



Independent and collaborative contributions of the cerebral hemispheres to emotional processing

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Presented is a model suggesting that the right hemisphere (RH) directly mediates the identification and comprehension of positive and negative emotional stimuli, whereas the left hemisphere (LH) contributes to higher level processing of emotional information that has been shared via the corpus callosum. RH subcortical connections provide initial processing of emotional stimuli, and their innervation to cortical structures provides a secondary pathway by which the hemispheres process emotional information more fully. It is suggested that the LH contribution to emotion processing is in emotional regulation, social well-being, and adaptation, and transforming the RH emotional experience into propositional and verbal codes. Lastly, it is proposed that the LH has little ability at the level of emotion identification, having a default positive bias and no ability to identify a stimulus as negative. Instead, the LH must rely on the transfer of emotional information from the RH to engage higher-order emotional processing. As such, either hemisphere can identify positive emotions, but they must collaborate for complete processing of negative emotions. Evidence presented draws from behavioral, neurological, and clinical research, including discussions of subcortical and cortical pathways, callosal agenesis, commissurotomy, emotion regulation, mood disorders, interpersonal interaction, language, and handedness. Directions for future research are offered.

Keywords: hemisphere, emotion, brain, valence, emotion regulation, subcortical, cortical, handedness

While the debate over hemispheric asymmetries for emotion perception and identification has been ongoing for over four decades, the most recent observations are a mixture of findings such as a right hemisphere (RH) superiority for negative emotions (Kumar and Srinivasan, 2011; Önal-Hartmann et al., 2012; Sedda et al., 2013), a RH superiority for both positive and negative emotions (Hagemann et al., 2005; Killgore and Yurgelun-Todd, 2007; Alves et al., 2009; Bourne, 2010; Cheng et al., 2012; Irish et al., 2013; Najt et al., 2013; Yuvaraj et al., 2013), no asymmetries for positive emotions (Tomarken et al., 1990; Smith and Bulman-Fleming, 2005; Kumar and Srinivasan, 2011; Zhang et al., 2011; Önal-Hartmann et al., 2012; Najt et al., 2013; Sedda et al., 2013), and no left hemisphere (LH) differentiation between emotional and neutral faces (Najt et al., 2013). A recent meta-analysis concluded that the RH processes both positive and negative emotion, but the LH may only process positive emotions (Abbott et al., 2013). Given the evidence to date, it appears that the RH is integral to processing all basic emotions (positive and negative) and is the seat of subjective affect (feeling). However, inconsistent and contradictory findings make the contributions of the LH to emotional processing highly debatable. It is most interesting that regardless of the methodology and populations studied, the RH consistently demonstrates emotional competence, but the LH sometimes does and sometimes does not. Even when couched in terms of approach and avoidance/withdrawal motivations (e.g., Kinsbourne, 1978; Davidson, 1992) to account for findings that anger (a negative emotion) and happy judgments have both been associated with

the LH (Harmon-Jones et al., 2013), findings are still mixed with regards to the LH (e.g., Alves et al., 2009; Brüne et al., 2013; Fetterman et al., 2013; Najt et al., 2013; see Miller et al., 2013a). When LH competency is observed, it is consistent only in the identification of positive emotions. However, a broader range of evidence suggests that the LH may play a more crucial role in emotional processing at levels beyond simple identification of emotionality that have yet to be extensively explored. The current paper presents a framework that unifies evand genuine comprehension of emotional stimuli, nor does seem to influence subjective affect that is consistent with the specific stimulus. Rather, being proposed is that the LH contributes an additional or secondary interpretation, based on information received from the RH. This secondary interpretation of the LH appears to be positively biased, making an important contribution to regulation of negative emotion and social interaction, both

of which are important for planning, decision-making, and self-preservation. Also, being proposed is that the LH maintains a propositional understanding of RH emotional information and enables verbalization that is more informational than experiential. As such, the LH does not seem to be integral to initial perceptual and experiential stages of emotional processing, but seems more attune to the outcomes of RH interpretation and its application to executive functioning, social well-being, and knowledge representation. Thus, the LH may direct our conscious interpretation of and interaction with stimuli, but does so based on the RH direct and genuine interpretation of the stimulus. This further suggests that complex processing of and responding to emotions require a cross-hemispheric collaboration that originates in the RH, and this is particularly true for negative emotions. Suggestions for testing these hypotheses are presented in Section "Future Directions" below.

LATERAL SUBCORTICAL AND BILATERAL CORTICAL EMOTION NETWORKS

The subcortical and cortical networks provide one indication that the RH is the primary interpreter of emotional stimuli and gen-

inter-hemispheric communication) and cingulate gyrus, whose axons are the genesis of the CC (Koester and O'Leary, 1994; Rash and Richards, 2001), and is functionally associated with different aspects of emotional processing, it follows that a large amount of emotion would be communicated across the hemispheres. Indeed, a high degree of bilateral activity has been observed among DMN structures (Saenger et al., 2012

or at the very least, that the LH does make interpretations of circumstantial cues in the absence of true comprehension of the causal stimulus. In their review of V.P. and several other findings, Baynes and Gazzaniga (2000) similarly (originally) conclude that the RH makes the situation-appropriate emotional contribution to the LH interpretation of events. Cleverly, they also propose that if this were true, it should be possible to “trick” the LH. This point will be returned to in the Section “Future Directions” below.

In addition to V.P., other commissurotomy studies demonstrate that the speaking LH appears to have lost access to the understanding of the emotional nature of a stimulus. For example, Bermond (1995) observed that CC dysfunction results in deficits in verbal descriptions of emotion, but intact experiencing of basic emotions. Classically, commissurotomy patients are able to use non-verbal indications that they comprehend emotion, but are unable to verbalize these feelings (Sperry et al., 1979

of alexithymia (Habib et al., 2003). Lumley and Sielky (2000) observed similar findings of an association between alexithymia and poor inter-hemispheric transfer in normal participants, as did Romei et al. (2008) and Parker et al. (1999). Importantly, alexithymia does not seem to be due to hypoactivity of the RH,

than directly perceiving and identifying the emotional nature of stimuli.

Heilman and Bowers (1990) also proposed an inhibitory role for the LH that is akin to emotional regulation. They suggest that LH dysfunction results in a disinhibition of the RH, which in turn, increases physiological arousal associated with emotion. Although their proposal was conjecture at the time of their writing, these more recent findings lend additional plausibility. One additional benefit to emotional regulation may be to maintain a coherent and consistent conscious experience, for which Ramachandran (1995)

because the LH appears to exhibit less intense emotions under normal circumstances, a damaged or hypoactive RH forces emotional processing onto the LH, which only seems to be independently capable of positive assessments.

The behaviors of manics and depressives also indicate that the LH is poor at interpreting the emotional nature of stimuli. First, depression or catastrophic reactions would be considered normal responses to an experience of traumatic brain injury, sudden disability, and traumatic life events (a frequent trigger for clinical depression). As such, the depression observed in LH damaged patients is actually more normal and appropriate to their situation suggesting that the RH at least accurately appraises the situation. By comparison, the manic reactions of the LH are truly inappropriate to the experience of brain injury and disability, and suggest that the LH does not have the capability to comprehend and apply the appropriate emotional response. Even in non-TBI popula-

outright denying physical deficits (e.g., anosognosia) (Vocat et al., 2010; Azouvi and Peskine, 2013)

and events. Conversely, inconsistent-handers may have a disadvantage for emotional processing that is better accomplished by the LH alone or by the hemispheres, independently. For example, inconsistent-handers may have more difficulty than consistent-handers ignoring a correct emotional experience or identification in favor of a popular or socially acceptable one. Inconsistent-handers may show processing advantages for identification of negative emotions and they may also have more difficulty separating the genuine experience of the RH from the LH idealized experience.

There have been very few papers directly investigating emotion processing by degree of handedness. One paper suggests that inconsistent-handers may experience emotion more genuinely than consistent-handers. Farina et al. (2012) report that inconsistent-handers show greater emotional distress than do consistent-handers to a traumatic event (earthquake). In this instance, an earthquake truly is traumatic, and experience of associated negative emotion is expected. Because the RH appears to be the on-line information processor of real-world emotional stimuli, inconsistent-handers may have a greater understanding (ability to process, feel) of the traumatic event. Consistent-handers however, may have less of a connection to the RH emotion and so display less distress. Another study by Mikkelsen et al. (2006) examined consistent and inconsistent hander differences in expressiveness and emotional control. While these authors report differences as having been observed (opposite to what is predicted, here), they do not report the statistical inferences that led to their conclusions. Certainly, more research will enable stronger speculations.

Two other papers, using different methodologies have seemingly opposing conclusions. For example, Bourne (2008), using a free vision chimeric happy-face task, observed that degree of handedness is related to degree of RH lateralization for both positive and negative emotions. This supports the RH

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of negative valence stimuli are processed by the RH, only. In the normal brain, where bilateral activity is observed during processing of negative valence, the LH must use information received from the RH for verbal and propositional contributions to emotion processing, and emotional regulation.

- The currently proposed theory suggests that the LH contribution to emotion is not at a basic, comprehension level. Instead, the LH receives this type of information from the RH and integrates it into higher level cognitions. As such, the LH and RH contribute to different components or levels of emotion processing. There are many methodologies that have been under-utilized in the study of hemispheric asymmetries of emotion that have been successfully utilized in other areas. As such, to date, we have little understanding of the degree to which each hemisphere processes emotional information or their relative contribution to the many aspects of emotion processing.

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