

fearful faces are rendered invisible, greater skin conductance responses to them predict a greater dislike of novel neutral faces presented subsequently (Lapate et al., 2014). In contrast, when individuals are aware of the emotional provocation, changes in physiological reactivity were uncorrelated with subsequent judgments. We interpreted these findings to suggest that awareness may serve an important emotion-regulatory function by “breaking” otherwise automatic associations between emotional reactivity and evaluative behavior.

Thus, *lack* of conscious awareness of an emotional-eliciting event and/or of its relationship with subsequent physiological changes may subject us to the whims of external stimuli. In the context of the emotion misattribution paradigm, the explicit goal is to evaluate a novel stimulus. If evaluations are instead determined by a previously-provoked emotional change, rather than by an objective appraisal of the stimulus at hand, the individual’s behavior is biased, and emotional-stimulus-driven (as opposed to task-goal-driven). In the absence of a lawful relationship between that affect and the stimulus that it binds to, emotion misattribution is often maladaptive—for instance, many are probably familiar with the unfortunate experience of snapping at a loved one during dinner following an earlier disagreement with a co-worker.

Conscious awareness may thus promote behavior that overrides stimulus-driven responses to favor the organism’s goals, particularly when they involve strategic regulation. Consistent with this idea, the implementation of cognitive control appears to benefit from conscious awareness, in particular when it is implicitly inferred, such as via an internally generated goal or a history of events (Kunde, Reuss, & Kiesel, 2012; van Gaal, de Lange, & Cohen, 2012). For example, awareness benefits the strategic intake of information in a decision-making paradigm (de Lange, van Gaal, Lamme, & Dehaene, 2011), facilitates conflict adaptation (the “Gratton effect”; see Kunde et al., 2012, and van Gaal, 2012, for reviews), and is associated with the strategic behavior of slowing down to perform trials associated with high reward cues (Bijleveld, Custers, & Aarts, 2010).⁴ Collectively, these findings underscore the significance of awareness for strategic, self-initiated regulatory behavior.

Although studies simultaneously examining the neural bases of conscious awareness and cognitive control in the same individuals are lacking, current evidence suggests that the dorsolateral prefrontal cortex (DLPFC) node of the frontoparietal

network may be an important neural substrate supporting the *co-emergence* of subjective awareness and strategic control.

DORSOLATERAL PREFRONTAL CORTEX: POSSIBLE NEUROARCHITECTONIC INTERSECTION OF AWARENESS AND COGNITIVE CONTROL

DLPFC Function Supports Subjective Awareness of Sensory and Emotional Representations

Activation of the frontoparietal network, including the DLPFC, correlates with stimulus awareness (Dehaene & Changeux, 2011; Lau & Rosenthal, 2011; Rees, 2007). Critically, DLPFC function may actually be *causally* involved in promoting awareness: individuals with lateral prefrontal cortex (LPFC) damage have a higher subjective awareness threshold for simple visual stimuli (Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009). Furthermore, when low-level signal strength and stimulus identification performance (i.e., objective awareness) are matched across conditions differing in subjective awareness, DLPFC (more specifically, Brodmann Area 46 (BA46)) is the only region whose activation increases with subjective awareness (Lau & Passingham, 2006). Direct evidence for a causal role for DLPFC in promoting awareness comes from a study demonstrating that altering BA46 function using an inhibitory transcranial magnetic stimulation (TMS) protocol reduces subjective awareness of simple visual stimuli, while maintaining stimulus discrimination ability (i.e., objective awareness) intact (Rounis, Maniscalco, Rothwell, Passingham, & Lau, 2010).

Conscious access, possibly promoted by “entry” of stimulus representation into the DLPFC node of the frontoparietal network, may thus co-emerge with (or enable) some of the processes that best characterize this node’s function: goal-oriented and context-appropriate behavior.

DLPFC Function Supports Context- Appropriate Behavioral and Emotional Regulation

The DLPFC is involved with non-routine, abstract representation of a stimulus that incorporates temporally extended information (Badre & D’Esposito, 2009; Barraclough, Conroy, & Lee, 2004; Tsujimoto & Postle, 2012; Wilson, Gaffan,

Browning, & Baxter, 2010)—and that therefore should allow for more strategic, goal-oriented (as opposed to stimulus-driven) considerations of how to respond (Petrides, 2005).⁵

For example, DLPFC-supported computations are associated with self-control in situations where a stimulus-driven impulse should be overcome for better long-term outcomes. Individuals on a diet who are better able to refuse a tasty and caloric food item show greater DLPFC engagement when making such choices (Hare, Camerer, & Rangel, 2009). Accordingly, disruption of LPFC via TMS shifts human behavior toward impulsiveness in a delay discounting task (Figner et al., 2010), and DLPFC maturation is associated with improvements in strategic sharing in a neuroeconomic game (Steinbeis, Bernhardt, & Singer, 2012).

DLPFC also seems to support the implementation of *emotion-regulatory* goals such as cognitive reappraisal (Davidson & Irwin, 1999), which involves changing the meaning of an emotion-eliciting event according to one's goal (Gross, 1998b; Ochsner & Gross, 2005). Accordingly, LPFC is reliably recruited during reappraisal (for a review, see Buhle et al., 2012), and the magnitude of DLPFC coupling with the amygdala during instructed reappraisal to decrease negative affect correlates with emotion-regulatory success (Lee, Heller, van Reekum, Nelson, & Davidson, 2012).

One prior study speaks more directly to a possible DLPFC-mediated *co-emergence* of conscious awareness and strategic control: In a neuroimaging experiment, participants performed a central target-identification task while being asked to ignore peripheral moving dots with a motion ratio that was either subliminal or supraliminal (Tsushima, Sasaki, & Watanabe, 2006). Individuals failed to inhibit attention to the distracting dots when their motion ratio was subliminal compared to when the motion was supraliminal, leading to greater disruption of performance when the distracting motion was actually smaller in magnitude and not consciously perceived (Tsushima et al., 2006). This failure to perceive the motion and ignore it was accompanied by lower DLPFC activation to subliminally moving dots, compared to when supraliminally moving (and successfully ignored) dots were shown.

Collectively, the data reviewed here suggest that DLPFC function may promote relatively more strategic emotion- and behavioral-regulatory choices, and/or enable those choices to be implemented more successfully.

PREVENTING EMOTION MISATTRIBUTION: MODULATION OF PFC-AMYGDALA CIRCUITRY BY CONSCIOUS AWARENESS AND A CAUSAL ROLE FOR DLPFC

Given the above-reviewed evidence linking DLPFC function with awareness and regulation, we examined whether function of PFC circuitry known to promote successful emotion regulation was impacted by emotional-stimulus awareness. To do so, we used continuous flash suppression (CFS) in the MRI scanner to manipulate awareness of fearful faces and flowers during an emotion misattribution paradigm (Lapate et al., 2016). Consistent with the idea that the amygdala subserves the encoding of emotionally meaningful visual stimuli, we found that the amygdala responded to fearful faces independently of visual awareness. Moreover, such emotional-stimulus encoding appeared consequential in the visually unaware condition: greater amygdala responses to fearful faces rendered invisible were associated with lower preferences for later-presented neutral faces. With regard to the role of PFC circuitry, we replicated prior findings of increased frontoparietal (including DLPFC) engagement with stimulus awareness. Critically, the extent to which DLPFC (as well as ventrolateral and dorsomedial PFC (VLPFC and dmPFC)) inversely coupled with the amygdala during aware fearful-face processing predicted *reduced* emotion coloring.

The relationship between PFC–amygdala functional coupling and emotional coloring behavior was absent and significantly attenuated in the unaware relative to the aware condition, suggesting specificity of function of this emotion-regulatory network to consciously aware emotional processing. Consistently, individuals with greater structural connectivity in the major white matter pathway connecting the prefrontal cortex and amygdala (the uncinate fasciculus) showed less emotion coloring, and greater inverse coupling between the amygdala and dmPFC in the aware condition only (Lapate et al., 2016). In summary, amygdala–prefrontal functional and structural connectivity, both neural correlates of successful down-regulation of negative emotion (Lee et al., 2012; Tromp et al., 2012), selectively operated during conscious processing of emotional information, suggesting that function of a PFC-dependent emotion-regulatory network may depend on conscious awareness to impact behavior.

Despite being compelling, the above-reviewed evidence is correlational and precludes causal inferences regarding the role of DLPFC in preventing emotional coloring. To address this gap and determine whether DLPFC function actually plays a *causal* role in promoting conscious awareness and preventing emotional coloring, we disrupted DLPFC function using TMS during an emotion misattribution task. Following inhibitory TMS to DLPFC (vs. a posterior control site), ratings of novel, otherwise neutral faces were significantly influenced by the valence of a previously-processed (happy or fearful) facial expression, giving rise to long-lasting, emotionally biased appraisals measurable inside and outside of the laboratory days after the TMS session (Lapate et al., 2017). Finally, the extent to which we provoked emotional coloring after DLPFC inhibition correlated with reduced metacognitive awareness of the emotional stimuli across individuals, providing initial support for the idea that DLPFC function may mediate the interconnectedness of conscious awareness and emotion-regulatory processes in humans.

CONCLUSION

This essay examined an idea inspired by findings from the emotion misattribution task: that conscious awareness may facilitate goal-oriented rather than emotional-stimulus-driven behavior. The evidence reviewed here suggests that DLPFC function is implicated in both supporting awareness and behavioral regulation across cognitive and emotional processing domains.

Limitations and Future Directions

Although the emotion misattribution task has been fruitful in probing the modulation of emotional processing by awareness, the field would gain valuable insight from novel tasks probing the proposed strategic advantages for behavior of consciously aware emotional processing. For example, participants' goals could be made more explicit and manipulated parametrically, and/or participants' goal-oriented performance could be incentivized. In addition, most of the work reviewed here manipulated awareness of an emotional stimulus—which implies that awareness of the stimulus–affect contingency was also likely prevented. Dissecting the relative importance of awareness of an emotional *stimulus* vs. awareness of the *emotional stimulus–affect contingency* will be a critical direction for future research.

Lastly, to address skepticism about subjective bias contaminating awareness assessments, many

investigators (including myself) have adopted strict criteria for stimulus unawareness (such as performance at chance in 2-alternative forced choice [2AFC] tasks with a large number of trials) when studying emotion-awareness interactions. This has the virtue of addressing partial-awareness concerns and subjective biases in awareness measures—however, such a cutoff for awareness eliminates *both* objective and subjective awareness, and in fact confounds them. For example, as mentioned previously, when objective awareness is matched across two conditions that differ only in subjective awareness, instead of a large and diffuse frontoparietal network, BA46 emerges as the only region differentiating subjectively aware and less aware conditions (Lau & Passingham, 2006). In the majority of the work reviewed here, objective awareness criteria were used to exclude objectively aware but possibly subjectively unaware participants, which obfuscates whether modulation of behavior by awareness is simply due to differences in low-level signal strength, or due to the *subjective experience* enabled by conscious access. It is possible that the subjective component of awareness may be the most critical for regulatory benefits, but that is currently unknown. Future work would benefit from adopting techniques that match for objective awareness while enabling subjective awareness to differ relatively between conditions (e.g., meta-contrast masking) in order to better isolate the source of qualitative differences observed in performance following awareness manipulations, and thus shed light on the function of conscious awareness in human behavior.

12.6 AFTERWORD

What Is the Role of Conscious Awareness in Emotion?

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Conscious awareness of a percept is commonly referred to as “processing accompanied by subjective experience,” and reportable under normal circumstances (Dehaene & Changeux, 2011; Lau & Rosenthal, 2011). All authors agree that some degree of emotional processing can occur in the absence of conscious awareness following exposure to innate (or highly conditioned) cues of danger or reward, such as facial expressions.

To examine the limits of non-conscious processing, the authors review studies experimentally