

Although males are far more likely to experience traumatic events in their lifetime, including accidents, physical assault, illness, and witnessing death (the notable exception being sexual assault), females are twice as likely to *report* symptoms of PTSD following these experiences (Tolin & Foa 2006). For example, boys who experience physical trauma (e.g., community violence) are no more likely to report these experiences than girls who experience nonphysical trauma (e.g., relational harassment; Ireland 1999; McCart et al. 2005; Nishina & Juvonen 2005; Seals & Young 2003; see also Sourander et al. 2004). Related research shows that self-reported "machismo" ideology, the desire to appear tough, is associated with acute anxiety over expressing submissive, but not dominant, emotions in males (Gold et al. 1992; Jakupcak et al. 2003; see also Updegraff et al. 2000).

Women, in contrast, are more likely to exaggerate and perhaps precipitate experienced distress, by using more *emotion-focused* coping strategies that employ higher rates of self-blame and *corumination* (rehashing personal problems with peers; Rose 2002), and through higher rates of felt guilt and shame (Benetti-McQuoid & Bursik 2005). Men, alternatively, use more "problem-focused" and "positive-thinking" coping strategies to deal with

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misfortune (Vingerhoets & Van Heck 1990). Girls and women are also more likely than males to underrate their self-described capacity attributes such as athleticism, talent, intellectual abilities, and physical attractiveness (Cole et al. 1999; DuBois et al. 1996; Patterson et al. 2001; Stetsenko et al. 2000). Among males, the reverse pattern is often found in the form of exaggerated pride (Tracy & Robins 2007) and over-rated self-descriptions of capacity characteristics in comparison to ratings by others and in comparison to females (Feingold & Mazzella 1998; see also Cole et al. 1999; Patterson et al. 2001).

Finally, males and females present different types of social personas, such that girls and women express higher levels of sympathy for others than do same-age males (Baron-Cohen & Wheelwright 2004; Sy et al. 2003; Warden & MacKinnon 2003). Females are also more willing to disclose their personal feelings (Dindia & Allen 1992) and to invest in and demand greater displays of intimacy across their peer and romantic relationships (Agrawal et al. 2002; Benenson & Christakos 2003; Hartup 1996; see also Rose & Asher 2004; Shackelford et al. 2002; Terwogt 2002). Sex differences in expressed compassion, again, peak around puberty, whereby girls exaggerate their self-ratings more than do boys (Fabes & Eisenberg 1998; see also Fabes et al. 1999). Other studies show that, even as early as toddlerhood, girls engage in more comforting behaviors (Zimmermann & Stansbury 2003), and prefer more egalitarian outcomes and attainment status (e.g., homework scores) with their friends (Benenson 1993; Benenson & Schinazi 2004; see also Sprecher 2001). As they grow older, girls report a greater dissonance, such as feelings of guilt, from exclusionary behaviors as compared to boys (e.g., Horn 2003).

Compared to females, males form stricter dominance-hierarchies (Geary et al. 2003); are more competitive (Sidanius et al. 1994; 2000), more violent (Holinger 1980; Wrangham & Peterson 1996), less willing to provide comforting behaviors to friends they perceive to be fearful (Terwogt 2002); and report a normative preference for more aggressive peers (e.g., Chang 2004; Farmer et al. 2003; Xu & Zhang 2007). Boys and men are likewise more sensitive to respond to aversive stimuli with automatic and reflexive displays of observable aggression (e.g., Archer 2004; Gold et al. 1992; Knight et al. 2002; Vigil 2008). Aggressive behaviors cause other people to distance themselves from the male, which may deny the comforting behaviors of others and demonstrate the capacity to protect oneself in times of stress (Vigil 2008). Other studies suggest that behavioral displays of toughness enhance boys' popularity, whereas submissive behaviors appear to reduce this popularity (Cashdan 1998, p. 217; see also Lobel et al. 2001). Male popularity is especially enhanced and given "leadership status" when aggressive boys are also perceived as possessing honest or verifiable signals of capacity (e.g., superior athleticism; Farmer et al. 2003; see also Rodkin et al. 2000) and when boys complement their assertiveness with more *selective* displays of prosocialism (Arsenio et al. 2000; Farmer et al. 2003).

3.3. Summary

From a socio-relational perspective, sex differences in the propensity to express higher levels of capacity displays (e.g., risk-taking, inflated self-evaluations, aggressive behaviors) in males and trustworthiness displays (e.g., expressed compassion, modest self-descriptions, sadness behaviors) in females may reflect asymmetries in the social ecologies and relationship demands in which males and females evolved (Geary & Flinn 2002; Geary et al. 2003; Vigil 2007). If males' evolutionary ecologies consisted of larger social networks among closely related kin, then they may have evolved a sensitivity to relax the display of trustworthiness cues in favor of interchanging more capacity cues for attracting and maintaining a greater number of daily relationships. Likewise, if females' evolutionary ecologies consisted of more frequent interactions with more distantly related kin and non-kin, then they may have evolved a sensitivity to inhibit the display of capacity behaviors in favor of cues that reduce the perception of threat and demonstrate their overall trustworthiness. Formation of smaller social networks among women may have facilitated a feminine social style that promotes the interchange of higher levels of displayed vulnerability and investment behaviors across fewer, more intimate, more secure, yet time-consuming relationships.

From this perspective, higher rates of depressive behaviors in girls and women may stem from an *adaptive* behavioral strategy that facilitates the advertisement of trustworthiness cues. These behaviors may be particularly functional under conditions when the individual experiences diminished capacity resources, and in ways that ultimately strengthen the intimacy and hence security of one's relationships. The emergence of increased sadness behaviors in females, but not in males, occurs at the time of reproductive debut, when females are hypothesized to have been exposed to, and dependent upon, relationships with distantly related peers for their own and their offspring's well-being. This interpretation is consistent with research showing a significant relation between stress reactivity and quality of intimate relationships of adolescent girls, but not girls in middle childhood or boys of either age (Booth et al. 2008). Evolved sensitivities to exaggerate displays of vulnerability (e.g., sadness) and appeasement (e.g., expressed compassion) during this stage of development may have ultimately facilitated the maintenance of more secure and dependable relationships among fewer, more exclusive, and more reliable social affiliates, compared to the social demands faced by women at other stages in their lives, and compared to the relational demands faced by males in general.

4. Theoretical implications for variation in expressive behaviors

At the base of the current framework is the assumption that different types of relationships have varying effects on the individual's fitness (Bronfenbrenner 1979). Some types of social interactions are potentially beneficial, for instance, for reciprocating expedient and/or continuous interpersonal investment, whereas other types of social encounters are non-reciprocal and thus potentially harmful. This combination of factors is hypothesized to represent the ecological constraints and opportunities in which ancestral humans evolved, and thus the social contexts in which children currently develop. One possibility is that these ecological conditions would have coevolved

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with relationship-formation systems that are capable of regulating different types of relationships, simultaneously, in dynamic ways that enhance personal fitness. Again, from the current perspective, such modification may be possible through the selective advertisement of reciprocity potential and adjustment of expressed capacity and trustworthiness cues, as well as through ways described in the following sections.

4.1. Social spheres model

In order to understand how and why humans may be equipped with the ability to modify multiple relationships in systematic, fitness-enhancing ways, it may be best to conceptualize the composite of all the people with whom individuals interact as representing a tangible quotient or ratio of cost-benefit trade-offs. For the sake of illustration I will refer to this quotient as the individual's *social sphere*. This construct is extremely important because it represents the aggregation of all the possible social interactions, and hence the socio-relational risks and opportunities, to which individuals are exposed at any given point in their lifetime. In more concrete terms, and similar to Newcomb (e.g., Newcomb & Chou 1989), I am hypothesizing that the quantity and quality of individuals' relationships qualify these relational possibilities. Specifically, social spheres may be understood in terms of the absolute number of cooperators and competitors with whom individuals may interact, thereby representing the *size* of the social sphere, as well as the perceived trustworthiness and hence reliability of these relationships, hereafter referred to as the *relational proximity* between the individual and each sphere-member.

Because individuals' reciprocity potential is finite in terms of time and physical resources, the number of possible relationships that people can maintain at any given time is inversely associated to the relational proximity of their relationships. Again, this is because having a larger social sphere necessarily reduces the amount of investment that individuals can devote to each of their relationships, whereas having a smaller social sphere increases the ability to invest in each relationship (Geary et al. 2003; Vigil 2007). Larger and smaller social spheres should therefore be associated with increased and decreased risks of social defection, respectively, and hence with varying safety levels, as well as with unique opportunities to solicit investment from different types of relationships. Research on social interaction patterns shows that the likelihood of receiving social support from family is inversely associated with the amount of support received from peers (Newcomb & Bentler 1986). These constraints are important because they create a series of adaptive cost-benefit trade-offs between having a larger pool of potential reciprocators with a reduced likelihood that each affiliate will actually reciprocate and hence an increased risk of harm, and having a greater likelihood of receiving extensive investment, but from a smaller pool of potential reciprocators (e.g., family members).

According to the model of sex differences in social styles discussed earlier, abbreviated displays of capacity cues are theorized to help maintain larger social spheres (boys' social networks), while advertisements of trustworthiness cues are predicted to be better for maintaining smaller, more intimate social spheres (girls' social networks). In other words, there should be an adaptive benefit to advertising higher levels of capacity and trustworthiness cues across larger and smaller social contexts, respectively. A direct investigation of these relations was conducted by Benenson et al. (2002), in which boys and girls were exposed to stress and placed into either groups or dyads. Both boys and girls who were placed into the larger groups responded with increased externalizing behaviors such as assertiveness, anger, and general meanness to others. In contrast, the children that were placed into smaller groups displayed more internalizing behaviors, including self-depreciation, sadness, and expressed empathy for the feelings of others (Benenson et al. 2002; see also LaFrance et al. 2003; Leaper & Smith 2004; Vingerhoets et al. 2000). Though tentative, these findings suggest that the relative size of the social context in which individuals are embedded may be a proximate factor that stimulates the expression of capacity and trustworthiness displays.

Finally, different types of relationships (e.g., family vs. friends) should present different opportunities for the types of resources that can be interchanged. Relationships characterized by a history of cooperation, such as between family and close friendships, are the most reliable relationships and should therefore be targeted to interchange the trustworthiness component of reciprocity potential. Again, these expressions may be manifested as intimacy behaviors such as the discussion of personal problems and providing compassionate support. In contrast, other types of relationships, such as between acquaintances and strangers, are not based on a history of investment and are therefore more risky relationships. These types of relationships are supported less by the exchange of trustworthiness cues, and perhaps more by the exchange of expedient and/or discontinued capacity resources, such as material gifts and socio-political opportunities. Research on cultural attainment shows that both reliable and risky relationships are crucial for contemporary success (e.g., occupational status; Blau & Duncan 1967; Breiger 1995), and are therefore presumed to have played a similarly imperative role throughout human evolutionary history.

4.1.1. Conditional variation in expressive behaviors.

Collectively, these dynamics lend to the hypothesis that humans may possess the inherent motivation to adjust the relative size and relational proximity of their social spheres in coordination with life experiences and situational circumstances that enhance the ability to advertise reciprocity potential, as well as the associated risks of not being able to do so. Examples of these hypothesized relations are presented in Figure 2. According to Figure 2, when individuals experience conditions that increase their social status or resource accrual, they should be motivated to increase the advertisement of capacity cues such as through displays of joy, pride, and confidence. These displays may be effective for attracting less familiar and hence riskier relationships and, ultimately, *increasing* the size of the social sphere. By increasing the proportion of risky people to reliable people with whom individuals interact on a daily basis (see Fig. 2), they are able to increase their overall *opportunity* to solicit reciprocation at the cost of having less secure

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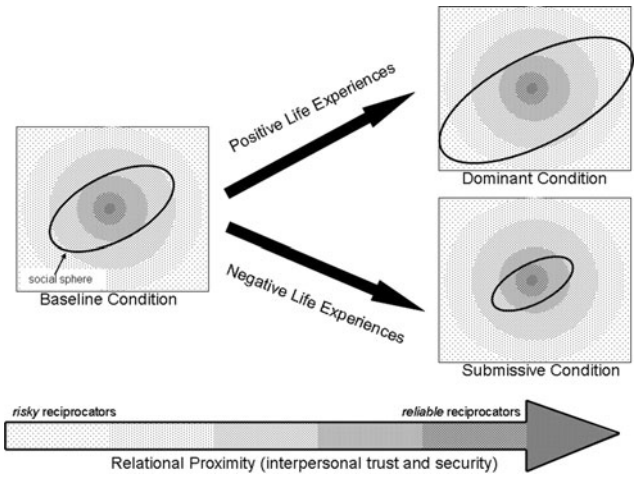


Figure 2. *Relational proximity* represents the probability of receiving reliable social support. The social spheres model predicts that individuals should respond to positive and negative life experiences by either increasing or decreasing the size of their social sphere. These modifications may be facilitated through the selective advertisement of the capacity and trustworthiness components of reciprocity potential, respectively (labeled "Dominant" and "Submissive" conditions). In response to positive life events, individuals *increase the ratio of risky to reliable affiliates* with whom they may interact in order to enhance the opportunity to reciprocate with more people. In response to negative life events, individuals *increase the ratio of reliable to risky affiliates* in order to enhance the probability of reciprocating with more reliable affiliates.

relationships and hence a lowered *probability* of actually receiving social support.

This trade-off is optimal under conditions in which the individual can endure the added risk of less reliable social support, again, following positive life events when the individual has experienced increased capacity attributes. Likewise, felt *happiness* in children and adults is associated with the perception of dominance (Montepare & Dobish 2003), broadcast sociability and willingness to help strangers (Eisenberg et al. 2003; Terwogt 2002), creativity and remote memory retrieval (e.g., in judgment tasks; Bolte et al. 2003; Isen 2000), calculated risk (see Fredrickson & Joiner 2002), and the motivation to explore novel relationships (Diener & Seligman 2002; Izard 1993). Felt happiness is also rated among the most preferred characteristics in a potential new friend (e.g., Vigil 2007). Collectively, these findings suggest positive life experiences and corresponding emotive responses may have been selected to facilitate the motivation to form potentially risky relationships, as well as the demonstrated ability to attract these types of social opportunities.

In contrast, the social spheres model predicts that when individuals experience events that decrease their social status, reduce their resource accrual, or otherwise inhibit their capacity, they should instead be motivated to rely more heavily on the behavioral advertisement of trustworthiness cues, such as through *sadness*, *worrying*, and *sympathetic* behaviors. Under these conditions, individuals may be additionally motivated to *decrease* the size of their social sphere in order to more efficiently advertise these cues and to reduce the likelihood of interacting with (e.g., attracting) less familiar and hence potentially risky affiliates (see Fig. 2). Events that decrease capacity attributes, such as experienced poverty and conditional vulnerability (e.g., during postpartum), are associated with *sadness* behaviors (e.g., Jackson & Warren 2000; Sutter et al. 1997), as well as with a greater overall threat interpretation of ambiguous stimuli (Chen et al. 2004), perceptions of subdominance, reticence, and reluctance (Montepare & Dobish 2003), self-perceived inferiority and feeling less influential (Zuroff et al. 2007), reduced aggression (Vigil et al., in press), and actual disengagement from less familiar and hence risky relationships (Caldwell et al. 2004; Keller & Nesse 2005).

Sadness behaviors increase the likelihood of receiving extensive social support from intimate affiliates such as family and close friends (e.g., Kaniasty & Norris 1995; Terwogt 2002). By consolidating their social spheres, individuals may be better able to allocate high levels of intimate investment behaviors into fewer, yet more secure, relationships. Strengthening the intimacy of these relationships may in turn increase the *reliability* of receiving high levels of investment from others under conditions when dependable social support is needed most (for related discussions, see Aureli 1997; Geary & Flinn 2002; Hagen 2003; Izard 1993; Taylor et al. 2000). Collectively, these affiliative and avoidant response patterns suggest that individuals may be equipped with domain-based algorithms that motivate them to either pursue or avoid specific types of relationships, depending on the costs and benefits of engagement (see also Andersen & Chen 2002; Bugental 2000; Kenny et al. 2001; Rudolph et al. 2005; see also Nail et al. 2000). From a socio-relational perspective, emotive behaviors evolved to mechanize these motivations, regulate the individual's relationships, and optimize the advertisement of capacity and trustworthiness cues in coordination with stochastic life experiences that affect the ability to advertise these cues.

4.1.2. Situational variation in expressive behaviors. A related prediction is that individuals will adjust the relative expressiveness of capacity and trustworthiness displays in the presence of different sphere members. This hypothesis is illustrated in Figure 3, which shows that individuals should be motivated to increase the expressiveness of capacity displays among larger group settings and less familiar affiliates, and instead produce more neutral capacity displays among smaller social settings and more reliable affiliates. Capacity displays (e.g., bragging, flashy body movements, raised voice volume) may be more observable than displays of trustworthiness (e.g., self-depreciation, modest body movements, lower voice volume), and thus more efficient for maintaining a greater number of expedient and discontinuous relationships (i.e., among acquaintances and strangers). This interpretation may help explain why people feel more compelled to display "positive" affect and to mask their sadness in the presence of strangers than when among close friends or alone, even though they feel greater genuine happiness among close affiliates (Jakobs et al. 1996; Lee & Wagner, 2002; Zaalberg et al. 2004). People also smile more in large than in small group settings, and this pattern is especially pronounced in females (see LaFrance & Hecht 2000). In contrast, males tend to increase assertive speech and overall body movements among strangers than among

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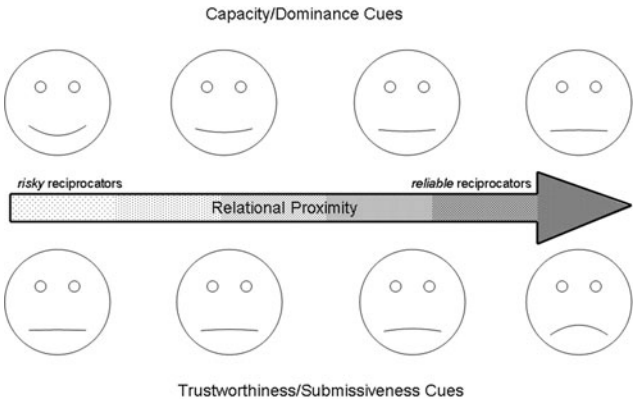


Figure 3. *Relational proximity* represents the probability of receiving reliable social support. The Social Spheres Model predicts that individuals selectively express varying intensities of capacity and trustworthiness cues, depending on the relational proximity of the audience. Individuals should increase the expressiveness of capacity displays in the presence of less reliable and hence riskier affiliates, and instead increase the expressiveness of trustworthiness displays in the presence of more reliable affiliates.

close affiliates, and more so than do females (Bente et al. 1998; Leaper & Smith 2004). Similar studies show that physical aggression and other displays of hegemonic (exaggerated) masculinity are associated with more broadcast, rather than intimate, popularity among males (Cillessen & Mayeux 2004; Levy 2005; Rodkin et al. 2000).

Figure 3 also predicts that people should demonstrate the reverse pattern for trustworthiness displays, such that individuals should increase the expressiveness of these behaviors among smaller groups (e.g., dyads) and more reliable affiliates, and much less so among risky affiliates. Likewise, people report a much greater willingness to express *sadness* behaviors, such as crying, when alone or in the company of a close friend than when in the presence of a stranger (Lombardo et al. 2001; Williams & Morris 1996; Vingerhoets et al. 2000). In one example, Buss and Kiel (2004) found that 2-year-old toddlers were more likely to selectively adjust the display of *sadness* expressions from other types of emotive behaviors (e.g., *fearful* and *angry* facial expressions) when they were engaged in mutual eye contact with their mothers, than when not. Once mutual gaze was broken, the children tended to revert back to their previous expressions (Buss & Kiel 2004; see also Shipman et al. 2003). Similar research has found that intimate affiliates such as parents and children discuss submissive emotions (e.g., sadness and fear) more extensively than dominant emotions (e.g., happiness; Lagattuta & Wellman 2002). People also use more affiliative speech in smaller, rather than larger group settings, especially among females (Leaper & Smith 2004).

In contrast, people are more likely to inhibit and conceal sadness and embarrassment behaviors (e.g., lip biting) in the presence of strangers than when alone (Costa et al. 2001; Jakobs et al. 1996). When people experience submissive emotions, they often try to avoid unfamiliar affiliations such as going out in public, and, when these encounters cannot be avoided, they tend to avert direct eye contact in ways that disallow strangers from detecting states of vulnerability (Webbink 1986). Collectively, these findings suggest that people may increase the expressiveness of submissive behaviors among trusted social partners and the types of interactions (i.e., long-term and committed relationships) that place the highest premium on these displays. At the same time, by maintaining more neutral submissiveness displays among larger group settings and less familiar people, individuals are able to conceal states of vulnerability from risky affiliates (see also the "save face" effect; Sabini et al. 2001).

4.1.3. Additional correlates of variation in expressive behaviors. *4.1.3.1. Personality correlates.* The current framework is based on the thesis that individual differences in observable characteristics are intricately associated with the motivation and opportunity to exchange the capacity and trustworthiness components of reciprocity potential across different types of relationships. Because personality styles are both observable and are usually modified in different social settings to some extent (Matthews & Deary 1998), these characteristics should, in theory, covary with systematic differences in the types of relationships (e.g., short term vs. long term) that individuals may seek to form and maintain. Early support for this hypothesis may be found in the literature on romantic relationships, which shows that individuals who self-report high ratings of *sensation-seeking* personality traits, such as disinhibition (Zuckerman et al. 1976) and extraversion (Eysenck 1976), report a greater number of sexual partners (see Simpson & Gangestad 1991). Other research suggests that high *self-monitoring*, the tendency to regulate one's self-presentation across different social contexts, is also associated with a greater number of lifetime sexual partners and with more serial relationships characterized by discontinued sexual experiences (Snyder et al. 1986).

In other words, individuals who rate high on sensation-seeking and self-monitoring personality traits may engage in a greater number of social interactions and thus maintain larger social spheres than do individuals who rate low on these traits. From the present perspective, the ease with which individuals are able to maintain larger social spheres may turn on the ability to advertise capacity cues, for instance, vis-à-vis personas that demonstrate one's willingness to engage in risky relationships (e.g., disinhibition) and ability to exchange resources across various types of relationships (e.g., high self-monitoring). Related predictions are that individuals who rate high on these personality traits should also report a higher number of non-reproductive peer relationships and rate themselves high on other types of capacity cues such as higher mood, self-confidence, assertiveness, and friendliness, among many others (e.g., see recent findings on trait-happiness; Weiss et al. 2008).

4.1.3.2. Peer relations. A similar prediction is that people will adjust self-presentations in conjunction with the relative size and intimacy levels of their social sphere. Specifically, individuals with fewer yet more intimate daily interactions should be more likely to express submissive behaviors, for instance, in the form of lower mood, higher felt pain, worrying behaviors, and expressed sympathy for others. In contrast, individuals with larger and more fluid social networks should be more likely to express dominant behaviors, such as greater joy,

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confidence, felt strength, and other capacity cues. Although several studies have found a relation between increased sadness and *lack* of adequate social support and desire for greater support (e.g., Brugha et al. 1990; Cramer et al. 1997), no study to my knowledge has examined the relation between frequency and overall number of daily interactions and variation in expressed mood.

4.1.3.3. Developmental variation. In theory, these relationships should exist for both sexes and covary with developmental changes in capacity attributes across the life span. For example, one possibility is that increased fertility (among the most fundamental capacity attributes) upon adolescence may covary with heightened sensitivity to exaggerate the expression of other types of capacity cues during this stage of development. This hypothesis is consistent with patterns of greater risk-taking behaviors, teasing behaviors, felt anger and hostility, and propensity to express physical aggression during adolescence and young adulthood, as compared to other points across the life span (Archer 2004; Birditt & Fingerman 2003; Holinger 1980; Keltner et al. 2001). Adolescents (both boys and girls) show less discriminate activation of the amygdala than other age groups, and hence more similar patterns of threat processing to adult males than to adult females (McClure et al. 2004).

Similarly, decreases in capacity attributes (e.g., fertility and physical abilities) that accompany the later stages of life may help explain why people report dramatic reductions in felt anger and aggression as they progress into older adulthood, with men experiencing sharper declines in these types of feelings than women (Mroczek & Kolarz 1998). By increasing the display of submissive behaviors in older adulthood, individuals may be optimizing the ability to advertise their reciprocity potential to others. Related predictions are that people should be motivated to form larger social spheres during adolescence and young adulthood, and to form smaller and more intimate social networks during older adulthood. In theory, many correspondences between capacity development and expressive behaviors should exist throughout the human life span.

4.1.3.4. Cultural variation. Another area in which the present framework may be applied is the study of cultural variability in expressive behaviors and the ability to detect expressed emotions. For example, several studies have found that participants from more individualistic cultures (e.g., European-Americans, African-Americans) tend to be more accurate at recognizing emotions, rate more intense reactions to emotions, and express more dominant emotions (e.g., anger and joy), compared to people from more collectivistic cultures (e.g., Asian-Americans [Bond 1993; Matsumoto 1993; Matsumoto & Ekman 1989; McLaughlin et al. 2007; Schimmack 1996; see also Elfenbein & Ambady 2003; Marsh et al. 2003]). Other research has found that Latin-Americans, a relatively collectivistic cultural group (Oyserman et al. 2002), in contrast report more *sadness* behaviors than other groups (Twenge & Nolen-Hoeksema 2002).

According to the present framework, these findings may result from variation in basic social dynamics, such as the relative size and relational proximity of the social spheres of people from individualistic versus collectivistic cultures. People from collectivistic cultures report stronger kinship ties and dependency (e.g., for decision making; Kim et al. 1994), effectively demonstrating relatively smaller and more intimate social spheres than people from other cultures. In theory, these social dynamics should covary with the associated biases to produce and recognize trustworthiness cues (e.g., sadness facial expressions, felt pain, surprise intonations in voice quality, conscientiousness), compared to people from more individualistic cultures. People from individualistic cultures are instead predicted to be more sensitive to producing and recognizing capacity cues (e.g., anger and joy facial expressions, felt pride, assertive intonations in voice quality, impulsivity). This prediction is consistent with findings that people from individualistic cultures report a greater tendency to respond to conflict with higher levels of assertion and confidence, compared to people from more collectivistic cultures (Brew et al. 2001; Mann et al. 1998; Ohbuchi et al. 1999). From the present perspective, cultural variation in expressive behaviors (e.g., mood, expressed confidence, body language, vocal intonations) may best approximate structural and relational distinctions in the social dynamics of individuals from different cultural backgrounds.

4.1.3.5. Climatic and geographical variation. From a socio-relational perspective, climatic and geographical variation in expressed mood may also be interpreted from the impact of these factors on the relative size and relational proximity of the individual's social sphere. For example, numerous cross-cultural studies have highlighted an association between living in northern latitudes and colder climates and greater reported *sadness* and *worrying* behaviors (Agumadu et al. 2004; de Graaf et al. 2005; Kovalenko et al. 2000; Okawa et al. 1996). Other research suggests that geographic isolation may also be associated with increased prevalence of mood disorders, with large nationally representative samples showing higher prevalence rates of depression among individuals living in rural versus urban neighborhoods (Probst et al. 2006; Wainwright & Surtees 2004). These differences are not always found, however, and may be associated with factors such as population density (Walters et al. 2004; Weich et al. 2003). Other research suggests that sex differences in mood and anxiety disorders tend to vary by city size, and are due to higher prevalence rates of depressive symptoms among rural men, compared to urban men (Diala & Muntaner 2003).

From the current perspective, rural dwellers and individuals living in colder climates may report higher levels of sadness behaviors because these factors create physical barriers to the ability to interact with multiple people, essentially resulting in smaller social spheres for people living under these conditions. In contrast, warmer climates and higher levels of urbanization provide greater opportunities to interact with more people, which may thereby create a bias to express higher levels of capacity displays. Higher temperature levels are generally related to greater societal *aggression* (e.g., violent acts; Bushman et al. 2005) and self-reported *happiness* (de Vliert et al. 2004; Rehdanz & Maddison 2005). According to the SRFB, contemporary sensitivities to climatic and geographic conditions may have evolved to optimize the ability to exchange capacity and trustworthiness cues with local community members, in association with the

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physical contingencies and social opportunities that diverse ecological conditions create.

4.1.3.6. Implications for the study of disease. Finally, the current framework may offer new and intriguing directions for our understanding of normative, yet seemingly paradoxical, health processes. One such process is the pattern for humans to respond to traumatic experiences with stress reactions that are broadly associated with significant health consequences and, in certain circumstances, may actually *cause* illness. Repeated activation of the Hypothalamic-Pituitary-Adrenal (HPA) system and the sympathetic nervous system (SNS) is associated with lower immune functioning, increased susceptibility to viral infection, and onset of disease-causing factors (e.g., pulmonary constriction [Cohen et al. 1998; Flinn & England 2003; Kunz-Ebrecht et al. 2003; Rotton & Dubitsky 2002; Segerstrom & Miller 2004; Uchino et al. 1996]). Findings like these have understandably caused many researchers to interpret stress responses from a pleiotropic, *disease-centered* model. From this perspective, short-term stress responses are believed to be adaptive for sensitizing the organism to prepare for action, whereas repeated stress exposure or *allostatic load* is thought to result in unintended and hence maladaptive mental and physical health consequences in humans and related species (McEwen & Seeman 1999; Sapolsky 1994). Longer-termed psychobiological and behavioral symptoms of chronic stress exposure (e.g., blunted HPA activity, low mood, fatigue, stress-related illness) are therefore believed to be the outcome of dysfunctional psychological and/or neuroendocrine regulation (Southwick et al. 2005).

An alternative approach to the disease-centered perspective of stress-induced morbidity is provided by models that highlight adaptive trade-offs of phenotypes that affect natural selection and senescence (Williams 1957), such as *disease behaviors*. For example, it is possible, though counterintuitive and certainly speculative at this time, that increased morbidity and susceptibility to illness caused by trauma exposure may be partly *functional* for regulating fundamental social dynamics, such as the size and relational proximity of the social sphere. If one considers physical health consequences and associated vulnerability in terms of expressive displays, then increased morbidity may reflect a broader behavioral strategy designed to advertise trustworthiness cues in times of adversity. From this perspective, certain illness-related outcomes of behavioral distress (e.g., felt pain suffering) may operate effectively as self-harming mechanisms designed to provide an *honest* advertisement of disability, reduced threat, and hence trustworthiness to others. In this sense, some physical illnesses may be associated with adaptive cost-benefit trade-offs in and of themselves, for example, manifesting when the social benefits of these conditions may outweigh the physical detriment that they cause.

4.2. Conclusion

Our current understanding of the natural history and present impact of variation in nonverbal behaviors is rapidly evolving. This research has drawn most heavily from the solid scaffolding provided by Charles Darwin's "Sexual Selection Theory" (1882) and, one hundred years later, by Robert Trivers's "Reciprocal Altruism Theory" (1971), as well as more recent contributions from countless researchers and theorists. My goal was to address variation in expressed emotion at the individual, situational, and group levels of analysis. My framework is similar to earlier treatments that suggest that emotions may function to modify the outcomes of social interactions (e.g., Frijda 1993; Tronick 1989), but extends these earlier models by proposing several overlapping dimensions, as well as essential cost-benefit trade-offs that are predicted to underlie specific patterns of variation.

The phenotypic expression of emotion is predicted to promote affiliative and avoidant reactions from others, in part, by advertisement of cues that signal the individual's abilities and intentions. If so, then theoretically similar emotions such as *anger* and *joy* should share a number of trait impressions (e.g., perceptions of dominance vs. submissiveness) and overlapping characteristics, including distinct neurological pathways (for support of this hypothesis, see Murphy et al. 2003; see also Adolphs & Tranel 2004). These trait impressions should covary with many forms of expressive behaviors, including variation in speech content, declarative versus inquisitive sentence usage, vocal intonations (e.g., low-pitched vs. high-pitched sounds), facial expressions (e.g., teeth-baring vs. closed-mouth expressions), eye-gaze patterns (e.g., narrow threat-stare vs. wide-eyed tear production), body-movement speed and positioning (e.g., basic hand gestures), social dispositions (e.g., independent vs. dependent personas), public policy displays (e.g., pragmatic vs. compassionate political ideologies), displays of rebellion and faith (e.g., religiosity), and so forth.

The second aim of the article was to provide an evolutionary explanation of sex differences in emotionality and to describe the social underpinnings of human masculinity and femininity. From a socio-relational perspective, these sex differences are specializations needed to communicate reciprocity potential with same-sex affiliates, and in specific social ecologies. In addition to the expression of emotion, sex differences have been found in many types of social behaviors, including morality and helping behaviors (see Eagly & Crowley 1986; Jaffee & Hyde 2000; Thoma 1986), implicit attitudes and judgments (e.g., Rudman 2004; see also Forgas 2003), intra-group biases and prejudice (Ekehammar et al. 2003), temperament and personality characteristics (e.g., Cohn 1991; Else-Quest et al. 2006; Feingold 1994), and public policy behaviors (e.g., opinions on judicial philosophy; Gault & Sabini 2000). Though many of these constructs have not been traditionally viewed in terms of expressive behaviors or advertisements in and of themselves, they can be viewed as simulations of preferred social characteristics. In this sense, a socio-relational perspective may eventually integrate emotional expression with a full range of social communication.

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Open Peer Commentary

When organization meets emotions, does the socio-relational framework fail?

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Frédéric Basso[a] and Olivier Oullier[b]

[a]*Center for Research in Economics and Management (UMR 6211), University of Rennes 1, Rennes, France; Graduate School of Business Administration (Institut de Gestion de Rennes – Institut d'Administration des Entreprises), 35708 Rennes Cedex 7, France;* [b]*Université de Provence, Aix-Marseille University & CNRS, 13331 Marseille cedex 03, France; Human Brain and Behavior Laboratory, Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, FL 33431.*

frederic.basso@univ-rennes1.fr **olivier@oullier.fr**

http://www.oullier.fr/ **http://www.neuroeconomie.fr/**

Abstract: We suggest that the framework proposed by Vigil is useful in laboratory contexts but might come up short for in vivo social interactions. Emotions result from cost-benefits trade-offs but are not solely generated at the individual level to establish emotional social spheres. In organizational contexts, emotion expression can be a constitutive part of a professional activity, and observed sex differences might vanish.

We wish to discuss Vigil's views regarding emotions in light of data collected either in a "neutral" context (i.e., lab experiments) or in a more *social* one (i.e., field research). From his target article we gathered that the exhibition (or perception) of *capacity displays* is associated with *risk-taking* tendencies (see sect. 3.3), whereas *trustworthiness displays* give rise to *altruism* (sect. 2.1.1.1). In addition, the author claims that *capacity cues* are more specific to male than to female behavior as opposed to *trustworthiness* ones (sect. 3.2.1.1). Nevertheless, both compose the *cost-benefits trade-offs* that constitute the core of the *social sphere*.

To apprehend individual *emotive behavior* from a functional and conscious perspective, we have decided to consider results from experimental economic games. In general, these protocols not only pay little attention to, but do their best to elude the role played by facial expressions and gesture in social interactions (but see Oullier & Basso 2010, for novel perspectives). In spite of this obvious reductionism, these games offer original insights on risk-taking and altruistic behaviors, therefore allowing the implementation of contexts in which interactions favor the analysis of *trade-offs* occurring in these *social spheres*.

Here, we focus on two settings from experimental economics: *The Dictator Game* (DG) and *Ultimatum Games* (UG). In both, a first player A offers a share of the amount of money he owns to a second player B. The DG is a true unilateral division of A's initial capital since what B decides regarding the money sent to him has no effect on what A can keep (Forsythe et al. 1994). The UG extends the DG to a situation where B can refuse A's offer. If he does so, both players lose their respective share (Guth et al. 1982). Player A is somewhat forced to anticipate B's emotions if he does not want to be punished. In the DG, the average share offered to B is 20% of A's capital, whereas another 20% is added in the UG (Elster 2009). The UG is therefore a true revelator of the functional role of emotions.

Interestingly, a meta-analysis of results collected in both games does not permit one to conclude that women exhibit more *trustworthiness* or less *capacity* than men (Croson & Gneezy 2009). However, men appear to have more capacity since they are less *risk-averse* than women. As such, empirical evidence seems to favor Vigil's views: "Recent findings suggest that women are more reluctant than men to engage in competitive interactions like tournaments, bargaining and auctions" (Croson & Gneezy 2009, p. 464). It is noteworthy that this claim is not verified for a certain category of women: namely, managers and entrepreneurs. For instance, it has been reported that such women's aversion to risk is of the same order as that found with men (Masters & Meier 1988). They are therefore less *risk-averse* than other women.

Two hypotheses can be made to interpret these observations. First, low risk aversion could be considered to be one of these women's intrinsic features that perhaps led them to become managers or entrepreneurs – a kind of *autoselection*. Second, it is possible that the particular training they underwent to prepare for these specific careers modified their aversion to risk (Johnson & Powell 1994). A recent study shows that differences could also emerge between managers and entrepreneurs in their attitude towards risk. Nevertheless, training as well as social and cultural norms are to be considered key factors that can minimize risk aversion (Lawrence et al. 2008). This second interpretation has major consequences for Vigil, for, as Croson and Gneezy (2009, p. 454) observe: "This result [i.e., modified risk-aversion] could also be an adaptive behavior to the requirements of the job."

The importance of one's professional activity in his or her relation to risk entices us into considering the role of organizations in our emotions. Thus, it appears difficult not to include organizations in the *socio-relational framework*. Economically, they account for 80% of America's economic activity (Simon 1996). Socially, they are the product of social interactions that are shaped by multiple kinds of emotions (Simon 1967). As suggested by the aforementioned study, emotions are not only to be considered at the level of our social *individual* sphere but also as a by-product of the organization, therefore leading to the concept of *emotional work* (Hochschild 1979).

Emotions in the *emotional work* exist, as pointed by Vigil, at the social and behavioral levels (*face-to-face* or *voice-to-voice*) and preserve their conscious and functional features. However, in that context, they somewhat lose their purely individual dimension. The *cost-benefit trade-off* is implemented to extend the social sphere of the organization while being put in emotional conformity with its expectations (Hochschild 1983; Rafaeli & Sutton 1987) or to influence of the emotions of others (Sutton & Rafaeli 1988) as suggested in quadrant II (*controlled and emotional* processes) of the typology provided by Camerer et al. (2005).

In summary, the *organizational context* brings the behavior and the individuals that constitute the organization much closer. Indeed, as we saw that women's professional activity can make them exhibit risk aversion similar to men's, it should also be noted that men, as members of an organization, can be constrained to adopt altruistic behaviors to the level generally exhibited by women (Simon 1996).

All in all, Vigil's conclusions on *social status* (sect. 4.1.1) might need to be put in perspective by stressing that "the imaginary presence of organization" (a kind of *panopticon*) influences the emotions of its members, although there exists a debate as to whether these prescribed emotions would not be basically inspired (or prescribed) by men (Mumby & Putnam 1992).

The role of emotions in adaptations for exploitation

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David M. Buss

Department of Psychology, University of Texas, Austin, TX 78712.

dbuss@psy.utexas.edu **www.davidbuss.com**

http://homepage.psy.utexas.edu/homepage/Group/BussLAB/

Abstract: Emotion expression serves functions in exploitative resource-acquisition strategies that may not include relationship reciprocity. These include rendering victims more exploitable and signaling one's status as non-exploitable. A comprehensive theory of emotion expressions must explain their role in adaptations for exploitation, as well as evolved defenses against those pursuing a strategy of exploitation.

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Emotion expression surely must be central to regulating social relationships, as Vigil contends. For internal psychological functions such as ratcheting up attention to strategic interference (Buss 1989) or recalibrating internal mechanisms (Tooby & Cosmides 2008), overt expression of internal emotional states would be superfluous, although of course these ultimately often contribute to the solution of social adaptive problems. Vigil also makes a compelling case for the role of emotions in signaling reciprocity potential. I propose that emotion expressions serve other functions as well, and I highlight one suite that has been relatively neglected by emotion theorists – their role in adaptations for exploitation.

Buss and Duntley (2008) argue that humans have evolved three fundamental strategies for acquiring reproductively relevant resources: (1) individual resource acquisition strategies (e.g., solo hunting or gathering), (2) cooperative resource-acquisition strategies (e.g., forming reciprocal and coalitional alliances), and (3) exploitative resource-acquisition strategies (e.g., expropriating the resources of others through deception, theft, coercion, terror, force, or murder). Although cooperative strategies have enjoyed a large volume of theoretical and research attention, exploitative strategies have been relatively ignored, with some notable exceptions (e.g., Buss & Duntley 2008; Jones 2007; Zuk & Kolluru 1998).

Without diminishing the role of emotion expression in strategies of reciprocity, I suggest that emotion expressions play a key role in strategies of exploitation and anti-exploitation defenses. Ominous expressions of *anger*, for example, could signal a perceived violation of reciprocity in one context, but signal a threat to a victim to cede resources immediately and non-reciprocally as a strategy of exploitation. Women may express an emotion of *sexual desire* to deepen a committed relationship in one context, or to expropriate a man's resources non-reciprocally through a "bait-and-switch" strategy in another context (Buss 2003).

Emotion expressions also function as anti-exploitability defenses. Displays of *anger* or *masculine prowess* may signal reciprocal resource capacity, but may also convey to would-be exploiters that one is a poor choice as a potential victim of exploitation. Expressions of *jealousy*, to take another example, may signal to romantic partners a lack of exploitability as a potential cuckold.

The intentional suppression of emotion expression, too, may figure centrally in anti-exploitability defenses. The suppression of subjectively experienced jealousy to one's intimate partner, for example, may function to conceal an exploitable mate-value discrepancy that otherwise might be perceived by a romantic partner (Buss 2000). The suppression of fear in the presence of coalitional partners may function not merely to signal reciprocity capacity, but also to activate exploitability adaptations in coalition partners in order to better expropriate out-group resources. Even displays of kindness and sympathy, rather than signaling reciprocity capacity, may function in some circumstances to deactivate the evolved anti-exploitability defenses in others.

A comprehensive theory of emotion expressions must explain their role in the successful enactment of adaptations for exploitation, as well as their functions in signaling non-vulnerability to those pursuing exploitative resource acquisition strategies.

Biofeedback mechanisms between shapeable endogen structures and contingent social complexes: The nature of determination for developmental paths

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Sari Goldstein Ferber

Department of Developmental Neuroscience, New York Psychiatric Institute, New York, NY 10032; Department of Psychiatry, Columbia Medical School, New York, NY 10032; and Department of Neonatology, Wolfson Medical Center, Sackler School of Medicine, Tel Aviv University, Tel Aviv, Israel.
sg2694@columbia.edu

Abstract: Biofeedback mechanisms (a) between individuals, (b) between the individual and the society structures which shape individual cognitions, and (c) within the individual genetic biochemical circulation, may explain the diversity of trustworthiness potential and the option of mutual trust for every individual in any given society.

Causal models predict different human inferences than taxonomic models do (Shafto et al. 2008); biofeedback perspectives, therefore, may correct the discrepancy between these cognitive capacities. Studies with humans on neuropeptides such as vasopressin and oxytocine suggest that variation in the genes encoding their receptors may contribute to variation in human social behavior by altering brain function (Donaldson & Young 2008). Likewise, the shapeable human social cognitions and the contingent social structures may imply a complex regulatory system of power; for example, submissive female sexuality can lead to dominance in gene reproductivity. Regulatory theories (Als 1999; Hofer 1994; Mareschal et al. 2007) in turn may suggest the need to measure the level of power within a given relationship in order to judge dominance and submissiveness and the complex interrelations between the two constructs.

Vigil claims that submissive behaviors express trustworthiness. This creates a one-way hierarchy of trust, in which the dominant can trust the submissive. As challenge and competition are considered part of give-and-take relationship, submissiveness may end in raising power challenges in the other and result in difficulties for trusting the submissive. Regulatory theories consider the concept of mutual trust and individual preferences.

Vigil refers to submissiveness in the adversity of the social framework through submissiveness as trustworthiness. The vulnerable may not receive social support in all human cultures or in other species. The assumption of welfare and charity found in Western society is problematic and may be replaced by the question whether the expression of vulnerability as well as the benefits of vulnerability, are instinctual. The examination of natural expressions of vulnerability compared with the cultural expression of it may suggest a complex of species-attributed behaviors interacting with socially and/or culturally attributed effects.

Sometimes individuals choose losing strategies or perpetuate their own victim state. Following this rationale, we would have to interpret (1) the attraction to abusive relationships as rewarding at some other levels; (2) the ability to discriminate what behavior is rewarding; and (3) what is the level of the observed reward. Alternatively, we can claim that attachment is a reward and that love has complex facets of frustration and reward. The examination of biofeedback mechanisms of alleles, genes, individuals, societies, or ecosystems, as suggested by theories of co-regulation, may show the complex of gender differences and that men with the similar biofeedback mechanisms may have feminine attributes, and vice versa. We ought to be cautious when we refer to individuals as entities that cannot be divided or summed, without considering biofeedback mechanisms of the vital human brain (Ferber 2008; 2009; Ferber & Makhoul 2004; 2008). Critical ages (Duffy et al. 2003) during early development and through the entire life span provide the window of opportunities and the possibility for determining which developmental paths may be considered along the course of life until a critical age for a certain capacity ends.

Vigil assumes a coherent and discrete self versus other, which are often hard to delineate – for example, in the case of pregnancy. There are also other states in early infancy without distinct discrimination between the self and other, along with the complex emergence of relationships and interactive behaviors between the infant and his/her family members (Ferber et al. 2007). Vigil assumes that there are only two vectors when facing the other – toward and away – and neglects the possibility of exploratory and curious observation and learning even in relation to a threat, or the cycle of retreating, reinforcing, and returning to marked experiences (Als 1999). The adoption of abusive behaviors that prove unprofitable even to the abuser, such as abusive parenting, is a situation where desire and abjection are more than normative regulations, and become a personality.

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Vigil mentions that there are neural-endocrinal correlates to trust. Oxytocin is the prime inducer of bonding between mother and infant; this means that we can understand such hormones and trusting behavior as organically linked, that is, as being the cause and effect of each other. Thus, it cannot be said that trustworthiness is merely an observed feature. It is an acquired relationship. The more *trustworthy* we are, the more *trusting* the other becomes toward us. Oxytocin causes mothers to bond with their child and not other people's children, and also explains the preference of monogamous species for one mating partner over multiple mating partners. This suggests that oxytocin-enhanced individuals will not only be more prone to bonding, but also more prone to reject those who are not bonded with. A mother's bond with her child means she will defend him or her against any threat or aggressor, making trusting and bonding behaviors trusted and bonded, but threatening and defensive against all others. Therefore, the coregulation between vasopressin and oxytocin seems more adequate for explaining trustworthiness.

Vigil describes the current state of affairs in a patriarchal society and grounds it as historically consistent. Still, Vigil provides us with the possibility of an alternative: "In foraging societies with *bride service*, the prospective husband is expected to reside with his bride's family to provide service to them before the marriage and often for some time afterwards" (sect. 3.1, para. 2, emphasis in target article). In this idea, Vigil pays attention to the contingent structure of society as a primary regulator of personality creation.

Vigil describes the correlation of hypothalamic pituitary adrenal (HPA) axis activation and the theory of sexually dimorphic competition domains. It could be argued that the activation of the HPA axis is not proof enough of a natural tendency of the two sexes to compete within or between groups, and that social construction leads to cognitive schemes that define stressful contexts and these activate the HPA axis accordingly.

The neural-endocrinal correlates are not proof of universality or biological origin, since they may be mediated by modular, shapeable cognitions as stated above. Therefore, contingency between shapeable cognitive structures and contingent social complex structures may need to be considered as interacting with genetic, environmental, and reciprocal complexes. The concept of female submissiveness versus male aggressiveness opens a window of opportunities for understanding developmental trajectories which one of them is the development of mutual trust.

Beyond our origin: Adding social context to an explanation of sex differences in emotion expression

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Agneta H. Fischer

Department of Social Psychology, University of Amsterdam, 1018 WB Amsterdam, The Netherlands.

a.h.fischer@uva.nl

http://home.medewerker.uva.nl/a.h.fischer/

Abstract: Vigil's socio-relational framework of sex differences in emotional expressiveness emphasizes general sex differences in emotional responding, but largely ignores the social context in which emotions are expressed. There is much empirical evidence showing that sex differences in emotion displays are flexible and a function of specific social roles and demands, rather than a reflection of evolutionary-based social adjustments.

The socio-relational framework presented by Vigil is a new challenge in understanding sex differences in emotion expression. Vigil's model accounts for the fact that there are general sex differences in specific emotional expressiveness: women cry more, laugh more, or show more depressive symptoms, whereas men display more contempt or antagonistic anger. These sex differences would reflect the extent to which men and women aim to maintain different social spheres and are motivated to display different social cues.

Although I appreciate the argument that social sphere plays an important role in this explanatory framework, the model lacks flexibility and sensitivity to the immediate social context (see also Deaux & Major 1987; Eagly & Wood 1999). Men and women may indeed differ in the ways in which they emotionally adapt in order to enhance their social fitness. However, social fitness should not be exclusively described in evolutionary terms, but should be defined as being able to adjust to one's current social environment, and to form and maintain social relationships in order to achieve one's life goals. These goals may be different for men and women, partly because of their different biological heritage, but also because of their current social roles (e.g., Diekman & Eagly 2008; Eagly 1997; Eagly & Wood 1999). In many societies, these social roles still co-occur with the different biological capacities of men and women; however, it is also clear that in an increasing number of societies men and women have more egalitarian social roles, and therefore meet similar social demands and social restraints.

Social demands and restraints that individuals are facing can be described in terms of both long-term and short-term social-relational goals in a specific situation. These can be roughly distinguished along similar lines as in Vigil's model; namely, approach and avoidance, or to promote relationships (either intimate or more formal) or to exclude oneself from relationships (running away, avoiding, excluding others). We have suggested that emotions have social functions (Fischer & Manstead 2008) that are derived from these social-relational goals. In other words, discrete emotions may serve either affiliation or distancing goals. A goal can be reached through different emotion expressions, however, depending on the social context and one's relational history with a specific person. For example, in a dispute with one's partner about a broken promise, the most important goal is to change the other's behavior. This goal can be reached via submissive behavior (disappointment, crying), but also via antagonistic behavior (direct anger, contempt). On the basis of Vigil's framework, we would predict that in an intimate context, women show submissiveness in order to maintain their intimate social sphere, whereas men would be aggressive in order to secure a larger social network. There is evidence, however, that sex differences in emotional expressions diverge from this general pattern, depending on specific social contexts.

First of all, results from meta-analyses have demonstrated that women show more aggressive behavior in intimate relations than do men (e.g., Archer 2004), but more importantly for the present argument, the type of anger expression varies with the type of social role. Women in egalitarian relations report more direct, or antagonistic anger compared to women in traditional relations (Fischer & Evers, under review); moreover, it was shown that women in traditional societies report less antagonistic anger in intimate settings than do women in societies with more egalitarian roles (Fischer et al. 2004). In other words, women's anger expressions seem to depend on the direct social demands that they are facing. This is supported by experimental evidence suggesting that women's anger can be predicted by the expected negative consequences of their overt anger (Evers et al. 2005).

Another example of the context specificity of sex differences in emotion expressions is the case of smiling. It is true that women generally tend to smile more than men, but results from a meta-analysis suggest that they do so especially in situations where they are expected to smile more; for example, in situations in which they are observed or evaluated (LaFrance & Hecht 2000; LaFrance et al. 2003). Sex differences in smiling therefore seem partly based on gender-specific display rules (see also Stoppard

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& Gruchy 1993). This is also evident from the fact that in social contexts with an explicit affiliation goal – for example, in caretaker roles – the sex difference in smiling decreases. This supports the general argument that social goals and one's social role in an interaction determine which emotional behaviors are functional to meet social demands.

A second critical issue with respect to Vigil's explanatory framework relates to the suggestion that making dispositional inferences in terms of capacity and trustworthiness cues is merely based on the characteristics of the display. It is likely, however, that such inferences are also context dependent. Smiling, for example, can be seen as signal of affiliation, appeasement, dominance, or negative self-conscious emotions, depending on the context (e.g., LaFrance & Hecht 2000; Shields 2002). The same applies to other – less ambiguous – emotional displays, such as crying. Crying can be interpreted as a sign of dispositional powerlessness (someone who is emotional), but also as a sign of temporary powerlessness (someone who is very sad), which may lead to quite different reactions. Perceivers may thus interpret emotional displays in different ways, not only depending on the actual dynamics of the display, but also on the construal of the perceiver, who may take into account the social role and identity of the displayer, and the social context.

We may thus wonder what we actually infer from emotional displays and why. There is as much evidence that we infer individual dispositions, such as capacity and trustworthiness, as social motives (Fridlund 1994), status characteristics (Tiedens 2001), or emotivational states (Roseman et al. 1994). Moreover, why would those inferences be context independent? Given that emotions are elicited in order to help an individual cope with problems in his or her environment, expressive displays are directly intended to change our social relations. This implies that we would infer information not only about the other person, but also about our relationship with this other person. In other words, we do not only infer from an angry face that someone has resources, but also that this person is more powerful and ready to retaliate.

Separating production from perception: Perceiver-based explanations for sex differences in emotion

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Jennifer M. B. Fugate,[a] Harold Gouzoules,[b] and Lisa Feldman Barrett [a,c]

[a]*Department of Psychology, Boston College, Chestnut Hill, MA 02467;*
[b]*Department of Psychology, Emory University, Atlanta, GA 3032;*
[c]*Massachusetts General Hospital – East, Charlestown, MA 02129.*
fugatej@bc.edu psyhg@emory.edu barretli@bc.edu
http://www2.bc.edu/~barretli/
http://www.psychology.emory.edu/nab/gouzoules/index.html

Abstract: In this commentary, we review evidence that *production-based* (perceiver-independent) measures reveal few consistent sex differences in emotion. Further, sex differences in *perceiver-based* measures can be attributed to retrospective or dispositional biases. We end by discussing an alternative view that women might appear to be more emotional because they are more facile with emotion language.

In his target article, Vigil suggests that sex differences in emotion are an adaptation to a presumed social structure exhibited by early hominoids, in which females migrated from their natal group and males tended to stay in their natal groups. As evidence for extant sex differences, Vigil reviews literature showing that women are superior to men at perceiving emotion in others, and then uses such evidence as the basis for inferring that women also produce more emotion than do men. In this commentary, we first discuss evidence that *production-based* (perceiver-independent) measures of emotion reveal few consistent sex differences. Next, we review evidence that *perceiver-based* measures, which do suggest women are more emotional, evoke retrospective biases that highlight gender stereotypes, or dispositional biases that attribute emotional responses to a women's nature. We end by discussing an alternative view that women might appear to be more emotional because they are more facile with emotion language.

Perceiver-independent measurements provide very little consistent evidence that women are "more emotional" than men (with the exception that women do cry more often). For example, some facial electromyographic (EMG) studies show sex differences in facial muscle activity in response to emotional stimuli (reviewed in the target article), but many do not (Lundqvist 1995, experiment 2; Lundqvist & Dimberg 1995; Kelley et al. 2005; Sloan et al. 2002). Even among papers that report sex differences, explanations based on orienting responses (Lang et al. 1993) or facial imitation (Dimberg & Lundquist 1990) cannot be ruled out. There is also inconsistent evidence for sex differences in smiling: some studies show that women smile more than men (LaFrance et al. 2003), but in others women smile less (Ansfield 2007). Similarly, there is no evidence for sex differences in psychophysiological responding to emotional stimuli (Kelley et al. 2005), nor in the acoustics of emotional vocalizations (Viscovich et al. 2003). Likewise, a recent meta-analysis of imagining studies found no major sex differences in how the brain responds to emotional stimuli (although males tend to exhibit more lateralized activation compared to females) (Wager et al. 2003).

Results from perceiver-based measurements of emotion generally tell a different story. Women, compared to men, report that they are more emotionally expressive (Barrett et al. 1998; Kring & Gordon 1998). Women also report experiencing more intense emotions than do men (Allen & Haccoun 1976; Allen & Hamsher 1974; Balswick & Avertt 1977; Larsen & Diener 1987), and perceivers typically agree (Kring & Gordon 1998). However, these sex differences are observed primarily when self-report measures draw upon memory for prior emotional experiences (Barrett et al. 1998; Robinson & Clore 2002b; Robinson et al. 1998). When men and women report their momentary emotional experiences in everyday life using experience-sampling procedures, they appear equally emotional (Barrett et al. 1998). Thus, one reason for perceiver-based sex differences is that women are simply better at recalling the information needed on global or dispositional self-report measures of emotional experience. Consistent with this suggestion, women also have more sophisticated emotion concepts that can serve as retrieval cues (Barrett et al. 2000; Seidlitz & Diener 1998). In addition, women recall emotional memories more quickly and frequently (Davis 1999), intensely (Seidlitz & Diener 1998), and ruminate more on negative events compared to men (Nolen-Hoeksema et al. 1994; Wood et al. 1990).

A second reason that women appear more emotional in perceiver-based measurements is that memory for emotional events is infused with gender stereotypes (Grossman & Wood 1993; Robinson & Clore 2002b; Robinson et al. 1998). Specifically, Robinson et al. (1998) showed that gender stereotypes are employed as a heuristic when people lack easy access to the target and situation-specific information (such as perceiving emotion in another person). Robinson and Clore (2002a, Study 3) showed that women reported more intense emotion, and men less intense emotion, when participants were not concurrently experiencing emotion but gender-based beliefs about emotion were primed. Thus, people might believe women are the more emotional sex because they are engaging in retrospective biases that highlight gender stereotypes.

Recent work within our laboratory highlights a third reason that perceivers experience women as more emotional: sex differences in emotionality might stem not from what men and women actually do, but from the explanations that perceivers give for those behaviors. Specially, Barrett and Bliss-Moreau (under review) found evidence that people are more likely to assign a dispositional

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cause to female displays of emotion, whereas a situational cause is more frequently assigned to male displays of emotion. Thus, people might believe women are the more emotional sex because they treat women's emotional behavior as evidence that women have an emotional nature, whereas men's emotional behavior is interpreted as evidence that the situation warrants such behavior.

Lastly, women, compared to men, might also report more emotion because they are more likely to conceptualize basic affective changes as emotional. This might be the result of women having a broader and more facile emotion vocabulary than do men. Consistent with this suggestion, parents tend to discuss emotions differently with their daughters and sons. Mothers elaborate about emotion more with their daughters than with their sons, and place emotions in a more interpersonal context with their daughters (Fivush et al. 2003). Mothers also use more emotion labels during conversations with their preschooler-aged daughters than with sons. Women consistently use more emotion words when describing their own and others' reactions to interpersonal conflicts (Barrett et al. 2000). Simply stated, then, more facile emotion language to which females are exposed might provide an *internal context* that shapes emotion perception.

In fact, a recent review (Barrett et al. 2007) summarized a number of different lines of evidence that support the idea that language is a key component in the conceptualization of emotion. Language might not only help determine the emotion categories people acquire but also how variable instances of core affect become conceptualized as a discrete emotion. More precisely, conceptual knowledge that is supported by language might explain why emotions are perceived as discrete entities even when the majority of production-based measures (including peripheral nervous systems responses, facial EMG, and neuroimaging) do not robustly and unambiguously differentiate among emotions (for a review, see Barrett 2006b; Barrett et al. 2007; Wager et al. 2008). As a result, we suggest that conceptual knowledge is a powerful tool that not only might explain sex differences in emotion, but also might shed light on the very nature of emotion (for further discussion, see Barrett 2006a; 2006b).

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Sex differences in emotion expression: Developmental, epigenetic, and cultural factors

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Carroll E. Izard, Kristy J. Finlon, and Stacy R. Grossman

Psychology Department, University of Delaware, Newark, DE 19716.

izard@udel.edu kfinlon@psych.udel.edu

sgrossman@psych. udel.edu

http://www.psych.udel.edu/people/faculty/izard.asp

http://www.psych.udel.edu/people/StacyGrossman.asp

Abstract: Vigil's socio-relational framework of sex differences in emotion-expressive behavior has a number of interesting aspects, especially the principal concepts of reciprocity potential and perceived attractiveness and trustworthiness. These are attractive and potentially heuristic ideas. However, some of his arguments and claims are not well grounded in research on early development. Three- to five-year-old children did not show the sex differences in emotion-expressive behavior discussed in the target article. Our data suggest that Vigil may have underestimated the roles of epigenetic and cultural factors in shaping emotion-expressive behavior.

We found much to admire in Vigil's target article. The novel constructs that he introduced to explain sex differences in emotion expression seem likely to become topics for further research, particularly among social psychologists. We also found some points that seemed underdeveloped or misleading.

1. Functions of emotion expression. In considering the functions of emotion-expressive behavior, Vigil focused on a rather narrow, though significant, area. He proposed that emotion expressions evolved to promote attraction and aversion in different types of relationships. He then operationally defined emotions as expressive behaviors – a highly restrictive view of emotions and their various properties. Though we see expression as an important aspect of emotion, it is but one of its components. Furthermore, expressions can and do occur without a matching experiential or feeling component, and the latter is widely considered as the motivational aspect of emotion (LeDoux, in press). In responding to a survey on the definition, functions, activation, and regulation of emotion, 35 distinguished emotion scientists identified social communication as one of six functions of emotion (Izard 2008).

2. First-order or second-order emotions. Vigil's allusion to socio-relational expressive behavior as reflecting basic or first-order emotions could prove misleading. The expressions that he describes as conveying reciprocity potential and trustworthiness are clearly higher-order emotions or emotion schemas that include complex cognitive content (Izard 2009). The latter undoubtedly reflects the cultural context of the individuals engaged in exchanging expressive-behavior signals. In the target article, Vigil shows little concern for the roles of cultural and epigenetic factors in shaping emotion-expressive behavior.

3. Epigenetic, cultural, and personality factors influence emotion expression. Memes are one of several epigenetic mechanisms that may influence the development and transmission of expressive behavior. Natural selection can act on "replicant" units (memes) that consist of cognition and action patterns. Experts on evolution hypothesize that memes emerged to serve unique adaptive functions in social interactions that are transmitted through imitative learning (Dawkins 1976/1989). Even newborns can imitate simple facial behavior (Meltzoff & Moore 1994), and they display identifiable discrete emotion expressions later in infancy (Izard et al. 1995). In the preschool years, make-believe play further enhances children's imitative skills. Clearly, both ontogenetic development and the evolutionary processes in phylogeny play significant roles in emotion expressive behavior (Izard 2009; Noble 2006).

People express emotions for reasons other than promoting interpersonal attraction and aversion, and emotion responding is always influenced by temperament/personality. One can express interest and engagement in a wide variety of nonsocial events or situations (Izard 2007; Silvia 2006). A person may become frustrated or angry when her computer malfunctions, frightened by a strange noise after a storm causes a power failure, and disgusted by foul tastes or odors. The same is true for experiencing and expressing other emotions (Izard 1991).

4. Sex differences in emotion experiences and expressions. Vigil maintains that females are better at detecting and identifying emotions in the expressions of others. Though research results on this issue consistently favor females, the size of the difference is typically quite small (McClure 2000). Moreover, Vigil claims that females are more expressive than males. There is little, if any, evidence to show that these differences are determined more by evolution than by culture and socialization. On the contrary, findings based on large data-sets relating to 3- to 5-year-old children typically show age differences but not sex differences in emotion knowledge – the understanding of the expressions, feelings, and functions of emotions (Finlon et al. 2009). We have found no evidence that girls are more expressive than boys. Our data show no consistent sex differences in emotion expressions during unstructured playtime (as indexed by independent observers' coding of facial cues, vocal cues, and body posture with our Emotion Behavior Coding System).

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In the one data set where we found sex differences, boys showed more expressiveness than girls, especially more happy expressions, but this difference was not consistent across cohorts.

Our data do support Vigil's claim that anger and joy should share trait impressions and overlapping characteristics. In 3- to 5-year-old children, during unstructured playtime, we found both increased anger and increased joy expression related to more positive interactions with peers and teachers and less solitary behaviors. We also found that increased sadness and increased anger were related to more negative interactions with peers and teachers. Contrary to Vigil's claims, there were no sex differences in these emotion expression-behavior relations.

The findings from our data sets are from low-socioeconomic status (SES), urban, minority populations. We suspect that most of the data reviewed in the target article came from middle-class Caucasian participants. Our data from children in low-income families help account for some significant differences related to ethnicity (Krauthamer-Ewing 2009), but not those determined primarily by evolutionary processes.

Vigil noted that Latino Americans, as a collectivistic culture, report more sadness-related behaviors than those from individualistic cultures. This finding is also contrary to what we have observed. In 3- to 5-year-old Hispanic and African American children, we found no differences in sadness expressions in the classroom, and African American mothers in our samples scored higher than Hispanic mothers on a depression inventory (although this finding was likely influenced by other demographic factors; Krauthamer-Ewing 2009).

5. Conclusion. In sum, we think that our finding of no consistent emotion-expression sex differences in several cohorts of Black and Hispanic 3- to 5-year-old children raises serious questions relating to Vigil's theory. In particular, our data suggest that Vigil may have gone too far in discounting familial (e.g., parental socialization of emotions), other social, and cultural factors in making an unjustifiably strong claim that evolution is the primary determinant of sex differences in the expression of emotions. Though we disagree with Vigil on this particular issue, we have long supported theories that view evolutionary processes as critical to understanding emotions and emotion processes (Izard 2009).

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Emotional expression of capacity and trustworthiness in humor and in social dilemmas

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Norman P. Li[a,b] and Daniel Balliet[a]

[a]*School of Social Sciences, Singapore Management University, Singapore 178904, Singapore;* [b]*Department of Psychology, University of Texas at Austin, Austin, TX 78712.*

normanli@smu.edu.sg **dballiet@smu.edu.sg**

http://www.normli.com

http://www.socsc.smu.edu.sg/faculty/social_sciences/dballiet.asp

Abstract: Humor and social dilemmas are two disparate areas that have been linked to emotions. However, they tend to have been studied apart from considerations of emotion and emotional expression. We provide an overview of how such areas might be illuminated by Vigil's socio-relational framework, and how capacity and trustworthiness are communicated in humor and social dilemmas.

Vigil's socio-relational framework broadly unifies research on emotion, proposing that emotional expression serves the function of communicating reciprocity potential along the dimensions of capacity and trustworthiness. We briefly consider how two disparate areas are tied into emotional expression and can be fruitfully viewed under the socio-relational framework.

Although not traditionally considered as a primary emotion or emotional display, per se, humor nevertheless has been associated with emotional intelligence (e.g., Yip & Martin 2006) and relationship formation and regulation (e.g., Shiota et al. 2004). Recently, Li et al. (2009) found experimental evidence that people initiate humor to indicate interest in romantic relationships with desirable others to whom they are attracted. Indeed, when people initiate humor as opposed to non-humorous conversation, their audience is more likely to perceive that the initiators are interested in a potential relationship, and the audience laughs and responds more positively if they reciprocate the positive evaluation and interest. In such social interactions, humor may be a process through which high self-capacity and high self-trustworthiness emotions are communicated and confirmation emotions are elicited.

When individuals assess themselves and each other to be high in both capacity and trustworthiness, reciprocity potential is particularly strong; hence, the individuals may be especially motivated to form relationships with each other. However, an important aspect of Vigil's model is that it highlights that people also need to communicate intra- and extra-appraisals where capacity and trustworthiness are not high. In this regard, specific types of humor may serve as effective mediums through which specific emotions are conveyed and feedback emotions are solicited. For instance, self-deprecating humor may be initiated to convey a state of high trustworthiness but low self-capacity, whereas aggressive put-down humor may convey high capacity but low trustworthiness. Similarly, perverse or sarcastic humor may suggest low self-capacity and low self-trustworthiness. In each case, to the extent that an audience agrees with the implied self-appraisal, they should react positively to the humor to indicate their agreement.

Humor may be an especially useful communication platform because it allows individuals to incrementally indicate their interest toward potential and existing relationships (Li et al., 2009). Similarly, humor may allow for less committed self- and other-appraisals of reciprocity potential. For example, when situations are new and somewhat ambiguous, one's own capacity and trustworthiness, as well as those of others, may not be clear. By using humor, individuals may be able to indicate the general direction of their appraisals and seek verification before committing to stronger appraisals. Thus, under the socio-relational framework, individuals who are adept at using and recognizing humor may be emotionally intelligent in that they are more effective at communicating and eliciting the appropriate emotional signals to form and regulate social interactions to their advantage.

There are, of course, plenty of situations where there is nothing to laugh about, including when relationships are in conflict. While traditionally considered to be in the domain of judgment and decision-making, social dilemmas may be intimately connected to dynamics of emotion. For instance, research on communication in social dilemmas has found that nonverbal communication between participants, including touch, oblique eye gaze, sight of the other, and just the sound of one's voice, can increase cooperation in social dilemmas (Balliet, in press; Kurzban 2001). However, no research has explicitly addressed how emotions may underlie the coordination of behaviors in social dilemmas. By looking to the socio-relational framework, it becomes clearer that emotions may be an integral part of communication in social dilemmas.

To illustrate, the framework predicts that individuals will respond to signals of high capacity and low trustworthiness with terror, fear, and/or aversion. Consistent with this, recent research on social dilemmas has found that people are less likely to contribute to a public good and more inclined to exit

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the social dilemma when an individual with a relatively higher endowment, and therefore, capacity to contribute to a public good, expresses anger (Wubben et al. 2008). Furthermore, people report lower expectations of contributions from an angry group member, compared to a guilty group member, thereby supporting the idea that angry individuals are perceived as less trustworthy in social dilemmas. These findings, which represent one of the few published studies on communicated emotions in social dilemmas, appear to fit well in a socio-relational framework and demonstrate that emotional expression can directly impact the outcomes of social dilemmas.

The socio-relational model can also generate hypotheses to guide social dilemma research on the role of emotional expression. For example, although individuals often possess cooperative intentions, certain circumstances (termed *negative noise*) may block individuals from acting on these intentions (e.g., a computer fails, thereby preventing one of the coauthors of this article from finishing his part of the collaboration). The individual still self-perceives trustworthiness, but would display sadness, grief, or shame in response to his or her own defection if the negative noise reduces his or her self-perceived state of capacity. In fact, negative noise in dilemmas tends to result in lower cooperation, unless an individual is given an opportunity to communicate (and presumably express appropriate emotions), in which case subsequent cooperation prevails (Tazelaar et al. 2004). The socio-relational framework predicts that by expressing sadness or grief, a defector can mitigate the defection's negative effect on the defector's trustworthiness as perceived by the partner. Consequently, if the defector's partner perceives greater trust, this could result in feelings and displays of sympathy toward the defector, which in turn are related to forgiveness and the ability to sustain a cooperative relationship. Therefore, the socio-relational model can be applied to predict how emotional expression coordinates cooperation between partners in social dilemmas.

We have briefly identified two disparate research domains that may both be intimately connected to emotion displays, and therefore, could benefit from an organized study of emotion expression and the communication of capacity and trustworthiness. Although we did not consider sex differences in this commentary, sex differences tend to be ubiquitous in these and other areas, and their consideration can only increase the utility of the socio-relational framework.

On the detection of emotional facial expressions: Are girls really better than boys?

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Vanessa LoBue and Judy S. DeLoache

Department of Psychology, University of Virginia, Charlottesville, VA 22904.
vl8m@virginia.edu **jdeloache@virginia.edu**

Abstract: One facet of Vigil's socio-relational framework of expressive behaviors (SRFB) suggests that females are more sensitive to facial expressions than are males, and should detect facial expressions more quickly. A re-examination of recent research with children demonstrates that girls do detect various facial expressions more quickly than do boys. Although this provides support for SRFB, further examination of SRFB in children would lend important support this evolutionary-based theory.

In his socio-relational framework of sex differences in the expression of emotion (i.e., the socio-relational framework of expressive behaviors [SRFB]), Vigil proposes that there should be gender differences in the processing of affective facial expressions, and he cites several specific examples of the ways in which males and females should differ in this domain. Here we focus on one in particular – sex differences in the detection of affective facial expressions and, in particular, whether there is evidence of such differences over the course of development.

Based on SRFB, Vigil claims that, because of their sensitivity to trustworthiness cues, females should detect affective facial expressions more quickly than males. The only exception might be in the detection of anger: since males should be particularly sensitive to dominance cues, they should detect angry facial expressions more quickly than females. The question of whether adults detect certain kinds of facial expressions more quickly than others has been of substantial interest to many researchers, making Vigil's claims easy to evaluate based on the existing literature.

Using a standard visual search paradigm, many researchers have examined the detection of threatening facial expressions, such as anger. However, with the exception of the few studies cited by Vigil, few report any gender differences. Most of these studies find that participants of both sexes are faster at identifying angry faces than happy faces overall (Calvo et al. 2006; Esteves 1999; Fox et al. 2000; Gilboa-Schechtman et al. 1999; Horstmann & Bauland 2006; Lundqvist & Öhman 2005; Mather & Knight 2006; Öhman et al. 2001; Schubo et al. 2006).

Although this research with adults offers no support for Vigil's theory, research with children might be particularly relevant to evaluating SRFB. Vigil's theory suggests an evolved or biological basis for gender differences in face detection, so it is possible that such differences would be apparent in childhood and even infancy. Recently, LoBue (2009) examined the visual detection of several affective facial expressions (e.g., happy, sad, angry, fearful) in both preschool children and adults. Participants in a series of studies were asked to find the single instance of a given category in a 3 x 3 matrix of color photographs. For example, they might be asked to identify the single angry face among eight happy ones (or vice versa).

Consistent with the adult literature, both preschool children and adults were faster to detect facial expressions that depicted threat-relevant expressions (anger, fear) than non–threat-relevant expressions (happiness, sadness). In another series of studies, LoBue and DeLoache (2008) reported that preschool children and adults were also faster at detecting pictures of threat-relevant animals (snakes) than non–threat-relevant ones (frogs or caterpillars). However, no gender differences were found in any of the experiments.

Despite the lack of significant sex differences, a slight advantage was apparent for female preschoolers in some of the studies. It is possible that the sample size in each study was too small (24 children in each study, 12 in each condition) for detecting subtle gender differences. Accordingly, we combined the data from all our visual search experiments to examine whether there was an overall advantage for females (data from LoBue 2009). There was in fact a significant effect of gender, indicating that girls detected the target faces more quickly than did boys. The advantage for females was stable across studies, and did not differ based on whether the target was threatening or non-threatening. Importantly, this advantage was significant only for the detection of affective facial expressions: When reanalyzing the data for the detection of snakes (data from LoBue & DeLoache 2008), there was no such advantage for girls.

These results indicate an advantage for young girls in the detection of affective facial expressions. Further, this advantage cannot be attributed to simple differences in motivation or compliance, since it was not found for the detection of non-facial stimuli. These results provide support for Vigil's claim that females should have an advantage over males in the detection of emotional facial expressions. However, Vigil's assertion that males should be particularly sensitive to threatening facial expressions was not supported – girls showed an advantage over boys across studies, regardless of whether or not the targets were threat-relevant.

While these findings provide some support for SRFB, whether there is a biological basis for these gender differences is still unclear. It is certainly possible that by preschool, children have

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developed gender differences in face processing based on experience. This question makes research with infants, who have less experience interacting with the relevant stimuli, critical for testing Vigil's hypothesis. Recently, LoBue and DeLoache (in press) did examine the detection of affective facial expressions in 8- to 14-month-olds, but found no gender differences. Further research in this area is needed in order to examine Vigil's claims more thoroughly.

Future research in other areas of development might also be informative for the SRFB. For example, Vigil suggests that females are better at posing affective facial expressions than are males. If so, this should also be true for children. Further, gender differences in infants' preferences for different kinds of faces might be an important consideration for future research. For example, Lutchmaya and Baron-Cohen (2002) reported an important gender differences in 12-month-old infants' looking preferences. They found that when infants were presented with videos of moving cars or moving faces in a looking-preference experiment, infant boys preferred to look at the cars over faces, while infant girls preferred to look at faces over cars. This result supports Vigil's claims and may warrant further investigation.

In conclusion, developmental findings on gender differences in the detection of affective facial expressions provide partial support for Vigil's view that females should detect affective facial expressions more quickly than do males. Research with infants and young children could provide further information relevant to assessing the SRFB.

The other side of the coin: Intersexual selection and the expression of emotions to signal youth or maturity

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George A. Lozano

Department of Zoology, Institute of Ecology and Earth Sciences, Tartu University, 51014 Tartu, Estonia.

george.lozano@ut.ee

www.georgealozano.com

Abstract: Vigil summarizes sex-related differences in emotivity, and presents a psychological model based on the restrictive assumption that responses to stimuli are dichotomous. The model uses for support the concept of intrasexual selection, but ignores intersexual selection. An alternative hypothesis might be that emotivity signals age: maturity in men and youth in women. Integration requires considering all evolutionary biology, not just agreeable concepts.

Vigil is to be applauded for tackling such a large and complex topic as the differences in emotivity between the sexes and for attempting to produce a model that reconciles psychological and evolutionary approaches. Vigil's summary of these differences (target article, sect. 3.2) is written crisply and directly, and will be a useful reference for anyone working in this area. With some adjustments and additions, his model or a derivative of it might successfully merge evolutionary and psychological approaches.

The model assumes that "approach" and "avoid" are the only possible responses to external stimuli. However, animals often respond to stimuli by taking a "wait and see" strategy to obtain more information. Second, to use Vigil's examples, food may be laden with toxins, and mates may sometimes become predators, so organisms seldom face a dichotomous choice, but rather must monitor many requirements and make the appropriate trade-offs. Third, even when it might be ultimately desirable to avoid a stimulus – for instance, a predator – there might be several viable short-term responses. The potential prey might freeze to avoid detection. If it is already being stalked, it might simply inform the predator that it has been seen so the latter can no longer mount a surprise attack. If the predator does attack, the best response might be to stand and fight. It is even more complex when, instead of responding to predators, animals must respond to highly social conspecifics with common and conflicting interests. Hence, the model would be stronger if it recognized that most responses to social stimuli probably fall within a large grey area between "avoid" and "approach."

Vigil then applies the model to sex-related differences in emotivity, using for support the concepts of intrasexual competition (Darwin 1871) and reciprocal altruism (Trivers 1971). The model would be stronger if it also considered related concepts, such as intersexual selection (Darwin 1871) and the ensuing sexual conflict (Trivers 1972). Vigil points out that most social interactions are with members of our own sex, and women have more intimate relationships and with fewer individuals than men do, and he attributes these patterns to sex-related differences in philopatry. It might be worth also considering that variance in reproductive success is higher for males than for females, so competition among males is stronger than among women, not just different in its style and in its setting. Second, one must also wonder why displaying emotions might be more useful in more intimate situations. The opposite could be argued. Powerful leaders throughout history, who happen to have been mostly male, demonstrate that displaying emotions can be a powerful means of controlling and motivating the masses. Third, as a sexually reproducing species, there is only one way for our genes to make it to the next generation – by interacting with the opposite sex. Maybe the model could incorporate intersexual selection (a.k.a. epigamic selection or mate choice) instead of focusing solely on intrasexual competition. Finally, sexual relationships are a constant struggle between common and conflicting interests. Within every sexual relationship, there is the potential for cooperation but also for deceit, manipulation, and exploitation. An enormous body of work over the past 40 years has been based on that premise (Andersson 1994; Arnqvist & Rowe 2005; Low 2001; Majerus 2003; Trivers 1972). It is peculiar that a treatise on the differences in emotivity between the sexes would not consider the one emotion that for millennia has provided a livelihood for thespians, singers, poets, and playwrights; humanity's greatest and most wonderfully labile and complex emotion and obsession: romantic love.

When mating, men have been selected to be relatively more concerned with quantity and women with quality (Betzig 1986; 1993; Buss 2003; Helle et al. 2008; Murstein 1986). Men compete for resources mostly with other men, but they also compete for the attention of women by displaying, emphasizing, and exaggerating their strength, status, and wealth. In contrast, women compete for high-quality males by displaying, emphasizing, and exaggerating their potential fecundity, beauty, and/or youth, all of which are highly positively correlated. Emotional displays are signals, and as such, their purpose is to persuade, cajole, and manipulate the intended receivers (Maynard-Smith & Harper 2003; Searcy & Nowicki 2005). There is nothing more potentially deceptive than a simple smile. A new hypothesis suggests itself: emotivity, or lack thereof, might be yet another way to attract the opposite sex. Given that children are more emotive than adults, men might conceal their emotions as a way to display their strength and maturity. In contrast, women might express more and more variable emotions in order to display their youth. In any case, consideration of intersexual selection offers a different and more complete perspective.

Vigil's social framework of emotions consists of a two-dimensional construct with "trustworthiness" on one axis and "capacity", or, perhaps more aptly, "ability", on the other axis. This conceptualization is similar to Leary's (1957) model, which had "love" and "dominance" as the two axes. Just like Leary's model, Vigil's is reasonable, interesting, and compelling, and it could have been derived without any knowledge of evolutionary biology. In

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applying the model to sex-related differences in emotions, evolutionary concepts are used only for support, not for illumination. Unfortunately, integration must encompass all evolutionary biology, not just selected concepts that agree with the model. If anything, the model highlights the fact that some areas of psychology and evolutionary biology, despite over 50 years of progress and a mutually acknowledged desire for integration, might be getting closer but are still entrenched in their own ways of thinking.

Following Darwin's (1872) pragmatism, Vigil addresses the *expression* of emotions, not emotions *per se*, as the latter are more difficult to observe, quantify, and classify (e.g., Nesse & Ellsworth 2009), and anyway, can only affect fitness when they alter behaviour. This important distinction might help us merge evolutionary and psychological approaches by allowing us to abandon arbitrary conceptualizations of what is inside a mind – the sensation of emotions – and instead lead us to focus on their ecology and functions. It is ironic that, evolutionarily, it only matters what emotions do, not how they feel.

Cry baby cry, make your mother buy? Evolution of tears, smiles, and reciprocity potential

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Minna Lyons

Liverpool Hope University and British Academy Centenary Research Project, Liverpool L16 9JD, United Kingdom.

Lyonsm2@hope.ac.uk

http://hopelive.hope.ac.uk/psychology/evolutiongroup

Abstract: In this commentary, the idea of reciprocity potential indicators is tied in with ultimate accounts on sex differences in social sensitivity. It is proposed that, rather than crying, smiling is a more likely cooperative signal. The possibility of coevolution and polymorphism in perceptual and signalling systems are also discussed briefly, with a reference to Theory of Mind and Machiavellianism.

Although Vigil provides a very plausible ultimate account on the evolution of sex differences in emotionality based on male philopatry and female dispersal, some of the premises of the socio-relational framework of expressive behaviours (SRFB) remain less convincing. The two main aspects of the model circle around advertising capacity (relating to masculine dominance behaviours) and trustworthiness (relating to feminine emotional expressions), which Vigil ties in with numerous examples from diverse literature. While dominance cues might provide the observer with information about the importance of the actor as a social partner, the idea that emotive signals such as crying have evolved as a display of trustworthiness is less compelling.

The purpose of adult crying is still very much disputed. Crying is a communicative signal (Zeifman 2001) functioning differently in multiple contexts (Peter et al. 2001). However, it is debatable whether adult tears represent an honest signal of cooperative intentions, and whether crying is perceived as such by receivers of the signal. Although some forms of crying do signify vulnerability and a need of help (Frijda 1997), it is more likely to induce others to help without the expectation of reciprocity. In fact, research suggests that, although crying amplifies the perceived sadness in the face (Provine et al. 2009) and elicits emotional support from others, crying individuals are sometimes perceived negatively (Hendriks et al. 2008), and even labelled as being manipulative (Buss 1992; Frijda 1997). Moreover, empirical, cross-cultural evidence on sex differences in crying is sparse, and the relative importance of socialisation and culture versus biological processes is not clear. Rosenblatt et al. (1976), for example, analysed sex differences in crying in 60 societies and found that in over half of the cultures, women did not cry more than men did. Ross and Mirowsky (1984) suggested that, rather than an evolved signal, crying in adults is socially conditioned behaviour, dependent on factors such as socio-economic status and sex-role identity of the individual. It is possible that crying in adults is an extension of attachment-related behaviour (Nelson 2005), but does not function as a signal signifying reciprocity potential.

Rather than crying, smiling is a more likely signal of reciprocity potential. Research has found that smiling is related to altruistic dispositions (Brown & Moore 2000; Brown et al. 2003) and is used in cooperative context (Mehu et al. 2007). Moreover, unlike crying, smiling induces trust and positive evaluations by the receivers of the signal (Mehu et al. 2008; Scharlemann et al. 2003). Sex differences in smiling and decoding of smiles could relate, ultimately, to the need to form reciprocal relationships with unrelated individuals. Females, both children and adults, are more expressive than males are (LaFrance et al. 2003; Provine 2000), and perform better in decoding emotional facial expressions (Hall et al. 2000; Rotter & Rotter 1988; Thayer & Johnsen 2000). Overall, females are better in processing and sending out signals that facilitate social interactions. At a neural level, a recent study found that when processing social information, females recruit areas containing mirror neurons more than males do (Schulte-Rüther et al. 2007), which could provide a possible proximate mechanism facilitating sex differences in social cognition. Ultimately, the superiority of women in reading and sending out nonverbal messages is probably a result of evolutionary pressures for heightened social sensitivity needed for competing and forming alliances in non-kin–based social networks.

The female advantage in sending and receiving social signals fits well with Vigil's idea of coevolution between perceptual systems aiding in identifying cooperators, and honest expressive behaviours in advertising trustworthiness. Ultimately, the coevolution could explain the problem of cooperation via the *Green Beard effect*, which postulates that altruists possess a conspicuous phenotypic behavioural of physical trait, which can easily be identified by others with the same characteristic (Dawkins 1976/1989). Although there is some evidence that people can recognise potential cooperators (Frank et al. 1993; Lyons & Aitken 2008; Pradel et al. 2008), not much is known about individual differences that might account for this ability. Moreover, it is possible that altruistic individuals are equipped with superior social intelligence, helping them in identifying the altruistic dispositions in others. There is some evidence that social intelligence in the form of Theory of Mind is related to self-rated cooperativeness (Paal & Bereczkei 2007), but it is unclear whether social intelligence is used when assessing the honesty of another person.

It is equally possible that evolution has produced polymorphism in perceptual and signalling systems, resulting in the existence of mixed strategies. Experimental work suggests that human populations consist of different cooperative types, which are under substantial genetic influence (Cesarini et al. 2008; Kurzban & Hauser 2005). Further research is needed in order to demonstrate how these types relate to individual differences in accuracy in assessing altruistic dispositions in others. Some individuals might be good in detecting trustworthiness, but not actually be trustworthy – a good candidate would be Machiavellian individuals (for the Machiavellian intelligence hypothesis, see McIlwain 2003; cf. Byrne & Whiten 1997). Others might, in turn, be trustworthy, but not competent in recognising the same trait in others (e.g., people with William's syndrome). It remains to be demonstrated how individual differences in social perceptiveness (e.g., Theory of Mind) and trustworthiness (e.g., Machiavellianism) relate to individual and sex differences in sending and receiving social cues.

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Human female exogamy is supported by cross-species comparisons: Cause to recognise sex differences in societal policy?

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Guy Madison

Department of Psychology, Umeå University, 901 87 Umeå, Sweden.
guy.madison@psy.umu.se
http://www.psy.umu.se/staff/guy_madison_eng.html

Abstract: A sex difference in the tendency to outbreed (female exogamy) is a premise for the target article's proposed framework, which receives some support by being shared with chimpanzees but not with more distantly related primates. Further empirical support is provided, and it is suggested that recognition of sex differences might improve effective fairness, taking sexual assault as a case in point.

In the target article, Vigil argues compellingly for a socio-relational framework of expressive behaviours (SRFB) that integrates a vast array of reported sex differences. The main selection pressure proposed to underlie these sex differences is female exogamy and its social consequences. *Female exogamy* refers to a drive to outbreed, effectively analogous to male *philopatry*: the tendency to remain at or return to the natal territory. The former drive is presumably based on natural selection benefits in terms of decreasing the effects of defective genes and increasing genetic variation. This may have been very important during phases of evolution when small groups were geographically isolated, and to leave a group posed a considerable effort as well as a considerable risk. It is conceivable that the selection pressure for exogamy must for such periods have been very strong and must also have required very strong motivational mechanisms to overcome the individual's natural tendency to remain in the familiar environment. In species with sexual reproduction, it is of course sufficient that one sex outbreeds. Since it would probably inflict adaptive costs if both sexes outbred, the optimal solution is a sex-specific one, in which the non-migrating sex can develop adaptive benefits related to philopatry. It is conceivable that a sufficiently effective and sex-specific motivational mechanism is quite a difficult device to develop by means of natural selection, and that a selection pressure to reverse its sex-specificity is unlikely to emerge once its development has commenced.

It is therefore notable that, although female exogamy is a rare behavioural characteristic in the animal kingdom, it is nevertheless shared by humans and chimpanzees (Ember 1978; Pusey 1979). It is estimated that around the time of sexual maturity, roughly one of every two female chimpanzees migrates to other territories (Pusey et al. 1997). Female exogamy is consistent with the group sociality centred on male rather than female kinship observed among chimpanzees (Mitani & Watts 2005; Williams et al. 2004; Wilson & Wrangham 2003), whereas other primates such as macaques and baboons exhibit a female-based social system. Chimpanzee sociality features male kin forming territorial groups that typically engage in competition with other groups, a pattern with some parallels in human behaviour (Alexander 1990; Wrangham & Wilson 2004). These observations are consistent with the notion that female exogamy is a genetic behavioural trait in humans, because chimpanzees are considerably closer in the human lineage than are primates with female-centred sociality. For comparison, the current estimate of the human-chimpanzee split is some 5 million years old, whereas the split between Hominidae and Old World monkeys (*Cercopithecoidea*) such as baboons and macaques is on the order of 25 million years (see, e.g., Boyd & Silk 2006).

Any evolutionary scenario can be questioned on the causality of its relationships, because its hypotheses can rarely be subject to experimental tests. This is particularly true in the case of humans, who, among other complicating factors, suffer from a long life cycle and an extremely elaborate set of cultures that may propagate non-adaptive action and experience tendencies. Main approaches for assessing the validity of theories such as SRFB are therefore analyses of cross-cultural commonality, correlational studies, and observations unlikely to have been affected by culture, such as infant behaviour.

In addition to the many empirical data reviewed in the target article concerning emotional expression per se, such as crying (DeFruyt 1997; Kraemer & Hastrup 1986), large sex differences have been reported for other behaviours that would also seem to be brought to bear on SRFB, such as sexual arousal (Chivers & Bailey 2005; Chivers et al. 2004; 2007) and the prevalence of sexual assault (Elliott et al. 2004). Moderate sex differences are also found for emotional reactions to music both in humans (McCown et al. 1997; Nater et al. 2006) and in chimpanzees (Videan et al. 2007). Female neonates display more interest for faces than for mechanical objects, whereas male neonates exhibit the opposite pattern (Connellan et al. 2001). Several studies have also reported on dose-response relationships between androgens and sex-typical behaviours of children, such as foetal testosterone in one-year-olds (Lutchmaya et al. 2002) and the severity of congenital adrenal hyperplasia (Nordenström et al. 2002; Servin et al. 2003).

Finally, I note that the SRFB may have implications for societal policies, in particular those pertaining to equality and fairness between the sexes. Given that, according to the SRFB, females on average have a stronger tendency for submissive displays (ultimately intended to advertise trustworthiness) and males have a stronger tendency for aggression and dominance displays (ultimately intended to advertise capacity), these two tendencies would seem likely to conspire in between-sex interactions. A conflict of interest would in such interactions be likely to exaggerate the male dominance display, being his default approach strategy, which would in turn exaggerate the female submissive display, being her default withdrawal strategy, and so forth in a vicious cycle. In a situation where the male desires sexual activity and the female does not, it is conceivable that the proposed sex-specific display strategies might increase the risk for sexual coercion and rape as compared to sex-neutral displays (cf. McKibbin et al. 2008; Thornhill & Palmer 2000).

Another aspect of this scenario is that sex-specific displays effectively may make men and women unequal in the eyes of the law. Indeed, it is common that rapists fail to be convicted because of insufficient evidence of violence. It is conceivable that the level of physical resistance and ensuing violence expected by the legal court as a display of refusal might be set by male standards, thereby seriously compromising the woman.

Sexual assault is but one example of instances where the recognition of sex differences might facilitate effective equality and fairness, in contrast to the typical denial from gender studies that biological sex differences exist. An important question, therefore, is: What empirical evidence and theoretical ground, such as the SRFB, might be required for recognising sex differences in societal policy?

Reciprocity of laughing, humor, and tickling, but not tearing and crying, in the sexual marketplace

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Robert R. Provine

Department of Psychology, University of Maryland, Baltimore, MD 21250.
provine@umbc.edu

Abstract: Laughing, humor, and tickling, but not tearing and crying, involve the give-and-take that provides value and a basis for exchange in the psychosexual marketplace.

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Laughter and humor are highly valued in the sexual marketplace. In a study of 3,745 personal ads published by heterosexual men and women in eight U.S. national newspapers on Sunday, April 28, 1996, men offered "sense of humor" or its equivalent ("humorous"), and women requested it (Provine 2000). Women, however, couldn't care less whether their ideal male partner laughs or not – they want a man who makes *them* laugh. Women sought laughter over twice as often as they offered it. The behavioral economics of such bids and offers is consistent with the finding that men are attracted to women who laugh in their presence (Grammer & Eibl-Eibesfeldt 1990). Without such a balance between the value of bids and offers, there would be no market for laughter and humor, and the currency of these behaviors would decline. It is significant that this orderly laughter scenario occurs at a low level of conscious awareness – laughter is not a matter of deciding to speak "ha-ha." Most people have difficulty laughing convincingly on command; it happens spontaneously in the appropriate social context. Laughter, like crying, is an *honest signal* that is hard to fake.

Although laughter is under low voluntary control, its stimuli are not, and show strong sexual dimorphism. Men are the most effective laugh getters (Provine 1993; 2000). Both men and women laugh more at male than female speakers, a likely reason why there are more male than female comedians. This trend starts early in life; most class clowns are boys. The essential stimulus of laughter is another person, male or female, not humor. Laughter is 30 times more frequent in social than solitary situations, and, when laughter occurs, only 10 to 15 percent follows comments that are jokes or other formal attempts at humor. Contagious laughter – laughing in response to perceived laughter – may be the ultimate example of the reciprocity of emotional expression. Contagious yawning may be another.

Tickle, the primordial laugh stimulus, joins humor as another laugh stimulus under voluntary control. The sexual component of tickle is suggested by its strongly heterosexual character (Provine 2000; 2004). Aside from physical play with children, adult males tend to tickle females, and vice versa. The ticklee of choice is not random. We tickle and are tickled by friends, family, and lovers. When was the last time you were tickled by a stranger? The reasons given most often for tickling are to "show affection" and to "get attention," not to antagonize. Even confirmed tickle haters may reconsider their position when they realize that the give-and-take of tickle battles is central to sexual foreplay and intercourse.

If you still doubt the sociality of tickle, consider that you can't tickle yourself (Provine 2000; 2004). It takes two to tickle. In contrast, you can tap your own patellar tendon and evoke a perfectly normal knee jerk. The sociality and reciprocity of tickle are neurologically programmed. Ticklees struggle, fend-off the tickling hand, laugh, *and* retaliate. Retaliation is the basis of the give-and-take of tickle battles, and what binds us together during the rough-and-tumble play of childhood and the sex play of adulthood. Bad tickle experiences are associated with the absence of reciprocity, such as when a person is held down and tickled. Nonconsensual tickle, like nonconsensual sex, is unwelcome and unpleasant. Vigil's emphasis on the reciprocity of emotional relationships is well placed.

Vocal crying and tearing are emotional signals that provide informative contrasts with laughing, humor, and tickling. The first study of tearing as a visual signal of sadness found that faces with tears appeared sadder than identical faces with tears removed by digital image processing (Provine et al. 2009). Tear removal produced faces that were not only less sad but of ambiguous emotional state. Thus, emotional tearing provides a significant visual cue of sadness, complementing the neuromuscular instrument of facial behavior that may not quite be up to the task. Emotional tearing, unique to humans, is a significant advance in *Homo sapiens* as a social species. The study detected no difference in the perceived sadness of teary and tear-free faces as judged by male and female subjects. However, as noted by Vigil, females cry much more than males, which provides females with more potential vocal and visual stimuli of the emotional state.

Tearing and vocal crying, solicitations of caregiving and expressions of neediness, may be exceptions to emotional reciprocity of the sort considered for laughing, humor, and tickling. Caregiving, although adaptive within the framework of reciprocal altruism, is unattractive and costly for the provider, a fact revealed in the psychosexual marketplace of personal ads. You are unlikely to find people advertising their neediness or seeking it in others.

Brain-based sex differences in parenting propagate emotion expression

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James E. Swain

Child Study Center, Yale University School of Medicine, New Haven, CT 06520.

james.swain@yale.edu **http://myprofile.cos.com/jameseswain**

Abstract: Parent-infant emotional expressions vary according to parent and infant gender. Such parent-infant interactions critically affect infant development. Neuroimaging research is exploring emotion-related brain function that varies according to gender, and regulates parenting thoughts and behaviors in the early postpartum. Through specific brain functions, parenting serves to program the infant brain for the next generation of sex-specific emotional expression.

In addition to interpersonal social ecologies important for understanding sex differences in emotional expression, as discussed by Vigil in the target article, parent-infant interactions are a specific, measurable, and evolutionarily significant arena (Feldman 2007). Indeed, by the third month postpartum, face-to-face, synchronous parent-infant interactions teach infants about a range of emotional social interactions (Feldman et al. 1999; Tronick 1989). These early-life interactions consist of brief behavioral units in dyad-specific patterns. One of very few studies that have considered such parent-infant interaction as a function of parental gender (Dickson et al. 1997) examined the co-occurrences of infant smile type and play type during interactions with each parent. During father-child interactions, object-oriented play was more frequent and tended to co-occur with basic smiles, whereas mother-child play included more vocalizations. In another study, time-series analysis of 100 first-time mothers and fathers interacting with their 5-month-old firstborn, coded with 1 second resolution, showed that during play with mother, infants cycled between states of low and medium arousal, often with one peak of high positive emotionality during the engagement episode (Feldman 2003). In this study, mother-child play focused on face-to-face exchange and included patterns of mutual gazing, covocalization, and affectionate touch integrated into timed configurations. In contrast, during play with fathers, the time-line of arousal contained several quick peaks of high positive emotionality, including joint laughter and open exuberance, and individual linear regressions showed that these peaks became more frequent as play proceeded. Furthermore, father-child interactions centered on physical games, or games with an object focus, rather than on attention to micro-level face-to-face signals. This latter finding is consistent with previous research (Lamb 1977; Yogman 1981).

However, despite parent-gender differences in content, no differences were detected in temporal parameters, suggesting that father-infant play may be as synchronous as mother-infant play. Father-son and mother-daughter dyads showed the

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highest levels of synchrony, with respect to coherence, more mutuality in the lead-lag structure, and shorter time lags to synchrony. It has been suggested that synchrony builds on the infant's biological rhythms and extends it to social relatedness (Lester et al. 1985; Wolff 1967). Perhaps female newborns' higher social orientations, increased periods of eye contact, smiles, and rhythmical mouthing contrast with male newborns' frequent peaks of excitement, quicker rapidity of buildup, and higher reflex startling (Korner 1969; Osofsky 1976) to more easily match and build on similar parent interactions that tend to build on these innate dispositions.

Thus, mothers and fathers provide infants two modes of coregulation. As infants interact with mother and father, they learn that interpersonal intimacy may come in different forms; some relationships focus on subtle shifts in facial signals, whereas others are directed to exploring of the outside world; some are moderate in intensity, whereas others may be more arousing and exciting. Also, some are consistent with the individual's biological tendencies, while others may require some adjustment. As one might expect, it has been shown that mother-son dyads take longer to repair from mismatched to matched states (Weinberg et al. 1999), which may be explained by gender mismatching of dyadic interactions between mother and son. Such experiments explain the well-established link between early father absence and the development of externalizing disorders (Cabrera et al. 2000).

Since synchrony is central for the development of self-regulation, father absence and lack of sufficient and naturally more synchronous same-gender early interactions may disrupt the acquisition of self-regulatory skills and lead to conduct disorders in boys. This may also point to possible protective therapeutic interventions to maximize opposite-gender parent-infant interactions. These findings fit with psychoanalytic notions that early relational patterns construct person-specific internalized models (Stern 1985), perhaps through the development of specific emotion-regulation brain circuits (Leppanen & Nelson 2009), to serve as templates for intimate emotional interactions throughout life (Cassidy & Shaver 2008). Unique contributions from mother-child interaction (Moran et al. 2008) and father-child interaction (Boyce et al. 2006; Grossmann et al. 2002) to evolutionarily favorable sex-specific emotional expressions of the developing child may significantly constitute the mechanism through which sex differences cross generations.

These sex differences in emotional expression, manifested and perhaps transmitted through parent-infant interactions, are presumably based on sexual differences in parental brain structure and function across species (Bridges 2008) and in humans in particular (Swain & Lorberbaum 2008; Swain et al. 2007). Such studies also lie within the larger and growing field addressing sex differences in brain structure, function, and chemistry (Cosgrove et al. 2007). For example, neurochemical modulators such as oxytocin and vasopressin (Donaldson & Young 2008) are likely to be important determinants of emotion expression, as well as contribute to psychopathology risk.

Furthermore, brain networks that differ according to sex likely also vary according to the type of emotional stimuli (Hamann et al. 2004; Proverbio et al. 2009; Schirmer et al. 2004; Wager & Ochsner 2005), including the involvement of empathys (Schulte-Rüther et al. 2008). For example, considering parent-related stimuli, infant laughing, and crying stimuli versus a control sound, the amygdala and anterior cingulate of non-parent women were more active than those of men (Sander et al. 2007). Perhaps these gender-dependent correlates of neural activity reflect neural predispositions in mothers for responses to preverbal infant vocalizations. Direct contrast of men versus women in the first weeks postpartum indicated increased activity in mothers compared with fathers in response to baby cry (Swain et al. 2004) and picture (Swain et al. 2006) in limbic brain regions. This fits with findings that fathers experience more anxious emotional thoughts and engage in more compulsion-like behaviors to reduce their worry (Kim et al., submitted; Leckman et al. 1999; 2004; Swain et al. 2005). Taken together, this research suggests that networks of highly conserved hypothalamic-midbrain-limbic-paralimbic-cortical circuits act in concert to support aspects of parent response to infants, including the emotion-regulation circuits that vary according to gender. An integrated understanding of the brain basis of parenting according to gender has implications for long-term parent and infant emotional expression and mental health.

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On the richness and limitations of dimensional models of social perception

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Alexander Todorov

Department of Psychology, Princeton University, Princeton, NJ 08540.
atodorov@princeton.edu **http://www.princeton.edu/~atodorov/**

Abstract: The two-dimensional model of social relations outlined in the target article has striking convergence with empirically derived dimensional models of interpersonal perception, inter-group perception, and face evaluation. All these models posit two-dimensional structures related to perceptions of valence/affiliation and power/status. Although these models are parsimonious, they may be insufficient to account for behaviors in specific contexts.

In an ambitious treatment of gender differences in expressive behaviors, Vigil's target article outlines a two-dimensional model of social relationships according to which people evaluate their relationships on two fundamental dimensions: trustworthiness and capacity. These dimensions are related to inferring the intentions (e.g., potential harm) and the ability of the relationship partner to implement these intentions (e.g., means to inflict harm). This model converges with a number of dimensional models that have been empirically derived from the study of specific domains of social perception. These include Wiggins's model of interpersonal perception (Wiggins 1979; Wiggins et al. 1989), Fiske's model of inter-group perception (Fiske et al. 2007), and Todorov's model of evaluation of faces on social dimensions (Oosterhof & Todorov 2008; Todorov et al. 2008).

All these models use a similar data-driven approach. Groups, people, or faces are initially characterized on a number of specific attributes (e.g., trustworthiness, competence, aggressiveness), and then the judgments on these attributes are submitted to statistical analyses that identify and model the common variance among these judgments. The final objective is to identify a simple model that accounts for most of the variance in these judgments and, ultimately, provide an explanatory framework for the domain of study. Using this approach, Fiske et al. (2007) have argued that the primary dimensions of perceiving social groups are warmth and competence and that these dimensions are related to competition and status. Wiggins et al. (1989) have argued that the primary dimensions of perceiving other people are affiliation and dominance. Todorov et al. (2008) have argued that the primary dimensions of evaluating faces are valence/trustworthiness and power/dominance.

I use our own approach to illustrate the data-driven character of these methods. To outline the structure of perception of faces on social dimensions (Oosterhof & Todorov 2008; Todorov et al. 2008), we first identified trait attributes that are spontaneously

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used to characterize unfamiliar faces. Then, we asked participants to rate faces on these attributes. Not surprisingly, judgments of these attributes were highly correlated with each other. In fact, it is almost impossible to find a social judgment that is uncorrelated with judgments of trustworthiness. A Principal Component Analysis of the trait judgments identified a simple two-dimensional solution that accounted for more than 80% of the variance of these judgments. The first dimension was interpreted as valence evaluation of faces and the second dimension as dominance evaluation. Trustworthiness judgments were the best approximation of valence evaluation, and dominance judgments were the best approximation of power evaluation.

Computer modeling of judgments of trustworthiness and dominance showed that whereas cues signaling correspondent approach/avoidance behaviors were important for the valence/trustworthiness dimension, cues signaling physical strength were important for the power/dominance evaluation. As shown in Figure 1, whereas faces on the extreme positive end of the trustworthiness dimension were perceived as happy and slightly surprised, faces on the extreme negative end were perceived as angry. Whereas extremely dominant faces were perceived as extremely masculine and mature faced, extremely submissive faces were perceived as extremely feminine and baby-faced (Fig. 1).

These findings converge nicely with the model proposed by Vigil: that relationship partners are evaluated on trustworthiness and capacity; that is, intentions and the ability to implement these intentions. Moreover, given the commonalities between these dimensions and the dimensions in the models of Fiske et al. (2007) and Wiggins et al. (1989), models that were empirically derived in different domains of social perception, it may be argued that these dimensions are universal dimensions of social perception (Fiske et al. 2007).

Yet, although these models can provide a powerful explanatory framework for a set of phenomena, their parsimony can come with a price. Specifically, these models may be insufficient to explain and predict social behaviors in specific contexts. In the data-driven methods, the general approach is to model common variance and discard variance that is unique to the specific input variables (e.g., non-error variance that is specific for trustworthiness per se and is not shared with general valence evaluation of faces). While this approach is justified to the extent that the objective is to arrive at a general framework that can account for a variety of specific effects, it may miss important effects that are not easily attributable to common variance. For example, perceptions of trustworthiness and dominance are sufficient to account for perceptions of threat (Oosterhof & Todorov 2008) but not perceptions of competence. In decision contexts (e.g., voting) where competence is the primary dimension of evaluation, cues specific to competence, and not trustworthiness or dominance, predict social decisions (Olivola & Todorov, in press; Todorov et al. 2005). The weight of attributes or importance of dimensions can also change as a function of the specific context. Whereas masculine-looking leaders, with the associated perceptions of leadership and dominance, are preferred in wartime, feminine-looking leaders, with the associated perceptions of trustworthiness and likeability, are preferred in peacetime (Little et al. 2007).

To what extent the socio-relational framework of expressive behaviors (SRFB) model would sacrifice specificity of prediction is an empirical question. As a general descriptive framework, this model is certainly supported by independent evidence from other dimensional approaches to social perception. Moreover, as outlined by Vigil, the descriptive framework of the model can be best understood in the context of social interaction. That is, displays of social cues are in the service of social interaction.

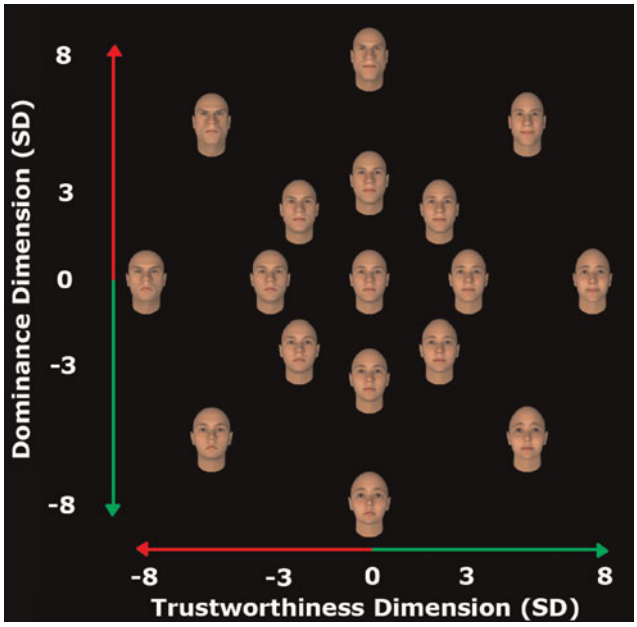


Figure 1 (Todorov). A data-driven computer model of variation of faces on the dimensions of valence/trustworthiness depicted on the *x*-axis and power/dominance depicted on *y*-axis. The variation of faces is in standard deviation units. The details of the modeling are described in Oosterhof and Todorov (2008).

Smiling reflects different emotions in men and women

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Simine Vazire,[a] Laura P. Naumann,[b] Peter J. Rentfrow,[c] and Samuel D. Gosling[d]

[a]*Department of Psychology, Washington University in St. Louis, St. Louis, MO 63130;* [b]*Institute of Personality and Social Research, University of California, Berkeley, Berkeley, CA 94720-5050;* [c]*Department of Social and Developmental Psychology, Faculty of Politics, Psychology, and Sociology, The University of Cambridge, Cambridge CB2 3RQ, United Kingdom;* [d]*Department of Psychology, University of Texas at Austin, A8000 Austin, TX 78712-0187.*

svazire@artsci.wustl.edu **www.simine.com**
naumann@berkeley.edu
http://www.ocf.berkeley.edu/~johnlab/naumann.htm
pjr39@cam.ac.uk
http://www.ppsis.cam.ac.uk/psy/staff/jrentfrow.html
samg@mail.utexas.edu **www.samgosling.com**

Abstract: We present evidence that smiling is positively associated with positive affect in women and negatively associated with negative affect in men. In line with Vigil's model, we propose that, in women, smiling signals warmth (trustworthiness cues), which attracts fewer and more intimate relationships, whereas in men, smiling signals confidence and lack of self-doubt (capacity cues), which attracts numerous, less-intimate relationships.

Vigil proposes that "gender-specific emotive behaviors would have coevolved with these [social] constraints in order to regulate interpersonal dynamics to enhance social fitness" (target article, sect. 1, para. 3). Vigil's framework can be used to make sense of apparently contradictory findings in the literature regarding the relationship between smiling and affect; moreover, the framework is useful for understanding our own recent empirical findings concerning gender differences in emotional expression.

Previous empirical evidence regarding the relationship between smiling and positive affect is equivocal, with some

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studies finding such a relationship (Brown & Schwartz 1980; Ekman et al. 1980; Friedman & Miller-Herringer 1991; Hall & Horgan 2003; Hecht & LaFrance 1998; Schwartz et al. 1980) but several others failing to find one (Gehricke & Fridlund 2002; Jakobs et al. 2001; Kraut & Johnston 1979; Ruiz-Belda et al. 2003). Consistent with Vigil's socio-relational framework of expressive behaviors (SRFB), we propose that sex is an important moderator of the relationship between smiling and affect.

The view that sex differences can help explain the contradictory findings regarding the relationship between smiling and affect is supported by several pieces of evidence. First, most of the studies supporting a positive affect–smiling link used predominantly or exclusively female samples (e.g., Ekman et al. 1980; 1990; Friedman & Miller-Herringer 1991; Hess et al. 1995; Larsen et al. 2003), whereas studies finding no such link tended to rely on male samples (e.g., Gehricke & Fridlund 2002). This suggests that, as Vigil argues, the links between affect and facial behavior could be different for women and men. Second, evidence suggests that positive and negative affect may have different biological markers in men than in women. One study found that salivary cortisol was associated with state positive affect only in women (Polk et al. 2005). Once again this finding supports Vigil's model by demonstrating that biological affective processes may differ for men and women.

We propose that these differences could result in different facial displays of affect, specifically smiling, for men and women. In line with Vigil's model, we predicted that, among women, smiling may be a signal of trustworthiness, associated with feelings of warmth, and thus should correlate positively with positive affect. Among men, smiling may be a signal of capacity, associated with feelings of confidence and lack of distress, and thus should correlate negatively with negative affect.

We tested this hypothesis by examining whether positive affect and negative affect predicted smiling in men and women. Seventy male and 87 female undergraduates (mean age, 18.7 years; SD = 2.0; 58% White, 24% Asian, 12% Latino, and 6% other ethnicity) completed a battery of questionnaires including the Positive And Negative Affect Schedule (PANAS; Watson et al. 1988). The instructions for the PANAS were to "indicate to what extent you have felt this way today" using a 1 to 7 Likert-type rating scale. Immediately after, participants were photographed by an experimenter who was blind to the purpose of the study. To capture naturally occurring smiling behavior, experimenters gave participants no instructions about what to do in the photograph except where to stand. Six coders viewed the photographs in different randomized orders and, on a forced-choice item, coded whether or not participants were smiling. The reliability of the codings was very high (ICC or intraclass correlation coefficient [2, k] = .95; ICC [2,1] = .76).

Consistent with the existing literature (e.g., LaFrance & Hecht 2000), there was a main effect for sex in the overall prevalence of smiling: 76% of women were smiling compared to only 41% of men (χ^2 [1, 157] = 19.26, $p < .01$). Men and women did not differ significantly in their levels of positive affect ($M_{women} = 4.46$, $SD_{women} = 1.04$; $M_{men} = 4.46$, $SD_{men} = 1.10$; $t[155] = .01$; NS) or negative affect ($M_{women} = 2.43$, $SD_{women} = 1.21$, $M_{men} = 2.28$, $SD_{men} = 0.95$; $t[155] = .89$, n.s.). Consistent with our hypothesis, smiling was correlated with positive affect in women (point-biserial $r = .41$; $p < .01$) but not in men ($r = .01$, n.s.). Conversely, smiling was negatively correlated with negative affect in men ($r = -.51$; $p < .01$) but not in women ($r = -.05$, n.s.). A binary logistic regression revealed that the interaction of sex and positive affect was a significant predictor of smiling ($\chi^2 = 8.58$ [1, 157]; $p < .01$; see Fig. 1).

A separate binary logistic regression revealed that the interaction of sex and negative affect was also a significant predictor of smiling (χ^2 [1, 157] = 15.44; $p < .01$; see Fig. 2). In short, positive affect is a strong positive predictor of smiling for women but not for men, and negative affect is a strong negative predictor of smiling for men but not for women.

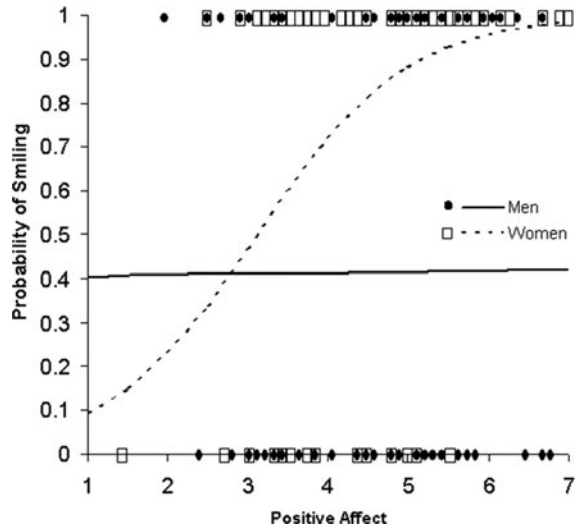


Figure 1 (Vazire et al.). Men's and women's probability of smiling as a function of positive affect. This plot is based on the results of two separate binary logistic regressions (one for men and one for women) predicting smiling from positive affect. The x-axis represents the possible range of positive affect scores, and the y-axis represents probability of smiling based on the results of the regressions. The individual dots represent data from individual men (circles) and women (squares) who did and did not smile. Smiling was coded as a binary variable, so the dots appear on the $y = 0$ and $y = 1$ lines.

These results support our hypothesis that smiling reflects different affective experiences for men and women. In line with Vigil's socio-relational framework, we propose that the sex

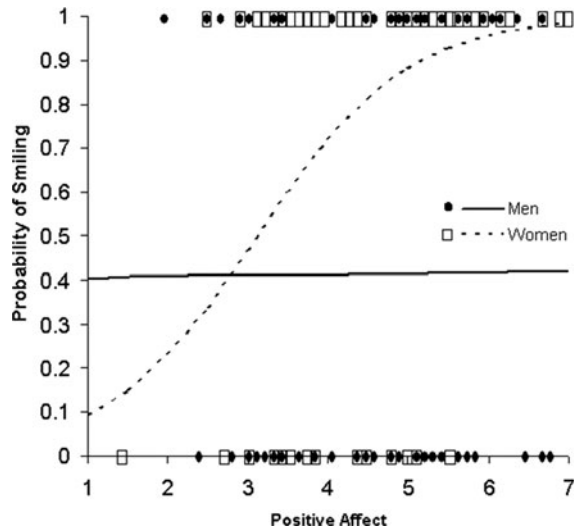


Figure 2 (Vazire et al.). Men's and women's probability of smiling as a function of negative affect. This plot is based on the results of two separate binary logistic regressions (one for men and one for women) predicting smiling from negative affect. The x-axis represents the possible range of negative affect scores, and the y-axis represents probability of smiling based on the results of the regressions. The individual dots represent data from individual men (circles) and women (squares) who did and did not smile. Smiling was coded as a binary variable so the dots appear on the $y = 0$ and $y = 1$ lines.

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difference observed here may reflect different strategies for enhancing fitness. Specifically, Vigil argues that the unique social constraints faced by women in a male-biased philopatry would create in women "a heavy reliance on behaviors designed to advertise their trustworthiness through higher levels of submissive displays" (sect. 3.1, para. 3). The strong relationship between smiling and positive affect in women suggests that, in women, smiling serves as a cue to trustworthiness by signaling warmth and enthusiasm (dimensions of positive affect), which serve to communicate a willingness to form intimate relationships.

Why might smiling be associated with lack of negative affect in men? According to Vigil, the evolutionary pressures faced by men may have led men to evolve a tendency to rely more heavily on capacity cues. Hence we propose that, in men, smiling may have evolved to signal confidence and calmness (i.e., lack of negative affect or self-doubt), which serve to attract numerous less-intimate relationships. In summary, the framework proposed by Vigil is corroborated by our findings that smiling reflects different affective states in men and women, and the framework also helps makes sense of the seemingly inconsistent findings in the literature on smiling and affect.

On the systematic social role of expressed emotions: An embodied perspective

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Nicolas Vermeulen

Université catholique de Louvain (UCL), 1348 Louvain-la-Neuve, Belgium; and National Fund for Scientific Research (FRS-FNRS), Belgium.

Nicolas.Vermeulen@uclouvain.be

http://www.ecsa.ucl.ac.be/personnel/vermeulen/

Abstract: Vigil suggests that expressed emotions are inherently learned and triggered in social contexts. A strict reading of this account is not consistent with the findings that individuals, even those who are congenitally blind, do express emotions in the absence of an audience. Rather, grounded cognition suggests that facial expressions might also be an embodied support used to represent emotional information.

The socio-relational framework of expressive behaviors (SRFB) proposes that expressed emotions are socially learned responses to external stimuli, especially to other social agents. In such a view, the central function of expressed emotions is to motivate other individuals to respond to the expresser. For instance, SRFB assumes that a smile systematically aims to motivate reactions in perceivers that will in turn enhance the smiler's fitness. Although this is undoubtedly one key function of facial expression, I am not comfortable with the strict view that expressive behaviors (among which are expressed emotions) are purely social in nature. There exist two important lines of research showing (1) that individuals (even congenitally blind people) express emotion even in the absence of an audience and (2) that facial expressions can also play another role in emotional life, which is to serve as the grounding for the processing of emotional information (Barsalou 1999). When taken together, I propose that such findings suggest that facial expressions also constitute a cognitive support used to reflect on or to access the affective meaning of a given emotional situation or emotion concept.

As a first body of evidence, the social psychology literature shows that individuals express emotion even when other individuals are not present to perceive it. In other words, people express emotion for themselves. Consistent with this notion, Matsumoto and Willingham (2006) found that 72% of the coded expressions of judo athletes occurred when the athletes were not directly facing anyone (facing towards the Tatami), as soon as 2.5 seconds after match completion. Of importance, too, Matsumoto and Willingham (2006) found no cultural (i.e., social) differences in the first expressions at match completion, which support the universality of these expressions, and it was instead on the podium (during medal ceremony) that cultural differences in expression were observed. Crucially, there were also no differences between congenitally blind and sighted athletes in spontaneous expression (Matsumoto & Willingham 2009). Collectively, these findings demonstrated that spontaneous expressions of emotion are not only dependent on observational (social) learning. Matsumoto and Willingham (2006) conclude that the initial expressions were probably not displayed because of the social nature of the event but were, rather, reflections of the athletes' emotional responses to the outcome of the match. This is fully in line with a second body of evidence coming from the embodied cognition literature.

In the growing embodied or grounded cognition literature (e.g., Barsalou 1999; 2008), research has demonstrated that individuals use simulations to represent knowledge. The simulations can occur in different sensory modalities (e.g., van Dantzig et al. 2008; Vermeulen et al. 2008) and in affective systems (Niedenthal 2007; Niedenthal et al. in press; Vermeulen et al. 2007). Thus, expressed emotion (such as facial expression) might also have the function of providing a grounded support of emotional knowledge (for a review, see Niedenthal 2007). Such a view is consistent with the observation that people automatically mimic a perceived facial expression (Dimberg 1982; 1990). The embodied cognition view suggests that mimicry constitutes part of the simulation (emotional mirroring) of perceived emotion to facilitate its comprehension. Such an interpretation can account for the fact that covert experimental manipulation of facial expressions (facial feedback hypothesis) influences emotional judgments. For instance, Strack et al. (1988) instructed their participants to place a pen in their mouth (as if they would write with it) either between the teeth (to produce a smiling face) or between the lips (to produce a sad face) while they assessed cartoons. The findings showed that smile induction increased positive ratings of the cartoons, compared to conditions where the smile was hampered (for further demonstrations, see also Niedenthal et al. 2001). In addition, the results of a study using electromyography (EMG) clearly confirm that the moderating impact of the facial manipulation was related to the muscular activity (Oberman et al. 2007).

Interestingly, recent studies show that the necessity to access the emotional meanings of words triggers discrete muscular activity in the face (Niedenthal et al., in press). Specifically, Niedenthal and colleagues found that their experimental participants expressed emotion when trying to represent discrete emotional content such as that related to disgust. For instance, when participants had to indicate whether the words *slug* or *vomit* were related to an emotion, they expressed disgust on their faces, as measured by the contraction of the levator labialis (used to wrinkle one's nose). Importantly, a follow-up experiment showed further that the blocking of facial activation (e.g., using a manipulation that requires holding a pen laterally between one's lips and teeth; Niedenthal et al. 2001) disrupted the emotional judgment. This latter finding suggests a causal role (rather than simply a correlational role) of facial activation observed in emotion word processing (Niedenthal et al., in press).

Collectively, the aforementioned literature provides good evidence that perceiving and thinking about emotionally significant information involves the re-experience (i.e., *embodiment*) of this emotion. And this re-experience often involves the display of a facial expression of emotion.

The SRFB relies in part on the findings that females and males do not express emotions the same way. However, gender differences in expressed emotions might also be a demonstration of gender differences in the conceptual organization of emotions. These may be related to previously demonstrated innate

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structural gender differences in brain activation during emotional situations (e.g., Aleman & Swart 2008; Gur et al. 2002). Furthermore, individual and cultural differences in emotional expression (e.g., Elfenbein & Ambady 2002) can be comfortably accounted for in theories of embodied cognition (e.g., Niedenthal & Maringer 2009). In sum, while the specifics of the appearance and timing of facial expressions are unquestionably influenced by social learning (and context), the precise developmental and functional proposals of the SRFB do not appear to me to account for all of the findings in the vast literature on the facial expression of emotion.

Expressed emotions, early caregiver–child interaction, and disorders

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Andreas Wiefel[a] and Renate Schepker[b]

[a]*Charité-Universitaetsmedizin Berlin, D 13353 Berlin, Germany;* [b]*Zentrum für Psychiatrie Südwürttemberg, D 88214 Ravensburg, Germany.*

andreas.wiefel@charite.de **renate.schepker@zfp-zentrum.de**

http://kjp.charite.de/patienten/baby_und_kleinkindsprechstunde

http://www.zfp-web.de/K2/index.php3

Abstract: In addition to the socio-relational framework of expressive behaviors (SRFB), we recommend integrating theoretical and empirical findings based on attachment theory. We advocate a dynamic interpretation of early caregiver–child interaction. The consequences of models from developmental psychology for the occurrence of psychopathology are demonstrated from a clinical perspective.

Vigil's interpretation is a major step in summarizing recent knowledge about emotional behavior guided by Darwin's concept of the variation of expression of emotion. We would like to add that human behavior in general necessarily has its roots in the earliest caregiver–child interaction. In humans, any kind of behavior occurs in a context of *extra-uterine social prematurity*; that is to say, in a psychophysical state when terms such as "capacity" or "dominance" cannot easily be applied.

To understand human emotional development, we must go beyond the concepts of "fitness," "cost-benefit," and so on, because human babies are "unfit" and depend so much on the caregiving function. Hamlin et al. (2007) conducted an amazing social-task experiment with 6- to 10-month-old healthy infants and found that "The capacity to evaluate other people is essential for navigating the social world" (p. 557). A baby's crying, for example, may not necessarily be a gesture of submission, but instead can be an act of dominance, inducing the appearance of a caregiver (and, of course, then constitutes a fitness advantage). If this fails to happen too often, helplessness and depression follow, and crying loses its meaning as a specific social signal and only expresses despair in lieu of other outlets.

Vigil's capacity and trustworthiness components represent "within" cues, whereas interaction competencies as "between" cues might be additionally meaningful in a broader sense of early mental development. Attachment theory (Ainsworth & Bowlby 1991), as a key feature in understanding human socio-emotional development in early infancy, could be an expansion of Vigil's theoretical framework. Bowlby's main construct is the infant's dependence on the presence of a sensitive caregiver responsible for providing a "secure base" in an asymmetrical relationship. Thus arise the "inner working models" in the infant that are supposed to influence developing personality traits. Continuing the concept of "emotional availability," Emde (1980) points out the dyadic and dynamic aspects of emotional development in the first year of life.

As an ethological model, attachment behavior shares the central topic of the socio-relational framework of expressive behaviors (SRFB) – that is, with either proximity-seeking (affiliative) behavior or withdrawn (avoidance) behavior – but in a reflexive and intuitive manner. Patterns of infants' behavior such as displays of vulnerability (e.g., bowed head, gaze aversion, slow movement patterns, crying, and worrying behavior) are usually reactions to over-stimulation and tiredness, indicating the need for a break; whereas ongoing avoidance may emerge after experiences of neglect or maltreatment.

Corresponding to Vigil's social sphere model, empirical findings based on the emotional availability concept show the great predictive power of alternatively auto-regulative or interpersonal affect-regulation styles in mother–child interaction when the child is at the age of 4 months (Kogan & Carter 1996). In this light, Vigil's model for correlating individuals' social spheres and phenotypic expression could be augmented by such a "mothering" link. Beside a large body of pediatric literature, this can be supported by our own data concerning breast-feeding and bonding (Böge et al., in preparation). In comparing a clinical sample with a non-clinical one, we have found that breast-feeding is associated with a reduced incidence of developmental problems and psychopathology in children later in life – irrespective of socioeconomic status, prematurity, and other risk factors. Oxytocin-inducing "good mothering" behavior and affiliative and/or trustworthy behavior, such as more intense eye contact and proximity among females than among males, might thus also be specific to females on account of heightened receptor sensitivity, ensuring the healthy upbringing of the species.

But phenotypic behavior does not automatically represent internal states. For example, misunderstanding, apparent sensitive behavior, as well as any other double-bind communication, cannot be explained by the mechanisms of SRFB as a monadic model. The findings of changes in temporal lobe and amygdala, as well as increasing oxytocin and vasopressin levels in conflicting communication, might be indicative of an early "flight-or-fight" decision. Either on the basis of intuitive attachment, or dominance versus submissive behavior, those findings have been largely confirmed – also by our own data of elevated levels of cortisol in 4-month-old infants of mothers with postpartum depression (Bartling et al. 2006). Thus, it would be worth widening the focus on conflicting states and clinical disorders, to disorders other than only stress-induced ones. As the expression of emotion relies heavily on mother–child contact and the child's potential for developing a theory of mind, autistic spectrum disorders, as well as depressive disorders, are the most interesting ones for investigation. Video interaction analyses in a clinical sample showed specific patterns in correlation with diagnostic clusters, not gender (Wiefel et al. 2005).

We especially like Vigil's notion, towards the end of the target article, that certain behaviors which were previously thought to be maladaptive (signs of weakness or submissiveness), might in fact be functional in humans. However, alternatively, those *involuntary defeat strategies* could be understood as a compromise between genetic drift and the result of attachment experiences from the first year of life, and, therefore, could be proof of a cost-benefit advantage; for example, the concept of *learned helplessness* in common depression. We even dare to pose the hypothesis that most of the gender differences found in childhood between girls and boys (more intense expression of emotion, more submissiveness, more group adherence) might be protective factors for children's mental health that wear off in later life, as girls are epidemiologically less prone to behavioral symptoms at a young age than are boys. From our clinical viewpoint, beneath the well-known gender differences in the incidence of several disorders we actually observed an even more rapid shift of this phenomenon over the early age span in infant psychiatry (Wiefel et al. 2009). Certainly we found diminished gender effects in our clinical sample when psycho-social circumstances (but not the caregiver's sensitivity as a central cue in the field) were integrated (Witte 2006).

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A social-cognitive model of human behavior offers a more parsimonious account of emotional expressivity

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Vivian Zayas,[a] Joshua A. Tabak,[b] Gül Günaydýn,[a] and Jeanne M. Robertson[c]

[a]*Department of Psychology, Cornell University, Ithaca, NY 14853-7601;*
[b]*Department of Psychology, University of Washington, Seattle, WA 98195;*
[c]*Department of Biological Sciences, University of Idaho, Moscow, Moscow, Idaho, 83844-3051.*

vz29@cornell.edu tabak@u.washington.edu gg294@cornell.edu jmrobertson@uidaho.edu
http://people.psych.cornell.edu/~pac_lab/

Abstract: According to socio-relational theory, men and women encountered different ecologies in their evolutionary past, and, as a result of different ancestral selection pressures, they developed different patterns of emotional expressivity that have persisted across cultures and large human evolutionary time scales. We question these assumptions, and propose that social-cognitive models of individual differences more parsimoniously account for sex differences in emotional expressivity.

Imagine a hunter-gatherer society in which men hunt, facing dramatic surprises and life-threatening situations regularly. Men with facility in emotion regulation would be better hunters, promoting higher overall fitness; in contrast, women would face weaker selection pressure for emotion-regulation abilities. Such an evolutionary construction could predict why a functional magnetic resonance imaging (fMRI) study of cognitive reappraisal found neurophysiological evidence that men were more effective than women at down-regulating emotional responses to negative stimuli (McRae et al. 2008).

This evolutionary explanation is plausible. But, so is the following cultural explanation: Western societal norms and gender stereotypes differentially encourage men to down-regulate emotional responses to negative events (Brody 1997). Thus, adherence to societal norms of expressivity, which pervade everyday life (e.g., Simpson & Stroh 2004), rather than prolonged evolution favoring sensitivities, could also easily account for the fMRI findings.

Evolutionary accounts do provide a provocative lens through which to view modern human behavior. However, as the foregoing vignette illustrates, a concern with most evolutionary psychological theories, such as Vigil's socio-relational framework for expressive behaviors (SRFB), is that their hypotheses rely on a number of assumptions that are difficult, if not impossible, to examine empirically in human populations.

We question the validity of basic assumptions of the SRFB, specifically (1) evidence of patrilocality in the ancestral populations that gave rise to contemporary humans, (2) the extent to which patrilocality led to purported differences in emotional expressivity in ancestral populations, and (3) the likelihood that the selection pressures mediating these hypothesized sex differences have persisted across large human evolutionary time scales to result in modern sex differences. In light of these concerns, we question the SRFB's utility as an integrative framework for understanding emotion and sex differences. We propose that current social-cognitive models of human behaviors provide a more parsimonious explanation of emotional expressivity and any purported sex differences.

1. How prevalent is patrilocality across cultures? The SRFB's explanation of sex differences in emotional expressivity rests on the assumption that women and men faced different social ecologies, which imposed different evolutionary constraints. However, in nearly one-fourth of human societies included in Murdock's (1967) ethnographic database, which includes data from a myriad of societies, including preindustrial ones, the residence pattern in which men stay with kin and women move with non-kin (patrilocal residence) is not observed. Thus, these findings cast doubt upon the SRFB's assumed universality of patrilocality and patrilocality-induced sex differences in emotional expression.

2. Did patrilocality lead to adaptive sex differences in emotional expressivity in ancestral populations? Even assuming that the majority of ancestral human populations exhibited patrilocal residence patterns, the adaptive value of Vigil's purported sex differences in emotional expressiveness is unsubstantiated. According to the SRFB, women had to advertise trustworthiness to non-kin through submissive emotions. However, other evolutionary arguments (Cosmides & Tooby, 2000) suggest that such displays might have also been associated with costs. As a result, the cost of expressing emotions in distant (non-kin) relationships might have been relatively more costly than expressing emotions in close (kin) relationships; in the latter, costs arising from emotional expressions might have been offset because of incurred inclusive (shared) fitness benefits. Thus, based on this account, it is unclear why women, who were moving into distant relationships, did not limit their emotional expressiveness, and why men, who remained near kin, did not exhibit greater emotional expression with kin and limit expression of vulnerabilities to competitors.

3. Is there evidence that directional selection favoring sex differences in ancestral populations persisted throughout modern human evolution? The SRFB rests on the assumption that men experienced prolonged selection pressures that favored less expressiveness, and that women experienced prolonged (and opposing) directional selection favoring more expressiveness. Prolonged directional selection is unlikely, because the environment for which this trait has evolved has changed over the long course of human evolution. However, neither hypothesis can be directly tested in extinct populations.

Moreover, prolonged directional selection would have resulted in relatively large sex differences in emotional expressivity (Grant & Grant 1992; Kocher 2004). This is clearly not the case. The empirical reality is that substantial sex differences in emotional expressivity are not observed; One comprehensive review of research on emotion as expressed through behavior, self-report, or physiology, unequivocally concluded that "sex differences in emotionality are small, inconsistent, or limited to the influence of specific situational demands. ... Reviews do *not* support belief in sex-based affective differences" (Wester et al. 2002, p. 639, emphasis in original).

Furthermore, because sex differences in emotion facilities, when they appear, tend to be small (e.g., Montagne et al. 2005; see also Brody 1997; Wester et al. 2002), between-sex variability in emotion expressivity is actually *smaller* than within-sex variability. Indeed, men's and women's distributions of scores on a measure of emotional expressivity, assuming a small effect size of $r = .1$, overlap by 84.3%. Applied to the SRFB, this suggests that a substantial proportion of women display "masculine" patterns of capacity and trustworthiness cues, and a substantial portion of men display cues in "feminine" patterns. The high variance of this behavioral trait does not fit with expectations of prolonged, directional selection favoring sex-specific patterns of expressivity, as proposed by the SRFB.

4. Social-cognitive models of human behavior: A parsimonious account of emotional expressivity and sex differences in emotional expressivity. Key assumptions of the SRFB remain speculative. Specifically, the adaptive significance of sex differences in expressivity in ancestral human populations and the conservation of such purported differences both across cultures and throughout modern human evolution cannot be validated. Moreover, extant research suggests women and men are much more alike than different in their emotional expression. The large within-sex individual differences, relative to small between-sex differences, suggest that emotional displays are strongly influenced by contemporary context (e.g., Ambady & Hall 2002; Callahan et al. 2005) rather than ancestral sex differences in sensitivities (see Brody 1997).

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A more parsimonious account of emotional expressivity, as well as any possible sex differences in emotional expressivity, is offered by current social-cognitive models of individual differences and human behavior (e.g., Zayas et al. 2002; see Mischel & Shoda 1995; Shoda & Mischel 1998). Such models highlight the adaptive value of flexible emotional expressivity for both women and men, and the importance of culture and contemporaneous situational influences in guiding appropriate emotional displays and behaviors.

By accounting for evolutionary constraints *and* empirical and theoretical contributions from broad areas of psychology and neuroscience, such social-cognitive models construe a person's behavior as a function of his or her processing system (e.g., sensitivity to displays) and the particular contingencies present in the situation. This position is in stark contrast to Vigil's current assumptions that sex differences in emotional expressivity reflect differences in ancestral selection pressures for men and women. Additionally, because social-cognitive models allow the generation of falsifiable hypotheses, they have broader potential for empirical scrutiny.

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Author's Response

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The socio-relational framework of expressive behaviors as an integrative psychological paradigm

Jacob Miguel Vigil

Department of Psychology, Center for Applied Research in Child and Adolescent Development, University of North Florida, Jacksonville, FL 32224-2673.

j.vigil@unf.edu **http://www.unf.edu/~j.vigil/**

Abstract: This response shows how the socio-relational framework of expressive behaviors may be used to understand and predict social psychological processes, beyond sex differences in the expression of emotion. I use this opportunity to elaborate on several key concepts on the epigenesis of evolved social behaviors that were not fully addressed in the target article. These are: evidence of a natural history of masculine and feminine specialization (sect. R1); phenotypic plasticity and range of reactivity of social behaviors (sect. R2); exploitive and protective functions of social behaviors (sect. R3); and the role of cognition in some affective responses (sect. R4). I conclude by highlighting (in sect. R5) future directions for psychological research from a socio-relational basis.

I am pleased that my target article is largely viewed as controversial yet useful for understanding sex differences and broader organization of social behaviors in humans. My goal was to present an integrative theoretical framework of key social selection pressures that may have been involved in the evolution and contemporary development of cognitive and behavioral mechanisms for regulating interpersonal relationships. I specifically focused on sex differences in masculine and feminine behaviors as an example of the many areas that the *socio-relational framework of expressive behaviors* (SRFB) may be applied. In the target article, I conceptualize just some of the cost-benefit fitness trade-offs that may have supported situation-based and condition-based variation in emotional expressivity. I use the current opportunity to comment on several key concepts that are fundamental to the commentary responses, but were necessarily truncated in the target article. I hope that by integrating these precepts into the existing framework, the reader is left with a broader conceptual basis with which to better understand and examine the human organism.

This response is divided into five sections to reflect the major themes of the commentaries. In the first section (R1), I discuss the commentators' concerns with some empirical and theoretical inferences from the target article. I then show how an evolutionary approach to studying sex differences may integrate many of the "alternative" models the commentators presented, while addressing corollary hypotheses that are difficult to explain from the discrete models themselves. In the second section (R2), I use the example of sex differences to describe how personal experiences operate within evolved ranges of reactivity to produce both evolved dispositions (e.g., overall group differences) and individual differences (e.g., within sex variability). In the third section (R3), I describe how social psychological mechanisms operate to exploit the reciprocity potential of others, while protecting the self from being exploited. In the fourth section (R4), I discuss the potential roles of some cognitive processes (e.g., emotional awareness, visceral sensations) for regulating affect. In the final section (R5), I describe how the SRFB may be useful for guiding some of the future research the commentators highlighted.

R1. Natural history of masculine and feminine behaviors

R1.1. Empirical issues related to the biology of sex differences

Of all the major findings that I described in the target article, a few empirical inferences were parsed by the commentaries. The first finding is greater facial expression–processing abilities in females, with the exception of anger, of which males are predicted to be more sensitive. Consistent with the SRFB, commentators **LoBue & DeLoache** show that females are better at detecting social, but not nonsocial, stimuli as compared with males. However, LoBue & DeLoache also present some data that suggest that both males *and* females detect threatening emotions (e.g., anger and fear) more efficiently than non-threatening emotions (e.g., happiness and sadness), leading the researchers to suggest that males and females may not differ in the ability to detect threat. I recently conducted a preliminary analysis that may shed light on the commentators' findings.

Using a large, representative sample of young adults ($n = 808$), I found that women were just as likely as men to perceive threatening (i.e., anger, fear, disgust) versus non-threatening (i.e., joy, sadness, surprise) emotions from ambiguous facial stimuli. However,

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when the emotional interpretations were re-coded as either signaling dominance (i.e., joy, anger, disgust) or submissiveness (i.e., sadness, fear, surprise), males were more likely to perceive the former (Vigil, submitted a). These findings suggest that males and females differ in how they interpret dominant and submissive cues in others. The SRFB explains these phenomena as reflecting a natural history characterized by the interchange of higher levels of capacity cues among males and trustworthiness cues among females. Likewise, the SRFB predicts that most sex differences in (social) perceptual and expressive biases should become exaggerated upon adolescence (not at the ages of children that **LoBue & DeLoache** investigated, for example). Historically, adolescence is when males and females may have required, and thus developed, specialized social skills for regulating different types of relationships. This age-dependent constraint may also explain why **Izard, Finlon, & Grossman** (**Izard et al.**) did not find sex differences in emotional expression in their samples of preschoolers (though see the comments further regarding racial differences in emotional expressivity). Clearly, we need more research to examine the universality of age and sex differences in the expression of emotion across people from varying cultural backgrounds.

Other empirical concerns were for the predictions that males are more sensitive to take risks (displays of capacity) and that females are more sensitive to display altruism (e.g., kindness). To address these hypotheses, **Basso & Oullier** highlight findings from two experimental tasks (the "Dictator Game" and the "Ultimatum Game") which involve the exchange of economic credits. The researchers found support for the prediction that males are less risk averse than females, but contend that females show no greater willingness to engage in true altruism (costly actions) than do males. The latter findings can be understood with a clearer description of what the SRFB actually predicts.

First, unconditional self-sacrifices are rarely adaptive in most contexts. It would therefore make no sense for either sex to endure an actual cost to personal fitness, without the possibility of a reciprocated reward. Rather, the SRFB predicts that females are only more sensitive to demonstrate the appearance of, or willingness to engage in, altruism, not the actual and unconditional provisioning of resources, as the experimental tasks demanded. I would therefore predict that, while not actually engaging in costly actions (e.g., expending one's credits), females will report greater compassion and felt guilt for their actions (e.g., not giving more credits to their experimental partners). Males, in contrast are predicted to demonstrate higher levels of capacity cues such as felt pride for successfully "cheating" their partners.

Further, the experimental tasks that **Basso & Oullier** describe are not as analogous to the functional display of emotions (especially trust cues) and for the overall negotiation of relationships as the commentators imply. This is because actual relationships are formed and maintained over time. In the experimental situations, participants are constrained by a limited number of options, aware of the eventual termination of the task, and not dependent on their experimental partners in any meaningful way (e.g., for sustained self-enhancement or protection). Another drawback of using economic games to simulate social interactions is that the games rely on the exchange of arbitrary (e.g., unearned) credits, again limiting the inherent interest of the tasks themselves. An extremely high level of creativity will surely be needed to design experimental protocols that can even remotely simulate the actual importance of non-kin relationships, as well as the scope of dynamic behaviors that humans use to regulate their relationships.

R1.2. Theoretical issues related to the biology of sex differences

The two major contentions that some commentators have with my theoretical models concern the utility of using an evolutionary approach to understanding human sex differences, as well as the specific types of sexual selection principles that would have favored their expression. The first set of issues is whether contemporary sex differences in social psychology even exist at all, and if so, whether they are solely the result of evolutionary forces. Alternative models to the evolutionary approach often highlight the importance of culture, proximate learning mechanisms, and motivational forces such as "norm formation" and "gender stereotyping." Several of the commentators (e.g., **Fugate, Gouzoules, & Barrett** [**Fugate et al.**]; **Vermeulen**) took this approach, and **Zayas, Tabak, Günaydýn, & Robertson** [**Zayas et al.**] described several reasons why sex-typical emotionality can be better explained by models that emphasize individual learning processes rather than naturally selected behaviors. Specifically, Zayas et al. contend that: (a) patrilocality is not favored across all human cultures, (b) patrilocality does not result in unique social selection constraints for males compared with females, and (c) human males and females do not express emotionality differently and, *if* they do, that the differences are not the result of biological dispositions. The authors conclude by describing a social modeling/learning explanation of gender development which appears to be more complementary than contradictory to the SRFB and the overall thesis that sex differences in social behaviors are rooted in evolutionary design.

First, human patrilocality is an example of a plastic or facultative phenotype. *Phenotypic plasticity*, or variability in the expression of traits, is an essential characteristic of ontogeny because it enables the individual to develop phenotypes that are specialized for different types of ecological conditions. As I described in the target article, patrilocality is the predominant social migratory system in traditional societies; however, as evidenced through anthropological records, this pattern does vary somewhat according to local, ecological conditions. These conditions appear to encompass historical ties between environment factors (e.g., regions where resources are scarce and groom labor is used as a bride service) and social customs (e.g., historically low levels of inter-group hostility). Under these special conditions, humans may benefit from alternative locality customs. Under more typical conditions (i.e., involving inter-group hostility), male-biased philopatry is associated with numerous biological incentives (see Geary 2009), as elaborated by **Madison** and as I describe in further detail below (see sect. R1.3).

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Second, **Zayas et al.** suggest that because certain types of social ecologies (e.g., consisting of acquaintances) are associated with fitness-reducing costs, nature would not have favored women to expose themselves to these conditions. However, according to evolutionary reasoning, it is *because* interacting with different types of affiliates is associated with both fitness benefits (e.g., genetic outbreeding) as well as costs (e.g., risk of rejection), that these behaviors have been designed by evolutionary trial and error to evidence plasticity. The existence of cost-benefit fitness trade-offs is a necessary condition for the evolution of phenotypic flexibility, and as such, the facultative expression of social philopatry, differential motivations to form distinct types of relationships, and the development of expressive behaviors that facilitate these goals. The importance of these processes is what motivated me to focus on *how* variability in social behaviors can be understood as a function of certain fitness-related cost-benefit trade-offs that covary with specific conditional factors (e.g., sex, age, personal experiences, social network dynamics, ecological factors such as climate) and situational stimuli (e.g., the presence of different audiences).

Third, **Zayas et al.** question the evidence that human males and females have evolved the proclivity to develop specialized social behaviors, based on the modest effect sizes that are sometimes found in this type of research. They support this concern by stating that "prolonged directional selection would have resulted in relatively large sex differences in emotional expressivity" and "this is clearly not the case." However, it is unclear how the commentators estimate what should be the appropriate effect size for psychological processes. From my perspective, nature selects biological designs to be highly specialized for their own set of environmental contingencies, and because such specialization often involves phenotypic plasticity, it is implausible to assume a degree of evolutionary design from the weight of a statistical effect size. In terms of sex differences, as long as a mean sex difference in psycho-biological processes exists, even at a proximate level of causation (e.g., memory retrieval, as suggested by **Fugate et al.**), the presumption should be that some degree of psychobiological specialization has taken place.

Finally, **Zayas et al.** suggest that sex differences in emotionality are driven by contemporary, individualistic factors (e.g., personal development of social norms) *rather than* evolutionary pressures. I don't agree with this dichotomy and instead believe that societal experiences (e.g., exposure to gender norms) and the psychological (e.g., learning) mechanisms that process these experiences are ultimately constrained by, and thus a reflection of, biological structures and sensitivities. As a result, models that rely exclusively on social learning/modeling explanations of sex differences, in the absence of evolutionary specialization, are not able to account for (a) why males and females usually identify with, and model, same-sex individuals; (b) why mothers and fathers interact with their children differently (e.g., talking vs. doing activities) across generations; (c) why males and females form distinct peer networks; (d) developmental and even prenatal sex differences in the rudiments of social behaviors (e.g., eye-contact and touching); and (e) cross-cultural universality of masculine (e.g., physical violence) and feminine (e.g., crying) behaviors.

R1.3. Theoretical issues related to the sexual selection of sex differences

Within the evolutionary school of thought, **Lozano** makes a number of excellent points regarding the utility of examining both *intra*-sexual and *inter*-sexual selection forces to account for human sex differences. Lozano highlights several biological scenarios that may be related to sex-typical behavior patterns, including the possibility that masculine and feminine dispositions are the products of inter-sexual selection pressures (e.g., similar to face and body shape) rather than skills that are needed to manipulate same-sex relationships. Of course, intra-sexual selection pressures often operate in parallel with mate preferences, resulting in behaviors with pleiotropic functions. According to the SRFB, for instance, traits that signal capacity (e.g., physical attractiveness) and trust (e.g., kindness) are essential for attracting all types of (non-kin) relationships. These traits should thus be advantageous for regulating interactions with romantic and non-romantic peers.

However, let me directly address the crux of **Lozano**'s hypothesis: that dominance may signal maturation and submissiveness may signal youth, and thus human mate preferences drove the evolution of masculinity and femininity. The reasons why sex differences in emotionality were probably not selected by mate preferences, irrespective of within-sex competition pressures, is because mate preferences cannot account for (a) implicit preferences for same-sex friendships, (b) social motivations to construct unique peer networks, and (c) sexually dimorphic social styles in early development (i.e., prior to puberty). Moreover, (d) sex-typical emotive gestures such as crying in females and aggression/threat promotion in males are not directly preferred in prospective mates, at least not to the same extent of well-established mating characteristics such as age, beauty, and resource acquisition. Finally, males' and females' social styles could not have been selected from mate choices, because (e) these are the very distinctions that often result in "miscommunication" between the sexes, a phenomenon that is more likely to deteriorate, rather than strengthen, pair bonding.

Lozano is therefore correct in stating that intra-sexually selected traits can also affect mate choices; it is evident (and predicted) that they sometimes do. However, I strongly believe that the majority of the dimorphisms (e.g., social motivations, emotional expressivity, and speech styles) that I reviewed in the target article are probably the result of intra-sexual selection pressures. In support of this hypothesis, I recently found that the previously mentioned pattern of males and females to perceive differential cues of dominance or submissiveness in facial stimuli is moderated by sex-typical relationship dynamics (Vigil, submitted a). Males with larger social spheres (i.e., numbers of friendships) were more likely to perceive dominant emotions (e.g., joy and anger) than males with smaller social spheres, and as compared to females in general. Regarding Lozano's related comment on the evolution of romantic love, it is unclear whether this sensation is expressed differently by males and

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females, and, if it is, whether such differences were selected by mate preferences and thus used to facilitate mating and/or parenting strategies.

I nonetheless agree with **Lozano** that the SRFB can only be enhanced with the integration of models that can incorporate the simultaneous operation of additional forms of selection pressures that are known to drive sex differences in social behaviors (e.g., differential parental investment). In this sense, I see male-biased philopatry as a supplementary adaptation to the basic human mating strategy of resource acquisition in males. If males can enhance mate value through resource inheritance and if patrilocality can enhance resource inheritance, then this form of philopatry may directly result from human mating constraints. Thus, we may be able to organize a tentative chain of selection pressures (e.g., parental investment → mate preferences → male-biased philopatry → sex-typed social styles) that can more fully account for the evolution of human sex differences in emotionality.

R2. Range of reactivity of phenotypic expression

R2.1. Ultimate versus proximate levels of analyses

It is important for social scientists to remember that psychological phenomena can be adequately explained through both *proximate* and *ultimate* levels of analyses (Tinbergen 1963). Proximate explanations incorporate physiological, situational, and experiential mechanisms and are able to answer *what*-type questions (e.g., what learning experiences contribute to sex differences). This level of analysis is essential for measuring individual differences in phenotypic expression. Ultimate explanations instead incorporate micro- and macro-evolutionary forces and are able to answer *why*-type questions (e.g., why are human males different or similar to human females). This level of analysis is essential for measuring the functionality (and thus often assumed existence) of the psychological phenomena. Sound ultimate levels of explanation operate in parallel with sound proximate levels of explanation, and to view them as contradictory is erroneous. At the same time, both proximate and ultimate levels of analyses are required to model the form and function of psychological adaptations. I attempted to do this in the target article by describing how some social, psychological processes in humans can be understood in the context of evolutionary cost-benefit fitness trade-offs that cause individuals to respond to personal life experiences and situational factors (e.g., audience characteristics) through sex-typical and sex-general behavior patterns. In the following subsections, I describe how two proximate sources of causation – individual life experiences and accompanying learning mechanisms – fit into the broader socio-relational framework.

R2.2. Range of reactivity

Some of the commentators contended that evolutionary approaches to understanding sex differences are too constrained, that they don't incorporate learning experiences, and that, because sex differences are sometimes not found, their existence should be denied all together. These contentions can be resolved through a brief description of the concept of *range of reactivity*. Ranges of reactivity simply refer to the continua of possibilities (and constraints) that any given phenotype can be expressed. Some types of phenotypes such as eye color are not as plastic and thus have very narrow ranges of reactivity; these phenotypes do not benefit from conditional modifications and are thus designed to be less influenced by environmental or experiential factors. Other types of phenotypes such as social behaviors are highly plastic and are more modifiable by life experiences. These phenotypes have wider ranges of reactivity that support the ontogeny of ecological specialization. As I mentioned earlier, phenotypic plasticity is driven by cost-benefit fitness trade-offs and operates to modify developmental trajectories in ways that optimize personal attributes, within the constraints and opportunities of the local environment.

An example of this concept for understanding sex differences in social behaviors is illustrated in Figure R1. Males and females have evolved different ranges of reactivity or proclivities to develop masculine and feminine behaviors. The specific points along the continuum at which people express their unique combinations of masculine/feminine traits are influenced by individual (e.g., genetic) and experiential factors and by the proximate learning mechanisms that process life experiences. Figure R1 shows that males and females both have wide ranges of reactivity to develop prototypically masculine/feminine behaviors, and more narrow ranges of possibility to develop atypical behaviors. Although there is a great deal of variance within each sex, males and females are sensitive to develop specialized expressive styles for regulating different types of social ecologies. This concept of range of reactivity thus makes it possible to integrate most of the "alternative," mostly proximate learning-based models that the commentaries have highlighted.

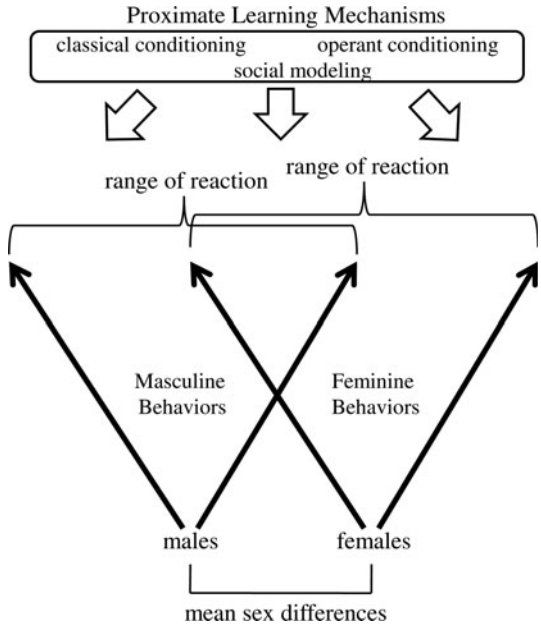


Figure R1. Epigenesis of evolved proclivities within a range of reaction. Males and females are sensitive to develop unique behaviors styles. Individual differences (e.g., genetics [not shown]) and learning experiences moderate the degree to which the behaviors are expressed.

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R2.3. Proximate learning mechanisms

For example, **Swain** describes interesting research showing that same-sex parent-infant dyads evidence more behavioral and arousal synchrony in their daily interactions as compared to opposite-sex dyads. These findings again highlight the utility of using intra-sexual models for understanding social behaviors, but also show how proximate learning experiences, such as *classical conditioning*, can strengthen sex-typical behavior patterns. As mentioned earlier (see **Fugate et al., Zayas et al.**), parents also reinforce sex-typicality through *social modeling* (observation and mimicking) mechanisms. Likewise, **Basso & Oullier** show how group demands (expected rules in organizational settings) can lead to acceptance and rejection, and thus how *operant conditioning* can alter sex differences in social behaviors. Similar arguments are made by **Fischer** and **Wiefel & Schepker**, who contend that different types of relational demands, such as history of trust, play a pivotal role in the expression of emotion.

The SRFB hypothesizes that sex differences in emotionality are largely based on the differential sensitivity to advertise trust cues. As noted by **Wiefel & Schepker**, the emphasis on trust links the SRFB to other models of social psychology such as "Attachment Theory" (Bowlby 1969). I believe the SRFB extends traditional applications of attachment models by showing why early childhood experiences (i.e., behavioral responses of others) are associated with the development of *specialized* and *functional* interaction styles. Infant-caregiver experiences probably form the basis of self-conceptualizations of reciprocity potential, as well as the basis for social expectations. For example, individuals who experience distrustful relationships in their life develop increased perceptual and expressive proclivities to detect and express anger (Vigil et al., submitted). Anger behaviors are in turn effective at provoking distancing responses from peers (e.g., Vigil 2008). Thus, this research shows that the types of learning that occur within relationships can and do alter the development of expressive styles (e.g., hostility) that primarily operate to regulate individuals' unique social conditions.

In an interesting caveat to the literature, **Izard et al.** found that minority children showed reduced sex differences in the expression of emotion. This finding is analogous to similar findings in adults showing reduced sex differences among African Americans as compared to European Americans (Vrana & Rollock 2002) and Asian Americans (Vigil, in preparation). The ethnic discrepancies are probably the result of variation in social, structural (e.g., in terms of social spheres), and relational demands (e.g., relative earning capacity and perceptions of peer trust) among males compared with females, for people from different cultural backgrounds.

In a related commentary, **Fischer** describes how females express more antagonistic aggression in intimate situations with less traditional and more egalitarian relationship partners. I agree with Fischer that the findings can be explained according to the expected outcomes of the anger behaviors. Specifically, the SRFB predicts that individuals should express more risky forms of aggression, such as antagonistic anger, when their relational partners are perceived to have lower *capacity* (to retaliate) than themselves (target article, Fig. 1). Lastly, I would like to clarify Fischer's insinuation that females express higher levels of aggression than males. These findings are typical for research relying on self-report measures, which usually include a multitude of non-risky behaviors (e.g., arguing with peers). In ethnographic studies that measure acts of violence that involve a greater risk of death (e.g., homicide), males are far more likely to express these behaviors than are females (e.g., Archer 2009).

R3. Social behaviors as exploitive and protective mechanisms

R3.1. Human psychology as an exploitive system

It is interesting that some of the commentators, such as **Goldstein Ferber**, tend to view my models as too individualistic and not focusing on mutual goal attainment, whereas other commentators, such as **Buss**, instead imply that I could have emphasized individual fitness gains even more strongly. Buss distinguishes three types of resource acquisition strategies (i.e., personal efforts, cooperative efforts, and exploitive efforts), whereas I consider all three strategies as operating off the same exploitive, and hence personal-fitness-enhancing, motivations. I agree with Buss that anger and related capacity displays (e.g., signals of prowess) operate to exploit the reciprocity potential (e.g., material resources, fertility) of others. However, I also believe that trustworthiness displays (e.g., expressed kindness and vulnerability) are equally exploitive. By advertising trustworthiness cues (e.g., via crying) to other people, individuals are able to exploit the motivation of others to advertise their own reciprocity potential such as via sympathetic responses. Relationship formation may thus ultimately function as the context within which individuals can readily interchange reciprocal displays of capacity and trustworthiness with others in the form of expedient and continuous investment cues, respectively.

R3.2. Fundamental mechanisms of exploitation

One of the most important commentaries is from **Todorov**, who has been constructing a neurocognitive model of affective processing that is remarkably similar to my own. What is impressive about this convergence is that Todorov and I derived our conclusions from two very different analytical strategies. Todorov derived his models from a *bottom-up* approach, using empirical findings to build a conceptual model, whereas my models were constructed from a purely *top-down* or theory-driven analysis. As predicted from my models, and as was found by Todorov, people evaluate others along two dimensions, what Todorov refers to as valence/trustworthiness and dominance/power impressions.

The SRFB extends **Todorov**'s findings in several ways that include: (a) conceptualizing the natural essence of these social properties as fundamental components of reciprocity potential; (b) extending the utility of the dimensional models to explain variation in expressive behaviors including displayed affect; and (c) describing some cost-benefit fitness trade-offs that support situation-based and condition-based variation in expressive behaviors. Todorov

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and I agree that social, perceptual processing of capacity and trust cues in others precipitates affective responses in the individual, and that affective responses ultimately function to induce affiliation versus avoidance from others. I simply extend this argument to model the fundamental dimensions of expressive behaviors as behavioral advertisements of these same social properties. According to the SRFB, all forms of expressive behaviors (i.e., behaviors that are both observable and modified by the social context) are dynamic advertisements of capacity and/or trustworthiness cues, which ultimately function to control how other people respond to the individual.

I recently found support for this hypothesis as it relates to affective processing by examining how perceptions of other people's capacity and trustworthiness trait levels are associated with interpersonal dispositions and discrete emotive reactions toward the people (Vigil, submitted b). Specifically, I showed that trustworthiness impressions are parsimonious predictors of the motivational desire either to affiliate with (i.e., "form a friendship") or to avoid (i.e., "stay away from") social objects. However, simultaneous impressions of capacity trait levels are necessary (and sufficient) for predicting discrete affiliative (e.g., sympathy vs. admiration) and avoidant (e.g., fear vs. disgust) emotions, as predicted in the target article's Figure 1. The types of emotional reactions that individuals express in turn affect whether other people respond to the individual with either affiliative or avoidant dispositions of their own (see Vigil 2008). Collectively, these findings suggest that both the perceptual processing and expression of human affect can be understood along several broad dimensions of social relevance. Affect behaviors operate by advertising the essential properties of reciprocity potential (i.e., capacity and trustworthiness cues) in order to regulate social fitness by selectively promoting affiliation versus avoidance across the individual's relationships.

In this regard, I disagree with **Todorov**'s suggestion that broad conceptual dimensions of affective processing are insufficient for predicting specific emotional reactions in vivo. In fact, in the target article, I attempted to outline several overlapping dimensions that can be simultaneously applied for just this purpose. Again, some of these dimensions can be conceptualized as (a) the perception and (b) the expression of capacity/trustworthiness cues, (c) the motivation to promote affiliation versus avoidance (target article, Fig. 1), (d) the signaler's sex (Fig. R1), (e) recent life experiences (target article, Fig. 2), and (f) characteristics of the signaler's audience (target article, Fig. 3), among several other probable dimensions (e.g., climatic ecology and health status).

The predictive validity of these hypotheses will ultimately rest on the universality of what I presented as basic behavioral responses. For example, **Goldstein Ferber** questions whether people from different cultures (and whether different species) respond to expressions of vulnerability in trusted affiliates with increased social support. I believe that this, as with most of the broad response patterns that I described in the target article (e.g., distancing reactions toward angry peers), are universal to humans. I would also suggest that submissive displays (i.e., trustworthiness cues) are far rarer in nature than is the demonstration of dominant displays (i.e., capacity cues). Specifically, submissive behaviors should covary with the social complexity of each species. Species that form continuous relationships (e.g., certain primates, wolves, dolphins, elephants, and lions) should be most likely to signal trustworthiness gestures (e.g., pain behaviors, high-pitched utterances, non-threatening eye contact), as these mechanisms are predicted to be functional for regulating longer-term relationships.

R3.3. Variation in affective responses

Several of the commentators are concerned with the ability to predict certain social reactions (e.g., indecisiveness about others) and emotive gestures (e.g., different types of laughing and crying behaviors) that were not fully addressed in the target article. **Lozano** and **Goldstein Ferber**, for example, find my approach/withdrawal heuristic to be too constrained to integrate what were described as more dynamic social reactionary strategies, including wait and see, freezing, and simply revealing oneself (e.g., to potential predators). They also contend that individuals must monitor and implicitly process multiple cost-benefit fitness trade-offs that are involved with interacting with different people. I agree that interacting with any sort of environmental stimuli, and especially other people, which are the least predictable stimuli humans can encounter, present multiple and simultaneous costs and benefits, as described earlier. However, I suggest that a dichotomous (affiliative/avoidant) heuristic can sufficiently account for variant response behaviors as well as simultaneous appraisal processes. This is possible as long as humans have the heuristical algorithms for processing the *net* outcome of either affiliating with, or avoiding, others. From my perspective, wait-and-see strategies, such as experiences of curiosity, may operate as low-intensity or low-valence approach dispositions; for instance, motivating the future appraisal of others. Freezing behaviors, in contrast, are obviously more beneficial for evading dangerous stimuli, by using a behavioral strategy that is specialized differently than other forms of avoidant reactions (e.g., displays of fear or violence).

According to the SRFB, discrete affective sensations (e.g., feelings of sadness) should covary with, and could thus be predicted by, discrete expressive displays (e.g., sadness behaviors) and the systematic reaction of others (e.g., approach from intimate affiliates and avoidance from unfamiliar affiliates). This thesis could be applied to the study of variant forms of expressive behaviors throughout the life span, including *crying behaviors* in infancy and adulthood. I agree with **Wiefel & Schepker** that babies utilize crying as a powerful tool for manipulating others, and that caregivers play a key role in shaping the development of affective processes in children, such as through the proximate learning mechanisms I have mentioned. Wiefel & Schepker also describe how infants use crying to solicit attention, and that the attention can be needed for various reasons, including hunger, fatigue, and overstimulation. It makes sense that infants primarily rely on trustworthiness rather than capacity cues to manipulate others, as submissive gestures can best accentuate an infant's actual vulnerability and because these behaviors are most effective for regulating intimate, co-dependent relationships.

Lyons also does an excellent job of outlining the many possible functions (exploitive benefits) of crying behaviors,

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but misinterprets an associated premise from the SRFB. Lyons implies that I suggest that vulnerability displays (e.g., crying) are only functional by displaying one's actual willingness to reciprocate with others. Rather, vulnerability displays such as crying, worrying, and perhaps pain sensations are also adaptive by signaling reduced threat, which may simply be effective at signaling a *safe context* within which other people can advertise their own reciprocity potential (e.g., via sympathizing behaviors). I believe that humans are systemically motivated to advertise capacity and trust cues continuously to other people, given every available opportunity, including conditional and situational openings. This would create an inherent fitness incentive for providing other people with the opportunity to demonstrate their own reciprocity potential. It is therefore possible that humans produce certain behaviors, such as playful aggression and crying, to disarm the threat interpretations of others and to signal the opportunity to reciprocate social demonstrations of reciprocity with others, in a safe relational context, irrespective of more specialized relationship behaviors.

On a related note, **Lyons** mentions that crying isn't always perceived as attractive, a fact that is predicted by the SRFB. According to the target article's Figure 3, for instance, crying and other displays of vulnerability should be expressed and most positively received by proximate affiliates (e.g., family and close friends). Instead, these behaviors should be attenuated and aversively responded to by distal affiliates (e.g., acquaintances). Again, these are the types of cost-benefit fitness trade-offs that would have selected for the facultative adjustment of behaviors such as crying that are effective at soliciting social support from certain types of affiliates, while simultaneously averting interactions with other affiliates. These trade-offs are part of the foundation of my *social spheres hypothesis* (target article, Fig. 2).

I agree with **Lyons** that *smiling* is also an affiliative gesture, and hypothesize that these behaviors should be especially attractive (e.g., in terms of increasing "positive" trait impressions) among more distal affiliates, rather than intimate relationship partners. Unlike crying, which serves as more of a relationship maintenance behavior, smiling and laughing are largely used to solicit potential relationship partners. Still, **Fischer** describes several forms and functioning of smiling behaviors, including serving as a signal of affiliation (Duchenne smile), appeasement (closed-mouth smile), dominance (pride smile), or experiencing negative self-conscious emotions (e.g., embarrassed smile). Some of these smiles signal capacity, namely the types of smiles that display the teeth; these smiles should covary with dominant emotions (e.g., joy and anger). Other smiles, especially those that conceal the teeth, should instead covary with submissive emotions (e.g., sympathy and shame). Thus, it would appear as though humans use the teeth (e.g., canines) to signal capacity, perhaps through demonstrations of bilateral symmetry and overall healthiness. By concealing the teeth, humans may instead produce heuristical demonstrations of modesty, which may ultimately reduce threat perceptions in others. Again, the SRFB predicts that submissive (i.e., trust) cues are just as powerful at exploiting the reciprocity potential of others as are displays of dominance (i.e., capacity).

The function of smiles differs somewhat by sex. This is supported by the work of **Vazire, Naumann, Rentfrow, & Gosling** (**Vazire et al.**), which shows that males and females evidence unique associations between smiling behaviors and felt emotional sensations. In females, smiling covaries with affiliative moods, such as pride, enthusiasm, and inspiration (referred to by the commentators as positive emotions). In males, however, smiling is more strongly and negatively associated with avoidant emotions, such as anger, fear, and shame (referred to as negative emotions). Because males have evolved the proclivity to advertise their capacity (e.g., prowess) and to conceal their vulnerability (e.g., shame, pain, crying, frustration, worry), it makes sense that they should advertise various forms of dominance behaviors (e.g., teeth-baring, threat stare, erect posture, lowering voice-pitch) in coordination with submissive emotional states, relative to females. Of course the opposite pattern – for females to display submissive cues (e.g., concealing teeth, head lowering, raising voice-pitch) when experiencing dominant emotional states – is predicted as well. In any event, Vazire et al.'s research shows how biological sex is an important dimension of affective processing in humans.

Along similar lines, **Provine** accurately describes the effectiveness and sexual dimorphism of other types of affiliative gestures such as *laughing*. According to Provine, laughter is an honest signal of reciprocation because it occurs implicitly, often without conscious awareness, and because it is hard to voluntarily produce and give the impression of sincerity. I agree with Provine that laughing is a behavioral mechanism that is used to show appeasement and hence trust cues (e.g., via high-pitched vocal utterances) to others. Indeed, people selectively laugh *for* (certain) other people and not about the humorous content itself. **Li & Balliet** provide support for this hypothesis by describing how people initiate *humor* to indicate affiliative intentions, and humor is in turn associated with, and effective at demonstrating, affiliative dispositions to other people. I agree with Li and Balliet that smiling, laughing, and humor operate by adjusting the display of both capacity and trustworthiness in ways that induce affiliation from others. I also agree that different types of humor may operate to serve specialized functions (e.g., maintenance of existing relationships vs. solicitation of novel relationships), which should covary with the structural properties of the humorous content itself (e.g., self-degradation vs. degradation of others).

Tickling and *tear production* are also elaborate affiliative gestures that are used to strengthen bonding with proximate (e.g., intimate) affiliates via the behavioral display of vulnerability. In the case of tickling, vulnerability is exaggerated by providing access to sensitive areas of the body (e.g., neck, abdomen) and becoming catatonic during intense laughter. In the case of tear production, vulnerability is exaggerated by occluding visual acuity with a bodily fluid. Here again, we see the natural organization of phenotypic forms, functions, and the reactions of other people. Given the power of these basic behavioral mechanisms for regulating social fitness, it is surprising that they are given much less scientific attention than more "cognitive" social, psychological processes.

R3.4. Social behaviors as exploitive defenses

Buss highlighted an interesting concept: behaviors that protect the self from being exploited by other people.

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From my perspective, this concept is captured by the entire set of responses that I referred to as *avoidant behaviors*. Individuals should produce these responses when they perceive a risk of being exploited by other people, either through direct interactions with a dangerous person or via indirect fitness-losses (e.g., reputational consequences and comparisons with higher-status people). I agree with Buss that defensive heuristics are sometimes manifested as hegemonic masculinity (e.g., physical prowess and less risk aversion) such as through exaggerated aggression by males. However, it should also be recognized that defensive mechanisms can also operate through trust cues, such as appeasement and vulnerability displays. Submissive gestures such as self-reported shame, guilt, and subservience (e.g., asking questions) may be effective for protecting oneself by lowering threat interpretations and inviting reciprocal displays of kindness or mercy from others, as described earlier.

R4. The role of social cognition in the SRFB

R4.1. The hierarchical organization of social psychology

The psychological sciences are currently hindered by the lack of unity on the organizational primacy and supporting roles of human thoughts versus feelings versus behaviors. Do thoughts and feelings ultimately support the adaptive qualities of expressive behaviors, or do behaviors ultimately facilitate the fitness objectives of thoughts? Alternatively, both thoughts and behaviors may be codependent, evolving in parallel and reliant upon support from the other for fitness enhancement. The answers to these hypotheses are imperative for understanding the form and function of human emotionality.

I ascribe to the general view that *only* behaviors can impact personal fitness. This is because a thought or feeling in and of itself cannot result in self-sustainment (e.g., survival) or self-enhancement (e.g., reproduction) without an associated modification in one's own behavior or in the behavioral reactions of other people (James 1884). It therefore makes sense that, across all animals, including humans, basic learning mechanisms and associated cognitive processes (e.g., attention, perception, sensational awareness, information processing, and rationalization) can affect fitness only by altering actual behaviors. From the basis of this perspective, emotions primarily serve social expressive functions. This position is further supported by studies that show that: (a) blind and perhaps cognitively impaired people are emotionally expressive; (b) children (e.g., infants) are sensitive to mimic and express emotions at earlier ages than they are generally believed to engage in operational learning; (c) normative emotional development unfolds through social interactions; and (d) emotive gestures (e.g., teeth or weapon baring) are more universal in nature than the sensations that we often refer to as "feelings." As **Lozano** aptly states, "evolutionarily, it only matters what emotions do, not how they feel."

Still, many of the commentaries took the contrary approach, instead emphasizing intra-individual cognitive processes (e.g., self-reflection, rationalization, and cultural norm appraisal) over the primacy of social expressive mechanisms. According to **Izard et al.**, these cognitive-based approaches represent the focus of the majority of emotion researchers. The commentators justified this position by citing the fact that affect is sometimes experienced in the absence of an apparent social situation. **Vermeulen** elaborates on this theme by describing how congenitally blind children express smiles similar to sighted individuals, the implication being that emotions are not always socially relevant and may therefore serve intrapersonal functions (e.g., self-reflection). As I suggested in the target article, this inference is analogous to the reasoning that: because people sometimes talk to themselves, and because deaf children can learn to speak, human language evolved to communicate to the self. In the following section I describe some potential reasons why emotions may consume the human consciousness and *feel* like important, self-reflective processes.

R4.2. The form and function of emotional experiences

The feelings or experience component of affective responses is usually the first concept that people think of when asked to define an emotion. However, according to the reasoning mentioned above, felt experiences are limited to a supplementary or facultative role in the evolution of emotionality; that is, they are only capable of enhancing fitness vis-à-vis modifications to specific behaviors. In the target article, I provided no justification for the inclusion of emotional experiences and may have implicitly de-emphasized the importance of felt sensations for daily functioning. If, as I proposed, the selective interchange of heuristical expressive cues *is* effective for regulating individual relationships (i.e., promoting attraction vs. aversion) and hence overall social fitness, then *why do humans (need to) feel emotional experiences at all*? This question can be further parsed by asking: Why are humans cognizant of emotional experiences; why are emotional experiences valence-based (e.g., felt along pleasant and aversive dimensions); and how does feeling an emotion enhance personal fitness?

The first question is difficult to analyze, but can be viewed along two opposing hypotheses. One hypothesis is that emotional awareness is simply a by-product of a broader adaptation to be consciously aware. Another hypothesis is that emotional awareness is instead specific and functional and hence an evolved adaptation in and of itself. I tend to lean towards the latter hypothesis for several reasons. First, humans are not aware of all bodily sensations (e.g., what it feels like to store iron in the liver), but only certain ones, suggesting a special design for the ability to acknowledge emotional sensations. Second, emotional experiences are not just consciously observed, but are also felt in *seemingly* important ways. Third, several cognitive psychologists have suggested that many of humans' comparatively unique mental faculties, such as intelligence, consciousness, and voluntary thought processing, were the products of, and ultimately serve, social manipulatory functions (e.g., Dunbar 1998; Geary 2005; Humphrey 1976). If these complex cognitive abilities evolved to regulate social relationships, then it is certainly possible that the awareness and experience of felt emotions may be designed for related purposes.

An associated hypothesis is that visceral experiences of pleasantness and aversion may have evolved to *calibrate* or otherwise differentiate the impact of significant life events in ways that enhance the efficacy of interpersonal interactions. By experiencing varying degrees of felt

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sensations (e.g., feeling slightly down vs. extremely down) in coordination with different types of life experiences, individuals may be better able to solicit sufficient degrees of responses (e.g., provisioning) from others. Likewise, inter-subjectivity (dual awareness) of the feelings of others (e.g., knowing what is feels like to experience mild vs. severe pain) may enable individuals to better qualify their own responses toward others without overextending personal resources such as time. From this perspective, humans are not just aware of arbitrary cognitive sensations, but rather, that these sensations exist and become accessible for fitness-enhancing purposes, by facilitating the *selective* interchange of reciprocity potential with other people.

Finally, I propose the thesis that *humans may experience the biological affects (e.g., emotions, moods, anxiety, pain) for the sole purpose of showing or talking about them to other people.* For example, one hypothesis is that emotional experiences may operate to *sustain* the behavioral advertisement of the felt emotions; this would be functional for prolonging the ability to solicit beneficial behavioral responses from others. A complimentary hypothesis is that humans may experience emotions (e.g., pride and guilt) in order to *better convince* others that one's behavioral advertisements are genuine. That is, by feeling emotions (or contextualizing emotions, as **Fugate et al.** suggest), individuals may be more effective at communicating the sincerity of one's relative state of capacity and trustworthiness attributes to others. From this perspective, it therefore makes sense that emotions *feel* important; they may be designed to do just that. By convincing oneself of the relevance of an emotional representation, humans may be better able to demonstrate to others that one's abilities and intentions are sincere.

Empirically, it is very difficult to separate cognitive processes (e.g., rationalization) that may be involved in emotion processes from the expressive properties of a self-report. Taken further, this confound opens up the possibility that many forms of self-reported information, such as self-descriptions (e.g., self-esteem) and social opinions (e.g., political ideologies), could largely operate to convey specific social impressions (e.g., demonstrations of dominance or submissiveness) to others (e.g., Vigil, submitted c). It is therefore likely that many types of self-reported information may be more closely associated with behaviorism rather than outcomes of cognitive reasoning processes. At the very least, the fact that the content of some self-reported information cannot be easily separated from the social impressions that the information communicates should give researchers caution to consider the possibility that they may be measuring behavioral expressions in addition to, or rather than products of complex computations. For these purposes, my definition of a social expression – a behavior that is both observable *and* moderated by the social context – should be especially useful for distinguishing communicative versus non-communicative mental processes.

R5. Future directions for the psychological sciences

Finally, I will briefly highlight some broad directions for future research that can be drawn from the target article and commentaries. One area is *emotional heterochrony*, or the timing of expression of emotional development. From a life-history perspective, the timing of any form of developmental process is an evolved adaptation in and of itself, and thus subject to the same principles of expression (e.g., plasticity within a range of reactivity) as other phenotypes. In this sense, the timing of expression of emotional development (e.g., emergence of discrete emotions throughout childhood) should reflect specificity (e.g., consistency in temporal development) and functionality (e.g., for regulating relationships) in ways that are not currently being investigated.

Another area for future research is how people regulate their relationships in coordination with stochastic life events (e.g., everyday ups and downs) and significant personal experiences (e.g., a history of child maltreatment). Interpersonal victimization and situational hardships are associated with differential mood adjustments (e.g., increased vs. decreased aggression, respectively [Vigil et al., in press; submitted]). According to the SRFB, variable mood states should be adaptive for regulating different types of social interactions in accordance with both historical and recent social experiences and a dynamic interaction of the two. Along these lines, several of the commentators (e.g., **Wiefel & Schepker**; **Swain**) presented novel hypotheses on potential physiological substrates that may help link early relationship experiences (e.g., attachment styles) and subsequent psychological functioning. Neuroendocrine chemicals that regulate social bonding, such as oxytocin, will prove invaluable for future research in the social neurosciences.

A complimentary line of research is in the field of *evolutionary medicine* as it pertains to the socio-relational precipitates and consequences of disease, including proximate and ultimate factors that link psychological processes to physical health. Physical illness has relevance for social fitness, and social fitness has implications for physical health, probably via mechanisms that are not always obvious. I firmly believe that many physical health–related systems (e.g., immune functioning, pain perception, endocrine stress responses) have been evolutionarily co-opted, and are thus moderated (i.e., attenuated and exaggerated) by affective processes in ways that result in social benefits (e.g., compromising physical health to solicit social support). I have recently been examining these hypotheses in relation to pain perception, based on my intuition that pain experiences and displays are moderated by social information (e.g., life experiences and situational factors), similar to other affect behaviors (see also Craig 2009). By investigating how social stimuli modulate pain perception, we should be able to develop innovative therapy techniques and technological devices that can either simulate pain-reducing social stimuli or otherwise modulate how people process this information.

Finally, **Madison** took the unique approach of discussing potential societal implications of the predictions from the SRFB, including the evolution of sex differences in emotionality. For example, Madison suggested that the SRFB may be useful for understanding the perpetual cycle of male-on-female exploitation, such as domestic violence and raping behaviors in which the male default display (i.e., dominance) reinforces the female default display (submissiveness), and vice versa. Of course, females evolved counter defensive mechanisms for

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protecting themselves from such exploitation, as well as powerful exploitive mechanisms (e.g., crying behaviors) of their own. Moreover, it would appear as if sex differences in psychological functioning pervade many aspects of our lives, from beliefs about social policies to the differential interpretation of empirical data among male and female scientists. Males and females undoubtedly have different styles of communicating, with males expecting and appreciating capacity (e.g., dominance) displays from others, and with females expecting and appreciating cues of trustworthiness (e.g., submissiveness). With respect to such specialization, miscommunication between the sexes would seem to be inevitable.

R6. Conclusion

My objective in formulating the SRFB was to construct a top-down analysis of how and why humans evaluate, attract, and protect themselves from each other, and form and maintain different types of relationships for personal fitness gains. While I hope that I was effective at presenting some broad predictions of the SRFB, the models are still in their infancy and will require continuous scrutiny, refinement, and innovations to reach their full potential for hypothesis generation. I am therefore extremely grateful to all of my distinguished colleagues that have already, and may continue to contribute towards this goal.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

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