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Eye Tracking Unconscious Face-to-Face Confrontations: Dominance Motives Prolong Gaze to Masked Angry Faces

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Abstract

In primates, dominance/submission relationships are generally automatically and nonaggressively established in face-to-face confrontations. Researchers have argued that this process involves an explicit psychological stress-manipulation mechanism: Striding with a threatening expression, while keeping direct eye contact, outstresses rivals so that they submissively avert their gaze. In contrast, researchers have proposed a reflexive and implicit modulation of face-to-face confrontation in humans, on the basis of evidence that dominant and submissive individuals exhibit vigilant and avoidant responses, respectively, to facial anger in masked emotional Stroop tasks. However, these tasks do not provide an ecologically valid index of gaze behavior. Therefore, we directly measured gaze responses to masked angry, happy, and neutral facial expressions with a saccade-latency paradigm and found that increased dominance traits predict a more prolonged gaze to (or reluctance to avert gaze from) masked anger. Furthermore, greater non-dominance-related reward sensitivity predicts more persistent gaze to masked happiness. These results strongly suggest that implicit and reflexive mechanisms underlie dominant and submissive gaze behavior in face-to-face confrontations.

Keywords

dominance, motivation, social competition, gaze behavior, reward sensitivity

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A typical bar brawl often starts with two individuals in a face-to-face dominance contest. Overt social aggression may be prevented when one of them communicates submission by word or gesture. These mechanisms in humans seem to share commonalities with frequently observed behavior during dominance contests in primate social systems. In primates, dominance/submission relationships are established primarily by individuals staring at one another (staring endurance) until one averts the eyes (gaze aversion) to signal submission and avoid aggression (Mazur & Booth, 1998). It has been argued that a psychological stress-manipulation mechanism is operative in these face-to-face competitions between group members: Opponents who are "outstressed" by the exchange of threats and the endurance of staring may relieve their discomfort by submissive gestures, such as gaze aversion (Mazur & Booth, 1998).

The angry facial expression serves as an important threat signal in these dominance encounters (Öhman, 1986). In humans, dominance/submission behaviors have not yet been investigated using genuine staring endurance and gaze aversion. However, an extensive line of research with pictorial emotional Stroop tasks has shown that self-reported and hormonally indexed traits of dominance and submission predict vigilant and avoidant responses, respectively, to angry faces (van Honk & Schutter, 2007). For example, the behavioral activation system (BAS), trait anger, and basal testosterone levels are strongly associated with vigilant responses to (masked) angry facial expressions (Putman, Hermans, & van Honk, 2004; van Honk, Tuiten, de Haan, van den Hout, & Stam, 2001; Wirth & Schultheiss, 2007). Furthermore, avoidant responses to masked anger have been demonstrated in socially anxious subjects and in subjects with high levels of cortisol (Putman et al., 2004; van Honk et al., 1998, 2000). On the basis of these data, van Honk and Schutter (2007) proposed that vigilant and avoidant responses to angry faces in emotional Stroop tasks index

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motives of dominance and submission. Moreover, these findings were predominantly obtained in backward-masking conditions, which suggests that the mechanisms are implicit and reflexive, and therefore not part of the explicit psychological stress-manipulation mechanism that is thought to operate in social dominance encounters (Mazur & Booth, 1998).

However, rapid color naming, the dependent variable in the emotional Stroop task, is a rather indirect and ecologically weak measure of dominant behavior. The hypothesis put forward by van Honk and Schutter (2007) can be truly confirmed only by measuring interactive gaze behavior directly. For that reason, in the present research we replaced verbal color-naming responses with ecologically valid behavioral responses—gaze aversion in face-to-face confrontations.

To facilitate direct comparison with previous studies, we devised a new task akin to emotional Stroop paradigms. The required response, however, was rapid aversion of gaze from subliminally presented angry, happy, or neutral facial expressions (see Fig. 1). The anger gaze is a signal of dominance (Mazur & Booth, 1998), and characteristics of dominance or submissiveness, respectively, should inhibit or facilitate aversion of gaze from facial anger (van Honk & Schutter, 2007). Compared with an angry expression, however, a happy facial expression is a nondominant gesture (Ellis, 2006). Although a smile is mimicked reflexively, women do so more than men (Hess & Bourgeois, 2010), and indeed this difference is argued to be rooted in males' dominance motivation and higher levels of testosterone (Dabbs, 1997; Ellis, 2006). Furthermore, particularly after subliminal presentation, happy faces evoke positive evaluations of pictures (Murphy & Zajonc, 1993) and promote appetitive motivation (Winkielman, Berridge, & Wilbarger, 2005). Unlike an angry face, a happy face is thus an automatic and nondominant cue for reward.

The Behavioral Activation Scale (Carver & White, 1994) may well tap into both dominant and reward-sensitive behavior. It consists of three subscales: Fun Seeking (BASF), Drive (BASD), and Reward Responsiveness (BASR). BASF (e.g., "I often act on the spur of the moment") indexes willingness to engage in novel rewarding situations and is a measure of reward sensitivity unrelated to dominance or anger. BASD and BASR index affective response to rewards. Although anger or dominance are never explicitly mentioned in these subscales (e.g., BASD: "I go out of my way to get things I want"; BASR: "It would excite me to win a contest"), they are linked to susceptibility to anger-evoking scenarios (Carver, 2004), self-reported anger (Harmon-Jones, 2003), expression of anger (Smits & Kuppens, 2005), and vigilance toward masked angry faces (Putman et al., 2004). Moreover, neuroimaging studies have shown that higher scores on these subscales predict increased responding to angry facial expressions in neural regions implicated in aggression (Beaver, Lawrence, Passamonti, & Calder, 2008), and that this effect occurs within 200 ms after stimulus presentation (Bediou, Eimer, d'Amato, Hauk, & Calder, 2009).

Neuroeconomic research has confirmed the implicit relation of BASD and BASR to dominance: Higher scores on these two subscales, but not higher BASF scores, predicted larger offers in an ultimatum game (Scheres & Sanfey, 2006), and researchers have argued that larger offers in this game originate from an increased concern for social status (Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010). The combined BAS subscales thus support a motivational interpretation of behavioral activation in which both dominance- and non-dominance-related reward sensitivity have their place (Carver, 2004; Harmon-Jones, 2004).

We hypothesized that increasing levels of dominance-related reward sensitivity (BASD and BASR) would predict slower gaze aversion from masked facial anger (relative to masked facial happiness). Given the experimental results described earlier, we expected that both inhibition of gaze aversion in high-dominant individuals and facilitation of gaze aversion in low-dominant individuals would underlie this effect (see van Honk & Schutter, 2007, for a review). Furthermore, because BASF measures non-dominance-related reward sensitivity, we hypothesized that higher BASF scores would predict a bias for positive reward cues that would be reflected in slower gaze aversion from masked happy faces (relative to masked angry faces). We tested these hypotheses with the newly developed gaze-aversion task.

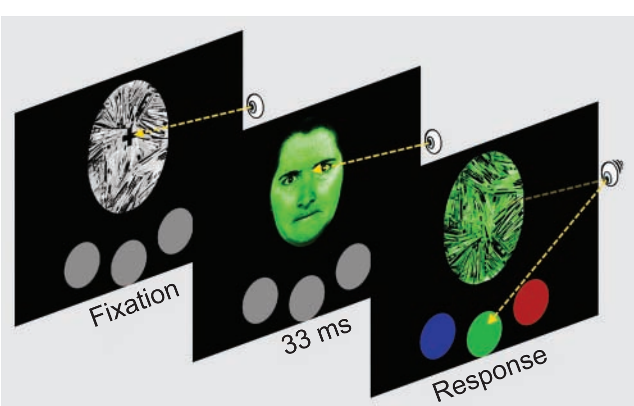

Fig. 1. Illustration of the gaze-aversion task. Participants fixated the screen; were presented with a backward-masked colorized angry, happy, or neutral facial expression; and responded by making a saccadic eye movement to the dot the same color as the face.

Method

Forty healthy volunteers (20 female; 20 male; mean age = 22.7 years, *SD* = 2.8) participated for either course credit or payment. The face stimuli for the gaze-aversion task were colorized (blue, green, and red) faces of 10 actors (5 female, 5 male), each expressing three emotions (angry, happy, and neutral; Ekman & Friesen, 1976). The 90 stimuli were presented once in random order. Each trial commenced with a fixation screen, which was followed by a 33-ms presentation of a colorized face stimulus and then a mask of the same color. The mask remained on the screen until the participant responded. Mask stimuli were cut-up and randomly reassembled faces. So that contrast and luminance levels would be constant over the whole trial, a (gray) mask stimulus was presented with the fixation cross during the gaze-fixation phase. As shown in Figure 1, three gray dots were presented below the stimulus. During presentation of the mask, each gray dot was replaced by a dot of a different color (blue, green, and red; colors randomly assigned in each trial). Participants responded by looking, as quickly as possible, away from the mask to the dot that was the same color as the preceding face stimulus. Before the task, participants completed 10 practice trials with neutral faces only.

The rationale behind this task is that the presentation of masked emotional expressions can evoke dominance (angry faces) and reward-seeking (happy faces) responses that can delay looking away from the mask (the location of the face). Thus, the difference between latencies on angry-face trials and happy-face trials can serve as a measure of implicit dominance or nondominance approach motives.

Eye movements were recorded with a Tobii-1750 binocular infrared eye tracker (sampling at 50 Hz, 0.5° accuracy; Tobii Technology, Danderyd, Sweden) with an integrated LCD display (8-ms response time). We used this system because it was recently shown that restriction of body movement greatly reduces approach-motivational responses (Harmon-Jones & Peterson, 2009), and this system is not head mounted, leaving participants fairly free in their movements. Stimulus presentation commenced when participants fixated the fixation cross for a randomly determined interval (1,000–1,500 ms, to avoid timing habituation), and saccade latency was estimated as the time between onset of the stimulus and the first gaze at the correctly colored dot. Latencies less than 100 ms or more than 2 standard deviations above or below the overall mean (2.5%) were removed from the analysis, which was conducted with two-tailed tests ($\alpha = .05$).

After giving informed consent, participants filled out the BAS questionnaire (Carver & White, 1994) and then performed the gaze-aversion task. Finally, they performed an objective awareness check intended to establish whether the emotion in the facial stimuli was masked successfully. In this awareness check, all 30 faces were shown once again with a mask. Colors were randomly assigned, but each color appeared 10 times. Participants had to report the presented emotion, choosing from three options (angry, happy, or neutral). Thus, with this awareness check, we tested not for awareness of the faces, but rather for awareness of the stimulus quality of interest: emotional expression.

Results

First, we assessed performance on the awareness check. An individual score of 15 or higher was significantly above the chance level of 10 correct responses (binomial upper limit with one-tailed α of .05 for $n = 30$ and an expected proportion of correct answers of 1/3). Thirteen subjects scored 15 or higher and were considered to have (some) explicit awareness of the presented emotions. Moreover, a negative correlation between performance on the awareness check and average saccade latency ($r = -.42$, $p < .01$) indicated that the face stimuli interfered most with performance on the gaze-aversion task when the faces' emotions were processed implicitly. Because several emotional Stroop studies have shown that the interaction between angry expressions and motivational traits occurs exclusively when the stimuli are masked (van Honk & Schutter, 2007), we created two separate groups of subjects. The implicit group ($n = 27$) scored at chance level on the individual awareness check, and the explicit group ($n = 13$) scored significantly above chance level. Average saccade latency was 448 ms (SD = 64 ms) for the implicit group and 422 ms (SD = 51 ms) for the explicit group. Repeated measures analysis of variance did not reveal any main effects of emotion (angry, happy, or neutral) on saccade latency in either the implicit group, $F(25) = 0.283$, $p > .7$, or the explicit group, $F(11) = 0.016$, $p > .9$.

To test our hypotheses regarding dominance- and nondominance-related reward sensitivity directly, we computed angry-happy contrast scores by subtracting mean latencies on happy-face trials from mean latencies on angry-face trials. High contrast scores thus represent longer gaze toward angry faces than toward happy faces. In the implicit group, the angry-happy contrast scores were significantly correlated with all three BAS subscale scores; the correlations were positive for BASD ($r_s = .39$, $p < .05$) and BASR ($r_s = .44$, $p < .05$) and negative for BASF ($r_s = -.39$, $p < .05$). There were no significant relations between contrast scores and BAS subscale scores in the explicit group ($r_s = -.10$, $p = .75$; $r_s = .04$, $p = .91$; $r_s = .38$, $p = .20$, respectively). Furthermore, BASF was not significantly related to BASR ($r_s = .26$, $p = .11$) or BASD ($r_s = .06$, $p = .73$), which indicates that the negative effect of BASF on gaze aversion in the implicit group was independent of effects of BASR and BASD. Because BASD and BASR scores were positively correlated ($r_s = .34$, $p < .05$), and both predict dominance motives (see the introduction), we pooled them into a single scale; scores on this scale were significantly correlated with angry-happy contrast scores in the implicit group ($r_s = .54$, $p < .01$; see Fig. 2).

To compare the implicit and explicit groups directly, we conducted a linear regression analysis with angry-happy contrast score as the dependent variable and group, Group × Dominance-Related BAS Score (BASR + BASD), and Group × Non-Dominance-Related BAS Score (BASF) as regressors. The overall model was significant ($n = 40$, $R = .574$, $p < .05$), and both interactions indicated a stronger relation between BAS score and angry-happy contrast score in the implicit group than in the explicit group, $t(38) = 2.15$, $p < .05$, and $t(38) = -2.9$, $p < .01$, respectively. Separate regression analyses for the two groups confirmed that dominance- and nondominance-related BAS scores were significant predictors of angry-happy contrast scores in the implicit group ($n = 27$, $R = .688$, $p < .001$), with dominance-related BAS scores making a

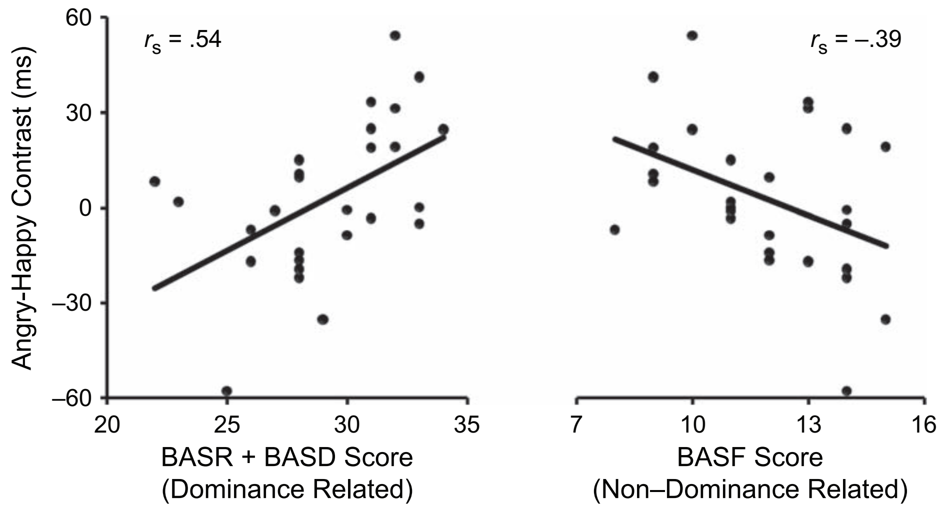

Fig. 2. Scatter plots showing the correlation between the implicit group's angry-happy contrast scores and their scores on the Behavioral Activation Scale. Angry-happy contrast scores were calculated by subtracting mean latencies on happy-face trials from mean latencies on angry-face trials; consequently, a high score indicates longer saccade latencies for angry-face trials (i.e., inhibition of submissive gaze aversion). Results are shown separately for the dominance-related questionnaire subscales pooled together (Behavioral Activation Scale Drive and Reward Responsiveness, or BASD and BASR, respectively) and for the non-dominance-related subscale (Fun Seeking, or BASF).

positive contribution to contrast scores ($\beta = 0.56$, $p < .01$) and non-dominance-related BAS scores making a negative contribution ($\beta = -0.47$, $p < .01$). The model for the explicit group was not significant ($n = 13$, $R = .15$, $p = .44$).

Discussion

We have shown that slower gaze aversion from masked facial anger is significantly predicted by the dominance-related BAS subscales, BASD and BASR. Accordingly, the present data provide direct support for the hypothesis that speed of gaze aversion from masked facial anger depends on motives of dominance and submission (van Honk et al., 1998, 2000, 2001; Wirth & Schultheiss, 2007). Additionally, the third BAS subscale, BASF, independently predicted relative engagement with masked happy faces, a result confirming that this subscale represents non-dominance-related reward sensitivity. Thus, our eye-tracking gaze-aversion task not only successfully provoked modulation of implicit face-to-face gaze behavior related to motives of dominance and submissiveness, but also revealed theoretically grounded dissociated responses to angry and happy expressions within the construct of behavioral activation (Carver, 2004; Harmon-Jones, 2004).

Crucially, the relation between dominance motives and gaze aversion was observed only in subliminal conditions. We cannot, however, exclude the possibility that humans use gaze contesting to consciously outstress opponents (Mazur & Booth, 1998), especially because genuine face-to-face confrontations generally persist long enough to initiate complex psychological mechanisms. Our findings do, however, support an extensive line of psychobiological research on rapid and reflexive initiation of dominance/submission behavior (van Honk & Schutter, 2007).

The neural mechanism underlying dominance/submission behaviors in primates was extensively described by Emery and Amaral (2002). They ascribed a vital role to the amygdala, which integrates sensory information, such as facial expressions, with social context and connects to endocrine and autonomic systems to facilitate appropriate behavior. Similar mechanisms have been described in humans. It is thought that when conscious evaluation of facial expressions is prevented, the sensory information is still crudely evaluated for threat in subcortical structures and relayed to prefrontal areas via the amygdala (Vuilleumier, 2002). Researchers have argued that this mechanism is an adaptive implicit alarm system that serves to direct attention and potentiate responding to threat (Liddell et al., 2005). The responses to masked facial threat in our high-BASD/high-BASR subjects possibly reflected enhanced responding of this implicit defense system, mediated by the motivation to stand one's ground and (if necessary) fight rather than flight. When confronted with an explicit threat, this fight-or-flight mechanism can be inhibited by higher-order cortical processes that maintain executive control (Nomura et al., 2004). Such inhibition might explain the lack of motivational modulation of responses in the group that explicitly processed the emotional stimuli in the present experiment, as well as the lack of such modulation in several previous emotional Stroop studies with angry faces (van Honk & Schutter, 2007).

Because both excessive reactivity of this implicit defense system and lack of prefrontal inhibition of such reactivity are often associated with aggressive behavior (Siever, 2008), an alternative explanation of our results might be that the reflexive fight response is not as effectively inhibited in dominant as in nondominant individuals. Recent evidence showing reduced white matter connections between the amygdala and frontal areas in psychopathy, possibly resulting in poor impulse control (Craig et al., 2009), seems to point in this direction. However, given that this higher-order mechanism requires conscious evaluation of threat, impulse control may largely concern the explicit mechanisms proposed by Mazur and Booth (1998). To further unveil the biological mechanisms of reflexive dominance, researchers will need to focus on interactions between subcortical and cortical brain structures.

In sum, the present data provide direct evidence for implicit and reflexive modulation of dominance/submission behaviors in humans. Furthermore, we have shown a dissociation between dominance- and non-dominance-related reward sensitivity within the BAS. High-BASF individuals implicitly track positive social signals, whereas high-BASR/high-BASD individuals persist in implicit angry face-to-face confrontations. Because success in dominance contests is achieved only when eye contact is never interrupted, such persistence may reflect an adaptive mechanism to ensure advantage in social dominance confrontations (Putman et al., 2004; van Honk et al., 2001). Likewise, facilitation of gaze aversion among individuals with submissive characteristics is adaptive, as it reduces the chance of injury and saves valuable resources (van Honk et al., 1998, 2000). Finally, utilizing saccade latencies as a social behavioral measure may have great potential for future social and motivational research.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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References

Beaver, J.D., Lawrence, A.D., Passamonti, L., & Calder, A.J. (2008). Appetitive motivation predicts the neural response to facial signals of aggression. *Journal of Neuroscience*, *28*, 2719–2725.

Bediou, B., Eimer, M., d'Amato, T., Hauk, O., & Calder, A.J. (2009). In the eye of the beholder: Individual differences in reward-drive modulate early frontocentral ERPs to angry faces. *Neuropsychologia*, *47*, 825–834.

Carver, C.S. (2004). Negative affects deriving from the behavioral approach system. *Emotion*, *4*, 3–22.

Carver, C.S., & White, T.L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS scales. *Journal of Personality and Social Psychology*, *67*, 319–333.

Craig, M.C., Catani, M., Deeley, Q., Latham, R., Daly, E., Kanaan, R., et al. (2009). Altered connections on the road to psychopathy. *Molecular Psychiatry*, *14*, 946–953.

Dabbs, J.M., Jr. (1997). Testosterone, smiling, and facial appearance. *Journal of Nonverbal Behavior*, *21*, 45–55.

Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., & Fehr, E. (2010). Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature*, *463*, 356–359.

Ekman, P., & Friesen, W. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.

Ellis, L. (2006). Gender differences in smiling: An evolutionary neuroandrogenic theory. *Physiology and Behavior*, *88*, 303–308.

Emery, N.J., & Amaral, D.G. (2002). The role of the amygdala in primate social cognition. In R.D. Lane & L. Nadel (Eds.), *Cognitive neuroscience of emotion* (pp. 156–191). New York, NY: Oxford University Press.

Harmon-Jones, E. (2003). Anger and the behavioral approach system. *Personality and Individual Differences*, *35*, 995–1005.

Harmon-Jones, E. (2004). Contributions from research on anger and cognitive dissonance to understanding the motivational functions of asymmetrical frontal brain activity. *Biological Psychology*, *67*, 51–76.

Harmon-Jones, E., & Peterson, C.K. (2009). Supine body position reduces neural response to anger evocation. *Psychological Science*, *20*, 1209–1210.

Hess, U., & Bourgeois, P. (2010). You smile—I smile: Emotion expression in social interaction. *Biological Psychology*, *84*, 514–520.

Liddell, B.J., Brown, K.J., Kemp, A.H., Barton, M.J., Das, P., Peduto, A., et al. (2005). A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. *NeuroImage*, *24*, 235–243.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men [Target article and discussion]. *Behavioral Brain Sciences*, *21*, 353–397.

Murphy, S.T., & Zajonc, R.B. (1993). Affect, cognition, and awareness: Affective priming with optimal and suboptimal stimulus exposures. *Journal of Personality and Social Psychology*, *64*, 723–739.

Nomura, M., Ohira, H., Haneda, K., Iidaka, T., Sadato, N., Okada, T., & Yonekura, Y. (2004). Functional association of the amygdala and ventral prefrontal cortex during cognitive evaluation of facial expressions primed by masked angry faces: An event-related fMRI study. *NeuroImage*, *21*, 352–363.

Öhman, A. (1986). Face the beast and fear the face: Animal and social fears as prototypes for evolutionary analyses of emotion. *Psychophysiology*, *23*, 123–145.

Putman, P., Hermans, E., & van Honk, J. (2004). Emotional Stroop performance for masked angry faces: It's BAS, not BIS. *Emotion*, *4*, 305–311.

Scheres, A., & Sanfey, A.G. (2006). Individual differences in decision making: Drive and reward responsiveness affect strategic bargaining in economic games. *Behavioral and Brain Functions*, *2*, 35. Retrieved from http://www.behavioralandbrainfunctions.com/content/2/1/35

Siever, L.J. (2008). Neurobiology of aggression and violence. *American Journal of Psychiatry*, *165*, 429–442.

Smits, D.J.M., & Kuppens, P. (2005). The relations between anger, coping with anger, and aggression, and the BIS/BAS system. *Personality and Individual Differences*, *39*, 783–793.

van Honk, J., & Schutter, D.J. (2007). Vigilant and avoidant responses to angry facial perceptions: Dominance and submission motives. In E. Harmon-Jones & P. Winkielman (Eds.), *Social neuroscience: Integrating biological and psychological explanations of social behavior* (pp. 197–226). New York, NY: Guilford Press.

van Honk, J., Tuiten, A., de Haan, E., van den Hout, M., & Stam, H. (2001). Attentional biases for angry faces: Relationships to trait anger and anxiety. *Cognition & Emotion*, *15*, 279–297.

van Honk, J., Tuiten, A., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., & Verbaten, R. (1998). Baseline salivary cortisol levels and preconscious selective attention for threat: A pilot study. *Psychoneuroendocrinology*, *23*, 741–747.

van Honk, J., Tuiten, A., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., & Verbaten, R. (2000). Conscious and preconscious selective attention to social threat: Different neuroendocrine response patterns. *Psychoneuroendocrinology*, *25*, 577–591.

Vuilleumier, P. (2002). Facial expression and selective attention. *Current Opinion in Psychiatry*, *15*, 291–300.

Winkielman, P., Berridge, K.C., & Wilbarger, J.L. (2005). Unconscious affective reactions to masked happy versus angry faces influence consumption behavior and judgments of value. *Personality and Social Psychology Bulletin*, *31*, 121–135.

Wirth, M.M., & Schultheiss, O.C. (2007). Basal testosterone moderates responses to anger faces in humans. *Physiology and Behavior*, *90*, 496–505.