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

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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 trust-worthiness 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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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.

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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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.

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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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 socialrelational 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

& 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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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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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, makebelieve 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).

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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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 sociorelational 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 selftrustworthiness. 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 otherappraisals 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

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 sociorelational 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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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 nonthreatening. 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 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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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. Émotional 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

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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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.

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

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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 sexneutral displays (cf. McKibbin et al. 2008; Thornhill & Palmer

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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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.

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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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, objectoriented 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 microlevel 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 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 selfregulation, 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 fatherchild 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 parentrelated stimuli, infant laughing, and crying stimuli versus a control sound, the amygdala and anterior cingulate of nonparent 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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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

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

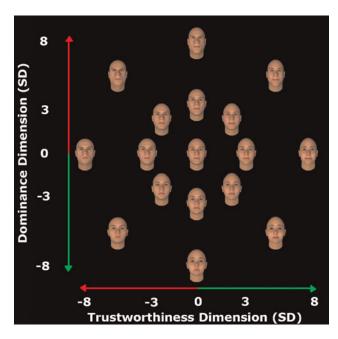


Figure 1 (Todorov). A data-driven computer model of variation of faces on the dimensions of valence/trustworthiness depicted on the *x*-axis and power/dominance depicted on *y*-axis. The variation of faces is in standard deviation units. The details of the modeling are described in Oosterhof and Todorov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

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.

Smiling reflects different emotions in men and women

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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 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.

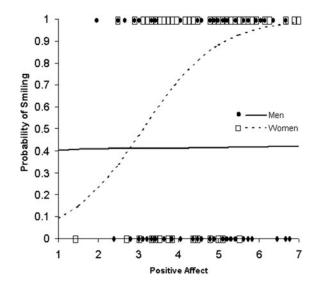


Figure 1 (Vazire et al.). Men's and women's probability of smiling as a function of positive affect. This plot is based on the results of two separate binary logistic regressions (one for men and one for women) predicting smiling from positive affect. The x-axis represents the possible range of positive 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

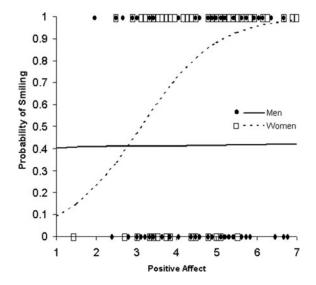


Figure 2 (Vazire et al.). Men's and women's probability of smiling as a function of negative affect. This plot is based on the results of two separate binary logistic regressions (one for men and one for women) predicting smiling from negative affect. The x-axis represents the possible range of negative 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.

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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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

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 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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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 socioemotional 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 breastfeeding 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).

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

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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 find-

ings 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

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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 costbenefit 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,

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).

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 costbenefit 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 costbenefit 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

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 sextypical 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

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 \rightarrow mate preferences \rightarrow male-biased philopatry \rightarrow 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.

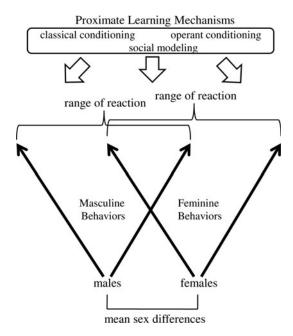


Figure R1. Epigenesis of evolved proclivities within a range of reaction. Males and females are sensitive to develop unique behaviors styles. Individual differences (e.g., genetics [not shown]) and learning experiences moderate the degree to which the behaviors are expressed.

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/trust-worthiness 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 costbenefit fitness trade-offs that support situation-based and condition-based variation in expressive behaviors. Todorov

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,

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 tradeoffs 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), appearement (closedmouth 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 appearement 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.

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 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 selfreported 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 healthrelated 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

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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