Unattended Facial Expressions Asymmetrically Bias the Concurrent Processing of Nonemotional Information

Jeffrey S. Maxwell, Alexander J. Shackman, and Richard J. Davidson

Abstract

■ Planned and reflexive behaviors often occur in the presence of emotional stimuli and within the context of an individual's acute emotional state. Therefore, determining the manner in which emotion and attention interact is an important step toward understanding how we function in the real world. Participants in the current investigation viewed centrally displayed, task-irrelevant, face distractors (angry, neutral, happy) while performing a lateralized go/no-go continuous performance task. Lateralized go targets and no-go lures that did not spatially overlap with the faces were employed to differentially probe processing in the left (LH) and right (RH) cerebral hemispheres. There was a significant interaction between expression and hemisphere, with an overall pattern such that angry distractors were associated with relatively more RH inhibitory errors than neutral or happy distractors and happy distractors with relatively more LH inhibitory errors than angry or neutral distractors. Simple effects analyses confirmed that angry faces differentially interfered with RH relative to LH inhibition and with inhibition in the RH relative to happy faces. A significant three-way interaction further revealed that state anxiety moderated relations between emotional expression and hemisphere. Under conditions of low cognitive load, more intense anxiety was associated with relatively greater RH than LH impairment in the presence of both happy and threatening distractors. By contrast, under high load, only angry distractors produced greater RH than LH interference as a function of anxiety. ■

INTRODUCTION

The ability to selectively respond to relevant aspects of the environment while inhibiting distraction and competing courses of action is essential for adaptive behavior and psychological well being (Casey, Tottenham, & Fossella, 2002; Rule, Shimamura, & Knight, 2002; Miller & Cohen, 2001; Aston-Jones, Rajkowski, & Cohen, 1999; Tipper, Howard, & Houghton, 1998). Mechanisms of attentional control and behavioral inhibition do not typically operate in isolation. Rather, in daily life, planned and reflexive behaviors often occur in the presence of emotional stimuli and within the context of an individual's acute emotional state (Davidson, 2002; Davidson & Irwin, 1999). Therefore, determining the extent to which emotion and attention interplay, and uncovering the neural mechanisms by which they do so, is an important step toward understanding how we function in the real world.

According to several theoretical accounts, neural processing is competitive and rivalries exist at multiple stages along the processing stream such that different sources of information compete for representation within their respective pathways; different pathways converge and compete for the mobilization of associated thoughts, memories, and behaviors; and the behaviors, memories, and thoughts that are ultimately implemented are those that receive the largest net degree of support (Corbetta & Shulman, 2002; Miller & Cohen, 2001; Desimone, 1998; Duncan, 1998). Typically, in the absence of other factors, the most salient signal (e.g., that with the highest contrast or most abrupt onset) wins. However, although an incoming signal's strength is partially determined by exogenous factors, top-down (endogenous) biases directly influence both the early and late stages of stimulus processing (Chelazzi, Miller, Duncan, & Desimone, 2001; de Fockert, Rees, Frith, & Lavie, 2001; Downing, 2000; Hopfinger, Buonocore, & Mangun, 2000; Luck & Hillyard, 2000). In a parallel fashion, we propose that affective experience and the perception of emotional stimuli are also able to bias these competitive interactions (cf. Bishop, Duncan, Brett, & Lawrence, 2004; Pessoa, Kastner, & Ungerleider, 2002) and, at times, do so in a lateralized fashion.

Several independent observations indicate that attention and emotion are at least partially subserved by common neural substrates. Reports from the animal and human lesion literature, clinical studies (e.g., ADHD, OCD, schizophrenia, Tourette's Syndrome), and electrophysiological and neuroimaging investigations converge

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Laboratory for Affective Neuroscience, University of Wisconsin-Madison

Journal of Cognitive Neuroscience 17:9, pp. 1386–1395

to suggest that several regions within the prefrontal cortex (PFC) are critically involved in suppressing automatic and intrusive behaviors, thoughts, and exogenous distractions (e.g., Casey et al., 2002; Chao & Knight, 1995, 1998), as well as in perceiving emotional information and implementing affectively governed behaviors (Rolls, 2004; Davidson, Putnam, & Larson, 2000; Damasio, Grabowski, Frank, Galaburda, & Damasio, 1994). Several additional brain regions (e.g., amygdala, locus coeruleus) and neurotransmitter systems (e.g., dopamine, norepinephrine) have also been linked to both emotional processing and attentional control (Davis & Whalen, 2001; Bush, Luu, & Posner, 2000; Arnsten, 1998; Arnsten & Goldman-Rakic, 1998).

In particular, affective facial displays, encountered daily and frequently unrelated to one's goal-directed focus, have the potential to interact with an individual's current emotional state and impinge upon mechanisms of behavioral inhibition. Several distinct regions within the PFC have been independently associated with the processing of emotional facial expressions and the suppression of automatically triggered responses, including the anterior cingulate (Bokura, Yamaguchi, & Kobayashi, 2001; Menon, Adleman, White, Glover, & Reiss, 2001; Blair, Morris, Frith, Perrett, & Dolan, 1999), inferior frontal (Garavan, Ross, & Stein, 1999; Nakamura et al., 1999), and orbito-frontal regions (Bokura et al., 2001; Blair et al., 1999). However, to date, no published investigation has directly tested whether systematic interactions occur between the perception of affective facial expressions and mechanisms of behavioral inhibition. Using a lateralized go/no-go continuous performance task (CPT; Figure 1), the current investigation tested several hypotheses concerning the impact of task-irrelevant emotional facial displays on the concurrent processing of task-relevant information and suppression of nonaffectively triggered motor responses.

First, given the right hemisphere's (RH) preferential involvement in sustained vigilance and arousal (Rogers, 2000; Ladavas, Del-Pesce, Mangun, & Gazzaniga, 1994; Liotti & Tucker, 1992), as well as in anxiety and avoiding danger (Davidson, 2002; Davidson & Irwin, 1999; Heller, 1993), it is strategically situated for the initial detection of novel (Martin, 1999), anomalous (Smith, Tays, Dixon, & Bulman-Fleming, 2002), and otherwise potentially harmful changes in the environment. In accordance with this notion, a number of investigations have suggested an RH bias in the perception of negative facial expressions (e.g., Fox, 2002; Mogg & Bradley, 2002; Adolphs, Damasio, Tranel, & Damsio, 1996; Johnsen & Hugdahl, 1991; Mandal & Singh, 1990); and negative relative to positive facial expressions (Nicholls, Ellis, Clements, & Yoshino, 2004; Jansari, Tranel, & Adolphs, 2000; Workman, Peters, & Tayler, 2000; Davidson, Mednick, Moss, & Saron, 1987; Reuter-Lorenz & Davidson, 1981).

To date, the majority of such studies have either employed split visual field presentation of face stimuli or the lateralized placement of expressive features, investigated patients with lateralized brain lesions, or both. Additionally, such stimuli have oftentimes been directly integrated with one's focus of attention (e.g., expression identification, intensity ratings) or spatially coincided with the information that they were observed to bias (e.g., attentional capture, emotional Stroop). Using a complimentary technique in healthy individuals, we tested whether centrally viewed threatening facial distractors, given equal access to both hemispheres, would preferentially disinhibit responses triggered by

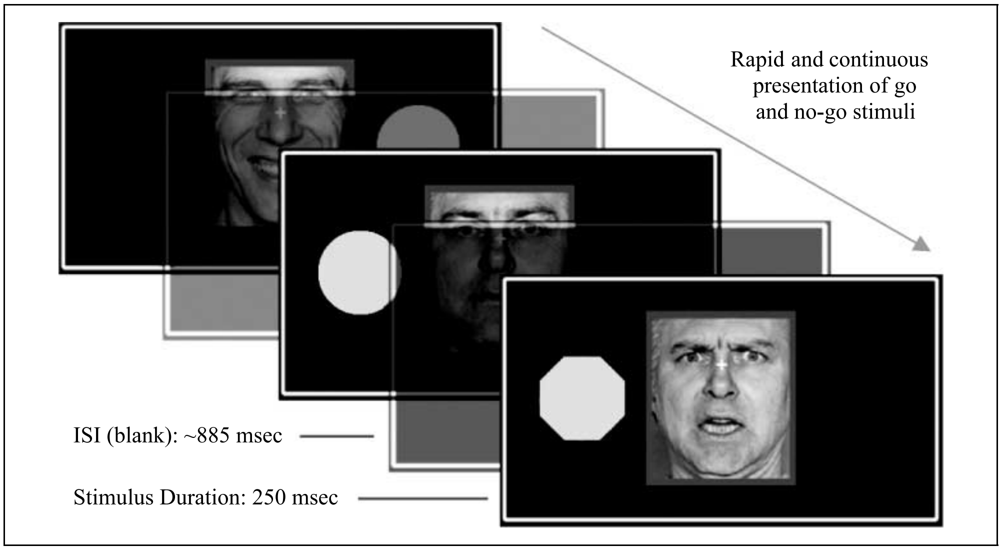

Figure 1. Lateralized go targets and no-go lures were presented in synchrony with centrally displayed, task-irrelevant, emotional facial distractors. Trials advanced at a rapid pace with a fixed target/distractor duration of 250 msec and an average ISI of 885 msec (100 msec jitter). Participants rapidly responded to all go targets (71.4% of trials) while attempting to suppress responses triggered by no-go lures (28.6% of trials). Go stimuli consisted of circles (80% green, 20% red) and no-go lures of octagons (50% green, 50% red). Overall, task-relevant images were comprised of 57.1% green circles, 14.3% red circles, 14.3% green octagons, and 14.3% red octagons. This relative proportioning of stimuli ensured that, in addition to establishing a prepotent tendency to respond on all trials, green (high load) no-go lures would trigger a stronger motor response and be more difficult to inhibit than red (low load) no-go lures.

left visual field (LVF) lures relative to right visual field (RVF) lures and LVF lures in the presence of neutral and happy facial distractors. We also assessed whether there was a reversal of this pattern in the RVF/left hemisphere (LH).

Second, recent observations suggest that higher levels of anxiety can amplify the extent to which emotional information biases the control of attention. For example, Mathews, Fox, Yiend, and Calder (2003) reported that individuals with high, but not low, levels of self-reported anxiety showed stronger attentional gaze-cueing in response to viewing fearful compared to neutral faces. Relatedly, Fox, Russo, and Dutton (2002) and Fox, Russo, Bowles, and Dutton (2001) found that high anxious participants had more difficulty disengaging their attention from angry compared to neutral faces; and reported mixed evidence concerning whether anxious participants exhibited comparable difficulty disengaging from happy expressions.

However, to our knowledge, no investigation has ever directly examined whether anxiety moderates the extent to which emotional information biases the control of attention asymmetrically across the LH and RH. We hypothesized that when galvanized by anxiety, the RH is readied for orienting toward and appraising potentially threatening changes in the visual scene. Additionally, because failing to detect a threat carries greater consequences than falsely orienting to an innocuous stimulus, we reasoned that higher levels of anxiety might generally bias RH processing toward any arousing change in the environment, irrespective of emotional valence. Therefore, when a potentially threat-relevant cue (e.g., teeth in an emotional facial expression) genuinely does signal a threat in the environment (e.g., teeth in an angry or fearful expression), the neural circuitry associated with escaping from danger will already be engaged and primed to react. Therefore, we predicted that higher levels of state anxiety (STAI-X) would be associated with relatively greater RH interference in the presence of threatening, and possibly also happy, facial distractors.

Finally, the extent to which voluntary attentional resources are not fully taxed determines how free they are to be reflexively captured and used for performing additional tasks (Pessoa, McKenna, Gutierrez, & Ungerleider 2002; de Fockert et al., 2001; Lavie & Fox, 2000). Consequently, as task difficulty increases, the automatic processing of task-unrelated (unattended) distractors should decrease. However, the processing of threat-related information is so highly prioritized that it may proceed relatively automatically, even when the source of threat is unattended or presented outside of one's explicit awareness (Vuillermier & Schwartz, 2001; Mogg & Bradley, 1999; Morris, Öhman, & Dolan, 1998; Whalen et al., 1998). Therefore, we predicted that the impact of task-irrelevant threatening facial distractors would be relatively less sensitive to increases in task difficulty than the processing of nonthreatening emotional distractors.

In sum, at a group level, we predicted that task-irrelevant threatening facial distractors would asymmetrically impair RH inhibitory performance relative to LH inhibitory performance and RH inhibitory performance in the presence of neutral and happy facial distractors. We also tested whether individuals with more intense levels of state anxiety would be vulnerable to greater RH than LH inhibitory impairment in the presence of threatening, and perhaps also happy, distracting emotional facial expressions. Finally, we examined whether the processing of unattended threatening facial distractors is relatively less dependent on the availability of attentional resources (i.e., more prioritized) than the processing of happy facial distractors.

RESULTS

Omnibus Analysis

Using the no-go accuracy data, we carried out a 2 (task difficulty: high, low cognitive load) × 2 (visual field: left, right) × 3 (facial expression: angry, neutral, happy) mixed-model GLM with self-reported anxiety as a continuous predictor. This analysis revealed a main effect of task difficulty with more inhibitory errors being committed to high load ($M = 27\%$ errors, $SD = 12\%$) than low load ($M = 15\%$ errors, $SD = 8\%$) no-go lures [$F(1,41) = 4.29$, $p < .05$]. No other main effects were significant (Fs < 1). We also observed a significant interaction between visual field and facial expression [$F(2,82) = 4.73$, $p < .01$], with an overall pattern such that angry distractors led to relatively more LVF/RH inhibitory errors (i.e., no-go commission errors) than neutral or happy distractors, and happy distractors to relatively more RVF/LH inhibitory errors than angry or neutral distractors (see Figure 2).

Control Analyses

To interrogate the specificity of these effects, we also analyzed the go reaction time data using an identical GLM. Importantly, there was no evidence for an interaction between visual field and facial expression, or between visual field, facial expression, and state anxiety (Fs < 1). Furthermore, given the rapidity with which certain emotional structures (e.g., amygdala) habituate to repeated presentations of the same negative facial expressions (Ishai, Pessoa, Bikle, & Ungerleider, 2004; Fischer et al., 2003), we considered whether only the first few experimental blocks might account for the bulk of these observations. Therefore, we reanalyzed the no-go accuracy data with time (first vs. second half of experiment) entered into the mixed-model GLM. Notably, there was no main effect of time nor did time interact with (or alter) the interaction between visual

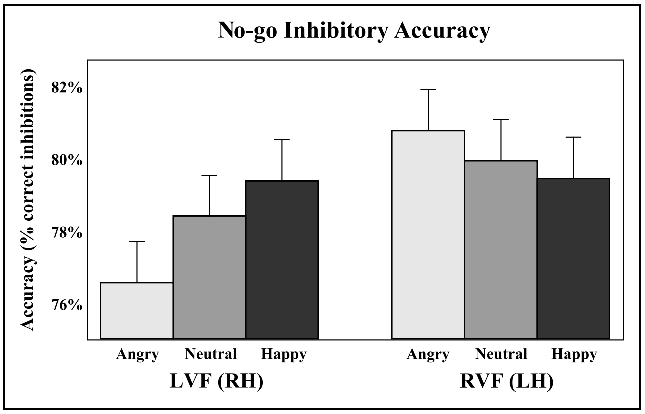

Figure 2. No-go performance accuracy (100% − errors of commission) for RH/LVF and LH/RVF lures in the presence of centrally displayed distracting facial expressions (angry, neutral, and happy). Within-subject standard error bars were calculated using pooled MS error (visual field, expression, and visual field × expression; Masson & Loftus, 2003). Lower numbers denote a greater percentage of inhibitory errors.

field and facial expression, or visual field, facial expression, and state anxiety (*F*s < 1).

Focused Group Analyses

Planned simple main effects analyses confirmed that centrally presented angry faces differentially interfered with the voluntary inhibition of prepotent motor responses triggered by LVF/RH lures relative to both RVF/LH lures [$F(1,42) = 8.19$, $p < .01$] and LVF/RH lures in the presence of happy expressions [$F(1,42) = 3.17$, $p <$ 05]. Three of the four remaining contrasts were also in the expected direction, albeit not significantly: LVF/RH angry versus LVF/RH neutral [$F(1,42) = 1.32$, $p < .13$]; RVF/LH happy versus RVF/LH angry [$F(1,42) < 1$]; RVF/LH happy versus RVF/LH neutral [$F(1,42) < 1$]. There was no difference between RVF/LH and LVF/RH performance in the presence of happy distractors ($F = 0.00$).

However, as Jaccard and Guilamo-Ramos (2002) cogently argued in a recent methodological report, ‘‘Simple main effects usually are of theoretical import. However, they do not bear on interaction effects, which address a different substantive question.’’ In other words, a reliable and meaningful interaction can be observed even if none of the pairwise contrasts is reliable; and even large interaction effects do not require that all, or most, of the simple main effects approach significance. This is because an interaction does not reflect individual pairwise contrasts (e.g., RH angry–RH happy) but, rather, the difference between two or more pairwise difference scores (e.g., RH angry–RH happy vs. LH angry–LH happy).

Therefore, to better understand the omnibus interaction between visual field and facial expression, we computed focused 2 (LVF, RVF) × 2 (expression 1, expression 2) GLMs separately for each possible pair of distractors: angry versus neutral [$F(1,42) = 1.56$, $p > .05$]; happy versus neutral [$F(1,42) < 1$]; and angry versus happy [$F(1,42) = 4.32$, $p < .05$]. These analyses indicate that, at a group level, the interaction between visual field and facial expression was most pronounced for angry versus happy distractors (i.e., oppositely valenced emotional expressions).

Interpreted alongside the significant simple main effects, the latter observation suggests that the interaction between visual field and emotional expression was primarily driven by angry facial expressions. However, when neutral faces are taken into consideration (as illustrated in Figure 2), a plausible alternative is that angry and happy expressions each exert qualitatively different effects upon LVF/RH and RVF/LH processing, both with respect to one another and in an opposite direction relative to an emotionally neutral baseline (control). This alternative interpretation receives support from the presence of a significant linear [$F(1,42) = 4.32$, $p < .05$], but not quadratic [$F(1,42) = 0.09$], trend in the 2 (visual field) × 3 (expression: angry, neutral, happy) interaction.

Individual Differences Analyses

A significant three-way interaction in the omnibus analysis revealed that the observed relation between emotional expression and visual field varied as a function of individual differences in self-reported state anxiety [$F(2,82) = 5.25$, $p < .01$]. By contrast, individual differences in baseline task performance (i.e., in the absence of distraction) were not significantly related to any of these measures. For the focused individual differences contrasts, in order to isolate asymmetries tied specifically to the perception of emotional expressions from those associated with face processing per se, asymmetric performance in the presence of neutral facial expressions (i.e., an individually defined constant) was subtracted from asymmetric performance in the presence of angry and happy expressions.[1]

On low cognitive load trials, more intense anxiety was associated with both angry ($r = .34$, $p < .05$) and happy ($r = .44$, $p < .05$) facial distractors asymmetrically biasing cognitive performance, increasing the percentage of inhibitory errors committed to LVF/RH lures relative to RVF/LH no-go lures (Figure 3). Additionally, on low cognitive load trials, the net degree to which state anxiety interacted with positive and negative facial expressions did not reliably differ [$t(40) < 1$]. However, in the face of high attentional demands (i.e., high load lures), only angry ($r = .33$, $p < .05$) and not happy ($r = .09$, $p > .20$) facial expressions produced reliably greater relative interference in the LVF/RH as a function of state anxiety. Underscoring this observation, the attenuating

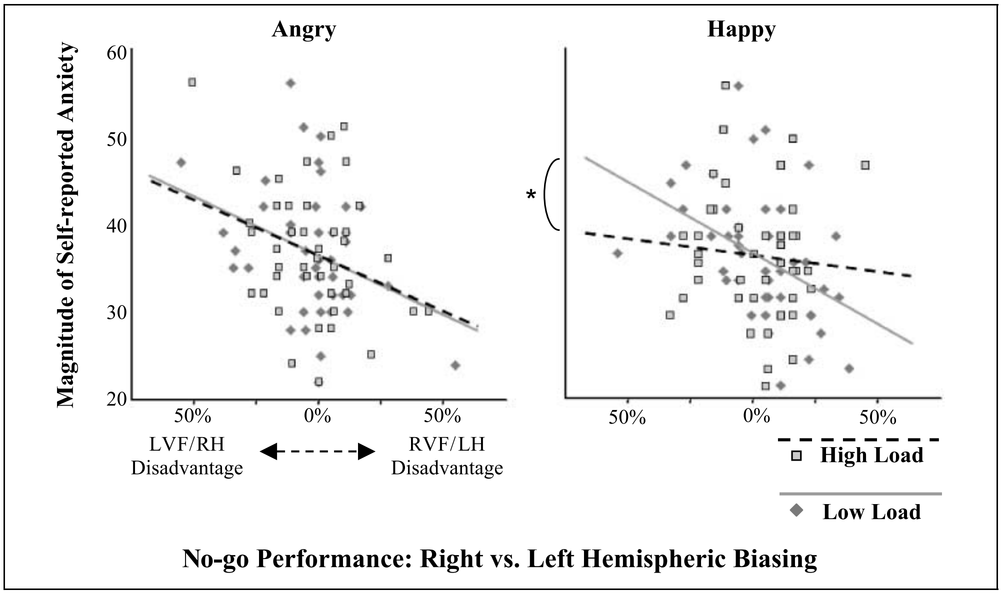

Figure 3. In the presence of low attentional demands (i.e., low load lures), more intense levels of state anxiety are associated with both angry ($r = .34, p < .05$) and happy ($r = .44, p < .05$) distractors producing greater relative LVF/RH interference (cf. better relative RVF/LH performance). However, in the presence of high attentional demands, only angry ($r = .33, p < .05$) and not happy ($r = .09, p > .20$) facial distractors produce reliably greater relative interference in the LVF/RH as a function of state anxiety. Baseline asymmetries in the presence of neutral faces have been removed.[1] Percentage values on the abscissa denote relative hemispheric biases (i.e., the absolute value of LVF–RVF accuracy) with 0% signifying equal performance for LVF/RH and RVF/LH stimuli.

effect of high attentional demands on the relation between state anxiety and happy-driven RH interference was statistically significant [$t(40) = 1.81, p < .05$; Figure 3).

DISCUSSION

These results support our hypothesis that the incidental perception of task-irrelevant emotional distractors can asymmetrically bias the processing of simultaneously presented task-relevant cognitive information. Moreover, these results demonstrate that individual differences in state anxiety are able to moderate interactions between affective perception and cognition, and suggest that task difficulty (cf. attentional demands) differentially influences the degree to which threatening and positive emotional expressions asymmetrically bias cognitive processing as a function of state anxiety. Several unique aspects of the current investigation increase the potential import of these observations.

In this investigation, the face distractors and task-relevant stimuli were simultaneously presented and cycled at a rate of approximately one trial per second. Additionally, stimuli and distractors were displayed for only 250 msec and the average response time during no-go inhibitory errors was 310 msec poststimulus onset. Therefore, although the current results do not provide a precise timeline for asymmetric interactions between emotional perception and cognition in the brain, they suggest that such biasing proceeds very rapidly (<310 msec) and does not depend upon spatial precueing.

The moderating impact of state anxiety on the interaction between emotional expression and no-go response inhibition further indicates that individual differences in affective state can bias the initial perception and processing of emotional facial expressions. Moreover, the notable lack of an interaction between visual field and facial expression in the reaction time data on go trials suggests that these no-go accuracy findings may be relatively specific to the inhibition of automatically triggered responses and are not simply the result of a speed–accuracy tradeoff or an overall impairment of both speed and accuracy.

Frequently, reported asymmetries in affective perception involve either split field presentations of emotional stimuli, lateralized brain lesions, or both. Additionally, such stimuli are oftentimes directly integrated with task performance and one's focus of attention (e.g., expression identification, intensity ratings) or spatially coincide with the information that they are observed to bias (e.g., attentional capture, emotional Stroop). Complimenting and expanding on these methods, participants in the current investigation viewed task-irrelevant, centrally displayed, face distractors while using their peripheral vision to perform an attentionally demanding CPT. Critically, these emotional facial expressions, although equally accessible by both hemispheres and sharing zero spatial overlap with task-relevant stimuli, nevertheless asymmetrically biased the concurrent processing of behaviorally relevant nonemotional information.

Competing evidence has often been presented concerning whether the RH is preferentially involved in processing all emotional stimuli irrespective of valence (Borod, Andelman, Obler, Tweedy, & Welkowitz, 1992; Bowers, Bauer, Coslett, & Heilman, 1985; Carmon & Nachshon, 1973) or whether negatively and positively valenced emotional stimuli differentially engage the RH and LH, respectively (Nicholls et al., 2004; Jansari et al., 2000; Workman et al., 2000; Davidson et al., 1987; Reuter-Lorenz & Davidson, 1981). The present results do not unambiguously speak to a strong version of either account, suggesting that these hypotheses might not be mutually exclusive, and reveal one potential factor that may help account for some of the observed discrepancies in the literature.

In accordance with RH accounts of emotional perception, we observed that, under conditions of low attentional load and high state anxiety, the incidental perception of both positive and negative facial expressions preferentially disinhibited responses triggered by LVF/RH lures. In contrast, supporting a valence-based account of emotional perception, a significant linear interaction between expression and hemisphere was superimposed on this anxiety-induced RH engagement by affective information, with an overall pattern, such that angry distractors were associated with relatively more LVF/RH inhibitory errors than neutral or happy distractors, and happy distractors with relatively more inhibitory errors in the RVF/LH than angry or neutral distractors. In other words, the linear effect of angry, neutral, and happy facial expression differed significantly across the LVF/RH and RVF/LH.

Additionally, simple main effects analyses suggest that these data present a somewhat less clear and potentially weaker picture concerning the processing of positive relative to negative emotional information, which is consistent with other recent work demonstrating an interaction between hemisphere and emotional expression that appears more pronounced for negative than positive faces (e.g., Nicholls et al., 2004). Specifically, angry facial distractors differentially interfered with RH inhibition relative to LH inhibition or RH inhibition in the presence of happy distractors, but no other simple main effects were significant.

One interesting issue regards the potential implications of this work for our understanding of interactions between affective and cognitive processing. For instance, is it somehow beneficial to disinhibit responses triggered by LVF relative to RVF stimuli when seeing someone making a threatening versus a happy face? Or rather, are these findings incidental, reflecting basic interactions between neural systems that happen to be involved in both attention and emotion processing?

Based on a large and diverse body of literature, Davidson (1992, 1998, 2003) has suggested that certain left and right prefrontal regions are specialized for approach (appetitive) and withdrawal (avoidant) processing, respectively. Segregating these motivations and perceptions into separate hemispheres might serve to reduce the competitive activation of mutually exclusive response options, such as predatory and agonistic tongue striking (Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998), and facilitate adaptive responding to biologically salient reward and punishment stimuli. For instance, although an intrahemispheric division of labor might anatomically segregate two distinct emotional functions at a single stage of processing (e.g., process X in hippocampus; process Y in amygdala), antecedents and consequences of those functions would nevertheless have the opportunity to interact at afferent and efferent target sites (e.g., thalamus and PFC). Interhemispheric segregation of functions, on the other hand, might enable differentially lateralized functions to proceed in concert and relative isolation from one another at many stages of processing.

For example, recent ecological evidence suggests that asymmetric visual processing is directly related to grit–grain discrimination success and dual task performance during feeding in pigeons, particularly when food discrimination is preferentially accentuated in the LH (Güntürkün et al., 2000). Relatedly, Rogers (2000) observed that while foraging, lateralized (light incubated) chicks were significantly faster than nonlateralized (dark incubated) chicks at detecting a simulated raptor flying through the LVF. Rogers concluded that the left eye (RH) is primarily used for predator monitoring when the right eye (LH) is occupied consuming food and discriminating grain from inedible distractors. Clearly, however, such hemispheric asymmetries might also come at a price. For example, according to Lippolis, Bisazza, Rogers, and Vallortigara (2002), the lateralization of appetitive and defensive behavior leaves *B. bufo* and *B. marinus* particularly vulnerable to predators attacking from the right and less able to detect prey appearing on the left. Nevertheless, their marked prevalence suggests that segregating consummatory from fearful and defensive drives, and biasing each of these processes toward a single hemisphere, confers an overall functional advantage to the organism.

In addition, it is important to consider that lateralization is not unique to affective processes, but a property shared by many behaviors and aspects of cognition (e.g., nonprosodic speech, Broca, 1861a, 1861b; handedness, Corballis, 1997; and vestibular reflexes, Previc, 1991), has been observed in a variety of species (e.g., cetaceans, Clapham, Leimkuhler, Gray, & Mattila, 1995; reptiles, Deckel, Lillaney, Ronan, & Summers, 1998; amphibians, Rogers, 2002; and spiders, Ades & Ramires, 2002) and is present in the form of macroscopic (e.g., heart, occipital lobe protrusions) and microscopic (e.g., dendritic arborization; Toga & Thomson, 2003) physiological manifestations, as well as patterns of genetic expression (e.g., nematode odor and taste neurons; Hobert, Johnston, &

Chang, 2002) and CNS neurochemical distribution (e.g., thalamic norepinephrine; Oke, Keller, Mefford, & Adams, 1978), each of which may be independently related to a host of behavioral, cognitive, and emotional asymmetries.

In light of this, it is possible that both affective and nonaffective asymmetries serve the general purpose of increasing processing efficiency for a wide variety of functions and behaviors. However, it does not necessarily follow that all asymmetric interactions between one or more lateralized processes are necessarily advantageous in their own right. Therefore, the present results (cf. Shackman et al., in press; Gray, 2001; Mogg & Bradley, 1999, 2000) probably speak more directly to our developing understanding of how particular emotional and cognitive processes asymmetrically interact than they do to adaptive (cost–benefit) models of hemispheric lateralization. Whether beneficial or incidental, findings such as these that illustrate asymmetric interactions between cognitive and emotional processing are likely to have both theoretical value (e.g., for understanding how these systems operate and interact at a basic level) and functional importance (e.g., predicting behavior and engineering optimal person–environment interfaces).

Future neuroimaging research will be required to determine the exact nature and location of these hemispheric interactions between cognition and affective perception. In particular, we believe that the underlying functional neuroanatomy is likely to include prefrontal and fronto-striatal regions. For example, anterior cingulate, inferior frontal, and orbito-frontal regions have all been previously associated with both the perception of emotional facial expressions (Bishop et al., 2004; Blair et al., 1999; Nakamura et al., 1999) and the effective suppression of automatically triggered motor responses (Menon et al., 2001; Garavan et al., 1999). Recent evidence has also implicated fronto-striatal dopaminergic activity in both the processing of emotional facial expressions, especially anger and disgust (Sprengelmeyer et al., 2003), and the successful suppression of no-go responses (Durston et al., 2002), complimenting the proposal that acute stress may, via a hyperdopaminergic mechanism, temporarily take the PFC "off-line" and allow habitual responses to govern behavior (Arnsten & Goldman-Rakic, 1998).

These data are informative, but leave many questions open pending further research. For example, although these data speak to the perception of affective information and the interaction between emotional perception and affective state, they are silent with regard to the generation and experience of emotion in the absence of affective stimuli, which may bias attentional processing in a fundamentally different manner. Additionally, angry and happy facial expressions may be processed differently than nonsocial emotional images (e.g., snake) and other facial expressions (e.g., fear), leaving open the possibility that comparably valenced but categorically distinct emotional stimuli may bias information processing in a different fashion (e.g., Bradley, Codispoti, Cuthbert, & Lang, 2001). Similarly, these results pertain to the inhibition of visually triggered, nonaffective, motor responses, but may not readily generalize to other attentionally demanding processes (e.g., response selection).

In sum, mechanisms of emotional processing and attentional control rely, in part, on common neural substrates and, at least outside of the laboratory, do not operate in isolation. As such, we have proposed to integrate emotional processing into competition-based models of attentional enhancement and inhibition. In particular, we have proposed that affective perception and emotional experience are able to, in some instances, asymmetrically bias attentional processing and control.

The present results provide initial support for this prediction and suggest that the incidental perception of unattended emotional facial distractors can asymmetrically disrupt the processing of nonemotional information and mechanisms of behavioral inhibition. Ultimately, it will likely be determined that the particular details of these and other attention–emotion interactions rely on a host of factors, including individual differences in affective style and reactivity; the specific system (e.g., appetitive, defensive) or emotion (e.g., anxiety, depression) involved and the manner in which it is engaged (e.g., affective experience vs. emotional perception); which aspect of attentional processing is examined (e.g., motion vs. color, orienting vs. disengagement); and whether the emotional experience (or affective stimulus) of interest is integrated with or incidental to one's primary task goals and focus of attention.

METHODS

Forty-three students and employees of the University of Wisconsin-Madison, 18–30 years of age (22 women, 40 right handed), with no history of neurological or psychiatric disorders, gave informed consent and were paid for their participation in this study, which was approved by the appropriate University of Wisconsin institutional review board. Sessions were discarded for seven additional study candidates because they either failed to establish a 98% baseline response rate on go trials, did not complete all items on the self-report questionnaires, or both. Gray-scale face images consisted of four male models selected from the *Pictures of Facial Affect* (Ekman & Friesen, 1976), displaying each of three facial expressions (neutral, angry, and happy). All face images were matched on luminance to within 0.05 standard deviations of the group mean and subtended a visual angle of 7.83° horizontally and 9.05° vertically. Target images consisted of isoluminant green and red circles and octagons that subtended 5.6° of visual angle in each direction and were centered 7.2° lateral to fixation in either the LVF or RVF.

Participants were seated in front of a ViewSonic 17GS computer monitor (operated at 60 Hz; RGB medium–short persistence phosphors) at a distance of 50 cm, eye-gaze monitored via a closed-circuit camera, head centered and stabilized with a chin rest, and used their peripheral vision to perform an attentionally demanding go/no-go CPT. Participants were instructed to ignore and, as much as possible, prevent being distracted by the task-irrelevant face images while responding as quickly and accurately as possible on the go/no-go task. Lateralized (LVF and RVF) go targets and no-go lures were presented in synchrony with centrally displayed, task-irrelevant, emotional facial expressions. To obtain a baseline index of task difficulty for each participant in the absence of any distraction, 25% of trials consisted of target or lure stimuli presented singly.

The go/no-go task required that participants make a rapid response to all go targets, presented on 71.4% of trials, while attempting to suppress their prepotent tendency to respond (i.e., make a nonresponse) on the remaining 28.6% of no-go lure trials (Figure 1). Go targets consisted of circles (80% green, 20% red) and no-go lures consisted of octagons (50% green, 50% red). Overall, task-relevant images were comprised of 57.1% green circles, 14.3% red circles, 14.3% green octagons, and 14.3% red octagons. This relative proportioning of stimuli ensured that, above and beyond establishing a prepotent tendency to respond to all task-relevant stimuli, green no-go lures would trigger a stronger motor response and be more difficult to inhibit (i.e., higher load) than red no-go lures. To ensure the establishment of a dominant response set, each participant performed multiple practice blocks (~15 min) prior to reporting anxiety (STAI-X; Spielberger, 1983) and beginning the experiment proper. Experimental trials advanced at a very rapid pace with a target duration of 250 msec and an average interstimulus interval (ISI) of 885 msec (100 msec jitter). Task stimuli and distractors were paired in every possible combination and randomly presented in six blocks (168 trials).

Acknowledgments

Support for this research was provided by a Ruth L. Kirschstein National Research Service Award (JSM) and NIMH grants P50-MH069315 (RJD) & R37-MH43454 (RJD). We thank Joshua D. Zeier for assistance with data collection.

Reprint requests should be sent to Jeffrey S. Maxwell, Department of Psychology, University of Wisconsin, 1202 West Johnson Street, Madison, WI 53706, or via e-mail: maxwell@psyphw.psych.wisc.edu.

Note

1. The fundamental relation between STAI, emotional expression, and RH/LH inhibition does not strictly depend on adjusting angry/happy asymmetry scores for baseline asymmetries in the presence of neutral faces: two of the three significant correlations remain significant (happy low load, $r = .33, p < .05$; angry high load, $r = .33, p < .05$); angry low load, although substantially attenuated, relates in the same direction ($r = .14$, $p = .39$); the complete absence of any relation between STAI, happy, and RH/LH inhibition under high load remains ($r = .01$, $p = .95$); and the attenuating effect of attentional demands on the relation between STAI and happy-driven RH interference again emerges [$t(40) < 1.66, p = .05$, one-tailed). Additionally, collapsed across expression (angry, happy) and attentional load (low, high), STAI is associated with relatively greater RH interference in the presence of emotional expressions in general both with ($r = .46, p < .01$) and without ($r = .31$, $p < .05$) baseline asymmetries in the presence of neutral faces subtracted.

REFERENCES

Ades, C., & Ramires, E. N. (2002). Asymmetry of leg use during prey handling in the spider Scytodes globula (*Scytodidae*). *Journal of Insect Behavior, 15,* 563–570.

Adolphs, R., Damasio, H., Tranel, D., & Damasio, A. R. (1996). Cortical systems for the recognition of emotion in facial expressions. *Journal of Neuroscience, 16,* 7678–7687.

Arnsten, A. F. T. (1998). The biology of being frazzled. *Science, 280,* 1711–1712.

Arnsten, A. F. T., & Goldman-Rakic, P. S. (1998). Noise stress impairs prefrontal cortical cognitive function in monkeys: Evidence for a hyperdopaminergic mechanism. *Archives of General Psychiatry, 55,* 362–368.

Aston-Jones, G., Rajkowski, J., & Cohen, J. (1999). Role of locus coeruleus in attention and behavioral flexibility. *Biological Psychiatry, 46,* 1309–1320.

Bishop, S., Duncan, J., Brett, M., & Lawrence, A. D. (2004). Prefrontal cortical function and anxiety: Controlling attention to threat-related stimuli. *Nature Neuroscience, 7,* 184–188.

Blair, R. J. R., Morris, J. S., Frith, C. D., Perrett, D. I., & Dolan, R. J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain, 122,* 883–893.

Bokura, H., Yamaguchi, S., & Kobayashi, S. (2001). Electrophysiological correlates for response inhibition in a Go/NoGo task. *Clinical Neurophysiology, 112,* 2224–2232.

Borod, J. C., Andelman, F., Obler, L. K., Tweedy, J. R., & Welkowitz, J. (1992). Right hemisphere specialization for the appreciation of emotional words and sentences: Evidence from stroke patients. *Neuropsychologia, 30,* 827–844.

Bowers D., Bauer, R. M., Coslett, H. B., & Heilman, K. M. (1985). Processing of face by patients with unilateral hemisphere lesions: Dissociations between judgements of facial affect and facial identity. *Brain and Cognition, 4,* 258–272.

Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation: I. Defensive and appetitive reactions in picture processing. *Emotion, 1,* 276–298.

Broca, P. (1861a). Perte de la parole, ramollissement chronique et destruction partielle du lobe antérieur gauche du cerveau. *Bulletin de la Société Anthropologique, 2,* 235–238. Translated by C. D. Green. Electronic resource developed by C. D. Green, York University, Toronto, Canada.

Broca, P. (1861b). Remarques sur le siége de la faculté du langage articulé, suivies d'une observation d'aphémie (perte de la parole). *Bulletin de la Société Anatomique, 6,* 330–357. Translated by C. D. Green. Electronic resource developed by C. D. Green, York University, Toronto, Canada.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences, 4,* 215–222.

Carmon, A., & Nachson, I. (1973). Ear asymmetry in perception of emotional nonverbal stimuli. *Acta Psychologica, 37,* 351–357.

Casey, B. J., Tottenham, N., & Fossella, J. (2002). Clinical, imaging, lesion, and genetic approaches toward a model of cognitive control. *Developmental Psychobiology, 40,* 237–254.

Chao, L., & Knight, R. T. (1995). Human prefrontal lesions increase distractibility to irrelevant sensory inputs. *NeuroReport, 6,* 1605–1610.

Chao, L., & Knight, R. T. (1998). Contribution of human prefrontal cortex to delay performance. *Journal of Cognitive Neuroscience, 10,* 167–177.

Chelazzi, L., Miller, E., Duncan, J., & Desimone, R. (2001). Responses of neurons in macaque area V4 during memory-guided visual search. *Cerebral Cortex, 11,* 761–772.

Clapham, P. J., Leimkuhler, E., Gray, B. K., & Mattila, D. K. (1995). Do humpback whales exhibit lateralized behaviour? *Animal Behaviour, 50,* 73–82.

Corballis, M. C. (1997). The genetics and evolution of handedness. *Psychological Review, 104,* 714–727.

Corbetta, M., & Shulman, G. R. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3,* 201–215.

Damasio, H., Grabowski, T., Frank, R., Galaburda, A. M., & Damasio, A. R. (1994). The return of Phineas Gage: Clues about the brain from the skull of a famous patient. *Science, 264,* 1102–1105.

Davidson, R. J. (1992). Emotion and affective style: Hemispheric substrates. *Psychological Science, 3,* 39–43.

Davidson, R. J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. *Cognition and Emotion, 12,* 307–330.

Davidson, R. J. (2002). Anxiety and affective style: Role of prefrontal cortex and amygdala. *Biological Psychiatry, 51,* 68–80.

Davidson, R. J. (2003) Affective neuroscience and psychophysiology: Toward a synthesis. *Psychophysiology, 40,* 655–665.

Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences, 3,* 11–21.

Davidson, R. J., Mednick, D., Moss, E., & Saron, C. (1987). Ratings of emotion in faces are influenced by the visual field to which stimuli are presented. *Brain and Cognition, 6,* 403–411.

Davidson, R. J., Putnam, K. M., & Larson, C. L. (2000). Dysfunction in the neural circuitry of emotion regulation—A possible prelude to violence. *Science, 289,* 591–594.

Davis, M., & Whalen, P. J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry, 6,* 13–34.

de Fockert, J. W., Rees, G., Frith, C. D., & Lavie, N. (2001). The role of working memory in visual selective attention. *Science, 291,* 1803–1806.

Deckel, A. W., Lillaney, R., Ronan, P. J., & Summers, C. H. (1998). Lateralized effects of ethanol on aggression and serotonergic systems in *Anolis carolinensis*. *Brain Research, 807,* 38–46.

Desimone, R. (1998). Visual competition mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London, B, 353,* 1245–1255.

Downing, P. E. (2000). Interactions between visual working memory and selective attention. *Psychological Science, 11,* 467–473.

Duncan, J. (1998). Converging levels of analysis in the cognitive neuroscience in visual attention. *Philosophical Transactions of the Royal Society of London, B, 353,* 1307–1317.

Durston, S., Thomas, K. M., Yang, Y., Ulug, A. M., Zimmerman, R. D., & Casey, B. J. (2002). A neural basis for the development of inhibitory control. *Developmental Science, 5,* F9–F16.

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

Fischer, H., Wright, C. I., Whalen, P. J., McInerney, S. C., Shin, L. M., & Rauch, S. L. (2003). Brain habituation during repeated exposure to fearful and neutral faces: A functional MRI study. *Brain Research Bulletin, 59,* 387–392.

Fox, E. (2002). Processing emotional facial expressions: The role of anxiety and awareness. *Cognitive, Affective & Behavioral Neuroscience, 2,* 52–63.

Fox, E., Russo, R., Bowles, B., & Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety. *Journal of Experimental Psychology: General, 130,* 681–700.

Fox, E., Russo, R., & Dutton, K. (2002). Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cognition and Emotion, 16,* 355–379.

Garavan H., Ross T. J., & Stein E. A. (1999). Right hemispheric dominance of inhibitory control: An event-related functional MRI study. *Proceedings of the National Academy of Sciences, U.S.A., 96,* 8301–8306.

Gray, J. R. (2001). Emotional modulation of cognitive control: Approach-withdrawal double-dissociates spatial from verbal two-back task performance. *Journal of Experimental Psychology: General, 130,* 436–452.

Güntürkün, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A., & Skiba, A. (2000). Asymmetry pays: Visual lateralization improves discrimination success in pigeons. *Current Biology, 10,* 1079–1081.

Heller, W. (1993). Neuropsychological mechanisms of individual differences in emotion, personality, and arousal. *Neuropsychology, 7,* 476–489.

Hobert, O., Johnston, R. J., & Chang, S. (2002). Left–right asymmetry in the nervous system: The *Caenorhabditis elegans* model. *Nature Reviews Neuroscience, 3,* 629–640.

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience, 3,* 284–291.

Ishai, A., Pessoa, L., Bikle, P. C., & Ungerleider, L. G. (2004). Repetition suppression of faces is modulated by emotion. *Proceedings of the National Academy of Sciences, U.S.A., 101,* 9827–9832.

Jaccard, J., & Guilamo-Ramos, V. (2002). Analysis of variance frameworks in clinical child and adolescent psychology: Issues and recommendations. *Journal of Clinical Child and Adolescent Psychology, 31,* 130–146.

Jansari, A., Tranel, D., & Adolphs, R. (2000). A valence-specific lateral bias for discriminating emotional facial expressions in free field. *Cognition and Emotion, 14,* 341–353.

Johnsen, B. H., & Hugdahl, K. (1991). Hemispheric asymmetry in conditioning to facial emotional expressions. *Psychophysiology, 28,* 154–162.

Ladavas, E., Del-Pesce, M., Mangun, G. R., & Gazzaniga, M. S. (1994). Variations in attentional bias of the disconnected cerebral hemispheres. *Cognitive Neuropsychology, 11,* 57–74.

Lavie, N., & Fox, E. (2000). The role of perceptual load in negative priming. *Journal of Experimental Psychology: Human Perception and Performance, 26,* 1038–1052.

Liotti, M., & Tucker, D. M. (1992). Right hemisphere sensitivity to arousal and depression. *Brain and Cognition, 18,* 138–151.

Lippolis, G., Bisazza, A., Rogers, L. J., & Vallortigara, G. (2002). Lateralisation of predator avoidance responses in three species of toads. *Laterality, 7,* 163–183.

Luck, S. J., & Hillyard, S. A. (2000). The operation of selective attention at multiple stages of processing: Evidence from human and monkey electrophysiology. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed., pp. 687–700). Cambridge: MIT Press.

Mandal, M. K., & Singh, S. K. (1990). Lateral asymmetry in identification and expression of facial emotions (Special Issue: Evaluative Conditioning). *Cognition and Emotion, 4,* 61–69.

Martin, A. (1999). Automatic activation of the medial temporal lobe during encoding: Lateralized influences of meaning and novelty. *Hippocampus, 9,* 62–70.

Masson, M. E. J., & Loftus, G. R. (2003). Using confidence intervals for graphically based data interpretation. *Canadian Journal of Experimental Psychology, 57,* 203–220.

Mathews, A., Fox, E., Yiend, J., & Calder, A. (2003). The face of fear: Effects of eye gaze and emotion on visual attention. *Visual Cognition, 10,* 823–825.

Menon, V., Adleman, N. E., White, C. D., Glover, G. H., & Reiss, A. L. (2001). Error-related brain activation during a Go/NoGo response inhibition task. *Human Brain Mapping, 12,* 131–143.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24,* 167–202.

Mogg, K., & Bradley, B. P. (1999). Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cognition and Emotion, 13,* 713–740.

Mogg, K., & Bradley, B. P. (2002). Selective orienting of attention to masked threat faces in social anxiety. *Behaviour Research and Therapy, 40,* 1403–1414.

Morris, J. S., Öhman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature, 393,* 467–470.

Nakamura, K., Kawashima, R., Ito, K., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Nagumo, S., Kubota, K., Fukuda, H., & Kojima, S. (1999). Activation of the right inferior frontal cortex during assessment of facial emotion. *Journal of Neurophysiology, 82,* 1610–1614.

Nicholls, M. E. R., Ellis, B. E., Clements, J. G., & Yoshino, M. (2004). Detecting hemifacial asymmetries in emotional expression with three-dimensional computerized image analysis. *Proceedings of the Royal Society of London, B, 271,* 663–668.

Oke, A., Keller, R., Mefford, I., & Adams, R. N. (1978). Lateralization of norepinephrine in human thalamus. *Science, 200,* 1411–1413.

Pessoa, L., Kastner, S., & Ungerleider, L. G. (2002). Attentional control of the processing of neutral and emotional stimuli. *Cognitive Brain Research, 15,* 31–45.

Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences, U.S.A., 99,* 11458–11463.

Previc, F. H. (1991). A general theory concerning the prenatal origins of cerebral lateralization in humans. *Psychological Review, 98,* 299–334.

Reuter-Lorenz, P., & Davidson, R. J. (1981). Differential contributions of the 2 cerebral hemispheres to the perception of happy and sad faces. *Neuropsychologia, 19,* 609–613.

Rogers, L. J. (2000). Evolution of hemispheric specialization: Advantages and disadvantages. *Brain and Language, 73,* 236–253.

Rogers, L. J. (2002). Lateralised brain function in anurans: Comparison to lateralisation in other vertebrates. *Laterality, 7,* 219–239.

Rolls, E. T. (2004). The functions of the orbitofrontal cortex. *Brain and Cognition, 55,* 11–29.

Rule, R. R., Shimamura, A. P., & Knight, R. T. (2002). Orbitofrontal cortex and dynamic filtering of emotional stimuli. *Cognitive, Affective & Behavioral Neuroscience, 2,* 264–270.

Shackman, A. J., Sarinopoulos, I., Maxwell, J. S., Pizzagalli, D. A., Lavric, A., & Davidson, R. J. (in press). Anxiety selectively disrupts visuospatial working memory. *Emotion.*

Smith, S. D., Tays, W. J., Dixon, M. J., & Bulman-Fleming, M. B. (2002). The right hemisphere as an anomaly detector: Evidence from visual perception. *Brain and Cognition, 48,* 574–579.

Spielberger, C. D. (1983). *Manual for the state–trait anxiety inventory: STAI.* Palo Alto, CA: Consulting Psychologists Press.

Sprengelmeyer, R., Young, A. W., Mahn, K., Schroeder, U., Woitalla, D., Büttner, T., Kuhn, W., & Przuntek, H. (2003). Facial expression recognition in people with medicated and unmedicated Parkinson's disease. *Neuropsychologia, 41,* 1047–1057.

Tipper, S. P., Howard, L. A., & Houghton, G. (1998). Action-based mechanisms of attention. *Philosophical Transactions of the Royal Society of London, B, 353,* 1385–1393.

Toga, A. W., & Thompson, P. M. (2003). Mapping brain asymmetry. *Nature Reviews Neuroscience, 4,* 37–48.

Vallortigara, G., Rogers, L. J., Bisazza, A., Lippolis, G., & Robins, A. (1998). Complementary right and left hemifield use for predatory and agonistic behavior in toads. *NeuroReport, 9,* 3341–3344.

Vuilleumier, P., & Schwartz, S. (2001). Beware and be aware: Capture of spatial attention by fear-related stimuli in neglect. *NeuroReport, 12,* 1119–1122.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., Mcinerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience, 18,* 411–418.

Workman, L., Peters, S., & Taylor, S. (2000). Lateralization of perceptual processing of pro- and anti-social emotions displayed in chimeric faces. *Laterality, 5,* 237–249.