

Comment: The Appraising Brain: Towards a Neuro-Cognitive Model of Appraisal Processes in Emotion

Tobias Brosch

David Sander

Department of Psychology and Swiss Center for Affective Sciences, University of Geneva, Switzerland

Abstract

Appraisal theories have described elaborate mechanisms underlying the elicitation of emotion at the psychological-cognitive level, but typically do not integrate neuroscientific concepts and findings. At the same time, theoretical developments in appraisal theory have been pretty much ignored by researchers studying the neuroscience of emotion. We feel that a stronger integration of these two literatures would be highly profitable for both sides. Here we outline a blueprint of the “appraising brain.” To this end, we review neuroimaging research investigating the processing of major appraisal variables, and sketch a neuro-cognitive process model of appraisal with a special emphasis on the chronometry and the recursive aspect of emotional evaluation. We hope that this contribution will stimulate more hypothesis-driven research on the neuroscience of appraisal.

Keywords

affective neuroscience, appraisal, emotion, neuro-cognitive mechanisms

Appraisal theories of emotion have greatly advanced our understanding of the elicitation and unfolding of emotional responses. However, whereas elaborate mechanisms have been described at the psychological-cognitive level, appraisal theories typically do not integrate neuroscientific concepts and findings. At the same time, theoretical developments in appraisal theory have been pretty much ignored by researchers studying the neuroscience of emotion. In a recent meta-analysis of neuroimaging studies, the authors discuss whether 234 studies conducted so far support basic emotion theory or constructionist theory, adding that “relatively little work from an appraisal perspective has investigated the brain basis of emotion (although see Sander, Grafman, & Zalla, 2003; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007). Therefore, we do not discuss appraisal models further in this article” (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012, p. 122).

We feel that a stronger integration of these two literatures would be highly profitable both for appraisal theories and for affective neuroscience. Drawing on neuroscientific methods and findings, appraisal theorists could tackle questions that cannot be answered by relying on overt behavioral responses, response time, or self-report alone. For example, one open question concerns the automaticity of the processing of appraisal variables (Moors, Ellsworth, Scherer, & Frijda, 2013). Neuroimaging techniques make it possible to measure brain responses to variables that are manipulated independently of the task or the attentional focus of the participant. For example, differential brain responses to novel versus familiar stimuli allow inferences about (a) which brain regions are involved in novelty processing, (b) how fast novelty is detected, and finally (c) whether “novelty” is processed automatically (allowing to test for processing features such as unintentional, goal independent, uncontrolled, efficient, and fast). Furthermore, appraisal theories may be constrained based on neuroscientific evidence, for example, by comparing the predictions of different theories regarding the sequence of appraisal.

At the same time, the neuroscientific investigation of emotion may greatly profit from adopting an appraisal framework. Recent research on affective processing emphasizes the role of large interacting neural networks and complex multilevel processes (Cunningham & Zelazo, 2007; Pessoa, 2008). Appraisal theories “by default” include complex interactions of cognitive and affective processes in recursive processing loops (e.g., Sander, Grandjean, & Scherer, 2005). Compared to a relatively inflexible and static basic emotions approach (still somewhat predominant in affective neuroscience), appraisal theories seem to be more appropriate to model the neural implementation of emotion.

In this article, we sketch a blueprint of the “appraising brain.” Complementing Moors (2013), who describes appraisal-based

emotion elicitation at the functional and the algorithmic level, we attempt a description at the implementational level, focusing on the neural activation underlying the appraisal process. While indeed not many neuroscientific studies have derived their hypotheses from appraisal theories, a substantial number of studies investigated the mechanisms underlying the processing of criteria that are central to appraisal theories, without linking them to emotion elicitation. Based on a review of neuroimaging studies in humans, we describe the neural mechanisms underlying the processing of major criteria predicted by most appraisal theorists: novelty, concern relevance, goal congruence, agency, and compatibility with norms and values.¹ In order to illustrate the “added value” of neuroimaging research, we discuss for each appraisal variable whether the neuroimaging data allow inferences about the automaticity of the processing.

We integrate our review of the mechanisms underlying the processing of appraisal criteria with findings concerning the neural processing of more “canonical” emotional information (such as emotional scenes or facial expressions), to sketch a neuro-cognitive process model of the appraisal process with a special emphasis on the chronometry and the recursive aspect of emotional evaluation.

Neural Mechanisms Underlying the Processing of Appraisal Criteria

Novelty

According to most models, the appraisal sequence begins with the detection of a change in the environment, a novel event that requires attention and further processing (see Ellsworth, 2013). The processing of novelty has been the focus of intense empirical research in cognitive neuroscience, revealing a neural network centered on medial temporal regions such as the hippocampus and amygdala, extending to lateral and orbital prefrontal cortex and temporo-parietal cortex (for review, see Ranganath & Rainer, 2003). Several types of novelty detection have been distinguished, such as stimulus novelty (an item has not been seen before), contextual novelty (an item has not been expected in this context), and categorical novelty (an item has not been seen before and is uncommon, i.e., not similar to anything the person has ever encountered). Reflecting the rapid detection of stimulus novelty, differential responses to novel versus familiar objects have been recorded in the perirhinal cortex and hippocampus as soon as 100 ms after stimulus onset (e.g., Brown & Bashir, 2002), and functional magnetic resonance imaging (fMRI) recordings furthermore have revealed increased amygdala responses to novel stimuli (Schwartz et al., 2003). Detection of contextual novelty has been linked more specifically to the hippocampus, a region involved in the formation of associative memory representations, and thus well suited to compare input about an object with previously formed associations with specific contexts (Kumaran & Maguire, 2007). The amygdala is involved in the detection of categorical novelty, showing increased responses to uncommon stimuli (Blackford, Buckholz, Avery, & Zald, 2010). Hippocampal and

amygdala responses to novelty have been obtained under passive viewing conditions, suggesting that novelty detection may occur automatically.

Concern Relevance

Most emotion theorists agree that the relevance of a situation for the concerns of the organism is the central element driving the elicitation of an emotion (see Frijda, 2007; Sander, in press). At the same time, most affective neuroscientists agree that the amygdala is a key region of the emotional brain, optimally positioned to rapidly receive sensory information about the environment and to orchestrate emotional responses. Whereas the important hub role of the amygdala in the emotional brain is well established, the computational profile of the amygdala is still debated (see Cunningham & Brosch, 2012; Sander, 2009, for discussion). The amygdala was typically thought to be a module specialized in the detection of fear-relevant information. However, more and more studies accumulated showing amygdala activation to non-fear-relevant negative stimuli or to positive stimuli, and pointed to an important role of the amygdala in reward learning. To account for the wide range of stimuli that activate the amygdala, we advanced the hypothesis that the amygdala detects concern relevance, the relevance of a stimulus for a person given the current needs, goals, and the values of the person (see Sander, Grafman, & Zalla, 2003, for further discussion; see also Cunningham & Brosch, 2012; Sander, 2009, in press). Whereas most investigations focused on the amygdala response to an emotional stimulus, independent of the current state of the organism (which appraisal theories refer to as “intrinsic pleasantness”), a few studies took into account the role of inter- and intraindividual differences in needs, goals, and values. For example, pictures of food evoked larger amygdala responses in hungry participants compared with satiated ones (LaBar et al., 2001). Furthermore, amygdala activation is modulated by current task goals. For instance, when participants evaluated emotionally charged names (such as “Hitler” or “Mother Teresa”), both positive and negative names activated the amygdala. When participants evaluated the positivity of a name, positive but not negative names activated the amygdala (Cunningham, van Bavel, & Johnsen, 2008). Participants endorsing egoistic values showed increased amygdala activation when they could earn money, compared to participants with more altruistic values (Brosch, Coppin, Scherer, Schwartz, & Sander, 2011). Taken together, these findings are consistent with the notion that the computational profile of the amygdala corresponds to a concern relevance detector. Intracranial electrodes have recorded rapid amygdala responses to emotional stimuli² (around 140 ms after stimulus onset; Pourtois, Spinelli, Seeck, & Vuilleumier, 2010) even when the stimuli were not task relevant and not in the focus of attention. Nevertheless, the automaticity of the amygdala response remains a debated issue (see Brosch & Wieser, 2011, for a brief review).

Goal Congruence

This appraisal evaluates whether an event facilitates progress toward the satisfaction of a goal or puts satisfaction out of reach.

Neuroscientific research on information processing during goal pursuit has identified a conflict-control loop consisting of anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (DLPFC). This circuit subserves the monitoring of performance toward a goal, the detection of goal conflicts, and the adjustment of top-down cognitive control to resolve potential conflicts. ACC implements the monitoring function, showing increased activation to simple response conflicts and behavioral errors (e.g., during the Stroop task), but also to complex conflicts posed by moral dilemmas (Botvinick, Cohen, & Carter, 2004). Conflict detection by ACC has been shown to occur 340–380 ms after conflict onset (van Veen & Carter, 2002), leading to an increase of top-down control exerted by DLPFC in order to prevent further conflict. Furthermore, ACC activation predicts increases in autonomic arousal and negative affect, suggesting that ACC may be the neural substrate linking the detection of goal-incongruent information to the elicitation of affective responses for adaptive action preparation. The sensitivity of the conflict detector is related to individual differences in higher order belief systems. Conservative and highly religious individuals show reduced ACC activity to personal errors (e.g., Amodio, Jost, Master, & Yee, 2007), suggesting the existence of appraisal biases linked to these personality traits (Scherer & Brosch, 2009). Whereas a large number of studies investigated the detection of goal-incongruent events and the resulting adaptive changes, only a few studies have looked at the processing of goal-congruent events, which make no adaptive action necessary, but may be related to the experience of positive affect. And indeed, in a study where participants had to learn a complicated task, feedback indicating successful learning resulted in increased activation of caudate nucleus, a key region in the processing of reward-related information (Tricomi & Fiez, 2008). Most neuroscience research has defined goals as task goals. Even though participants are not explicitly instructed to monitor their performance, they can be expected to be attentive to their failures and successes. Thus, no conclusions can be drawn about whether the detection of goal congruence occurs automatically. It may be informative to investigate the neural correlates of unconscious goal pursuit, testing whether the detection of unconscious goal conflict would involve similar neural mechanisms.

Agency

This appraisal concerns the causation of an event: was it caused by oneself, someone else, or the circumstances (e.g., Roseman, 2013)? Initial neuroscientific investigations have focused on a very simple case of agency: was an observed movement elicited by oneself or someone else? These studies showed that different neural regions underlie internal and external agency attributions, respectively, with temporo-parietal junction (TPJ), precuneus, dorsomedial prefrontal cortex (DMPFC), presupplementary motor area involved in attributing external agency, and insula and motor-specific regions involved in attributing self-agency (Sperduti, Delaveau, Fossati, & Nadel, 2011). The insula has been linked to bodily interoception and self-awareness (Craig, 2009), whereas TPJ, precuneus, and DMPFC are part of

a neural network for social cognition, underlying impression formation, theory of mind, and the inference of others' goals, intentions, and desires (van Overwalle, 2009). Thus, self-agency attributions may be based on a comparison of motor commands with sensory information about the executed movements. If these are congruent, self-agency is attributed. However, if causation cannot be attributed to oneself, regions underlying mental inferences come online, even in the case of simple motor behaviors. Showing considerable overlap with the research on motor agency, an investigation of agency attributions for more complex social behaviors revealed that external agency attribution was linked to the left TPJ, precuneus, and regions in the medial and superior frontal gyrus (Seidel et al., 2010). Self-agency attributions, in contrast, were related to increased activation in the right TPJ, suggesting that self-agency attribution for very simple behaviors relies on different mechanisms (interoception) than attribution for complex behaviors (inferences). Taken together, these findings suggest that agency appraisal may, depending on the type and the complexity of the behavior, rely on different types of processes and neural substrates, presumably with different degrees of automaticity.

Compatibility with Norms and Values

This appraisal concerns the compatibility of an action with external and internal moral standards. Accessing knowledge about norms (i.e., concepts about socially acceptable behaviors) is related to activation in the superior anterior temporal lobe (Zahn et al., 2007). Values are internal standards that are tightly linked to the self-schema and have the motivational power to guide behavior. Accessing information about one's values is related to activation in the medial prefrontal cortex, a region involved in self-reflexive processing, and the dorsal striatum, involved in information integration during action selection (Brosch, Coppin, Schwartz, & Sander, 2012). When distributing money between themselves and a charitable organization, participants endorsing egoistic values donated less money to charity and showed stronger activation of amygdala and ventral striatum when keeping money for themselves (Brosch, Coppin, et al., 2011). This suggests that value compatibility can modulate the motivational saliency and the basic reward value of behavioral options. In contrast, when participants have to comply with norms, especially norms that conflict with internal interests, high-level control regions in the DLPFC are involved, suggesting that prepotent behavioral tendencies need to be inhibited (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006). These initial findings suggest that value compatibility may be assessed automatically, whereas norm compatibility may require more controlled processing.

Process Characteristics of Neuro-Cognitive Appraisal Mechanisms

Much research in affective neuroscience was based on basic emotion theory, and thus considered an emotion as the triggering

of an affect program implemented by specific neural response systems. As a consequence, many studies tried to isolate the roles of distinct brain regions to map them on individual emotions. In addition, emotional processing was conceptualized as the activation of a few “emotional” core structures operating in separation from “cognitive” areas such as DLPFC (see Sander, *in press*, for discussion).

However, accumulating neuroimaging research suggests that affective processing involves the interactions of large neural networks in complex, recursive multilevel processes. A linear view of information processing, where information is first analyzed in the sensory cortex then moves “upward” to regions underlying more complex processing to finally arrive in the prefrontal cortex, has been replaced with models emphasizing that information flow in the brain occurs in multiple sweeps of activation, with numerous feedforward and feedback loops that refine neural processing patterns and the underlying computations with each iteration (Pessoa & Adolphs, 2010).

This allows for the dynamic, increasingly more complex evaluation of a stimulus, highly compatible with the predictions of appraisal theory. In a series of recursive processing cycles, stimulus appraisal may start with a rapid, relatively coarse first pass, which can be adjusted during successive processing to take into account additional sensory, contextual, and motivational information. Studies measuring the time course of the processing of emotional information using electroencephalography (EEG) or single-electrode recordings (see Olofsson, Nordin, Sequeira, & Polich, 2008, for a review) have shown rapid response increases in the sensory cortex, amygdala, and orbitofrontal cortex (as soon as 100 ms after the onset of an emotional stimulus), as well as later responses in widespread cortical regions including the prefrontal, cingulate, and parietal cortex (300 ms and above). Thus, a first feedforward sweep of coarse sensory stimulus information may be projected from the sensory cortex to the hippocampus, amygdala, and orbitofrontal cortex for initial appraisal. A rapid appraisal of novelty and concern relevance may thus occur even before sensory analysis in visual cortex is complete. Consistent with this, an EEG study investigating the time course of appraisal as predicted by the component process model (see Scherer, 2013) observed electrophysiological markers of novelty appraisal 95 ms after stimulus onset, and markers of goal/task relevance appraisal at 160 ms (Grandjean & Scherer, 2008). These times are highly consistent with depth electrode findings reviewed in previous lines concerning the speed of the initial response of perirhinal cortex/hippocampus (100 ms) and amygdala (140 ms).

Thus, a first appraisal of concern relevance by the amygdala may occur as soon as 140 ms after stimulus onset, enabling the rapid initiation of an emotional response (e.g., physiological changes and action tendencies). The amygdala can then orchestrate the further processing of an incoming stimulus that is appraised as relevant, boosting sensory processing and recruiting further cortical areas involved in the refinement of the appraisal (Brosch, Pourtois, Sander, & Vuilleumier, 2011). Depending on the requirements of the situation, this may include ACC for appraisals of goal incongruence, TPJ for agency, superior anterior

temporal lobe for norm compatibility, and medial prefrontal cortex for value compatibility. These appraisals may require more processing time due to their higher complexity. For example, electrophysiological markers of goal-conduciveness appraisal have been measured in a time range of 400–450 ms (Grandjean & Scherer, 2008), broadly consistent with the conflict detection response of the ACC (340–380 ms).

As the appraisal continues, subsequent feedforward sweeps from sensory regions may be added to the analysis, providing more fine-grained details about the stimulus, as well as interoceptive information about the current body state encoded in the insula. Due to the recursive nature of the process, later appraisal results may be fed back into the amygdala to modulate the ongoing appraisal and emotional response. Consistent with the suggestion that subsequent evaluative iterations may occur at a frequency of 4–8 Hz (Cunningham & Zelazo, 2007), depth electrode recordings of the amygdala showed discrete increases in gamma power amplitudes in the theta band at 200 ms, 400 ms, and 600 ms during the presentation of emotional pictures (Oya, Kawasaki, Howard, & Adolphs, 2002). The initial amygdala response may be driven by relatively simple stimulus information based on feature detection or overlearned associations (Brosch, Pourtois, & Sander, 2010), whereas later iterations may integrate information about the current motivational state and context provided by other brain regions, refining the amygdala response and the subsequent modulation of further cortical processing by the amygdala (see Brosch & van Bavel, 2012, for an example of how emotional attention prioritization can change as a function of allocated processing time).

After several evaluative iterations, the appraisal may reach a stable state. A meta-analysis of neuroimaging studies of the ventromedial prefrontal cortex (VMPFC) suggested that this region underlies the representation of subjective value, self-perception, memory, future projection, and visceromotor control (Roy, Shohamy, & Wager, 2012). Based on this convergence of functions, the authors suggested that VMPFC represents the “affective meaning” of a situation, a conceptualization of the appraisal outcome which may be used to inform future decisions and behavior.

Concluding Remarks

In this article we have sketched a blueprint of the “appraising brain,” with the aim of motivating a stronger integration of appraisal theory and neuroscience. However, more hypothesis-driven research about the neuroscience of appraisal is needed. We hope that this contribution will elicit some curiosity on both sides, making neuroscience findings more concern relevant to appraisal theorists, and appraisal theory more goal conducive to neuroscientists.

Notes

- 1 Whereas other criteria have been suggested, to our knowledge, hardly any neuroimaging research has been published concerning other appraisal criteria such as coping potential or urgency.

- 2 This study used facial expressions of emotion as stimuli, and thus measured effects of intrinsic pleasantness rather than concern relevance as defined earlier.

References

- Amodio, D. M., Jost, J. T., Master, S. L., & Yee, C. M. (2007). Neurocognitive correlates of liberalism and conservatism. *Nature Neuroscience*, *10*, 1246–1247.
- Blackford, J. U., Buckholz, J. W., Avery, S. N., & Zald, D. H. (2010). A unique role for the human amygdala in novelty detection. *NeuroImage*, *50*, 1188–1193.
- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, *8*, 539–546.
- Brosch, T., Coppin, G., Scherer, K. R., Schwartz, S., & Sander, D. (2011). Generating value(s): Psychological value hierarchies reflect context-dependent sensitivity of the reward system. *Social Neuroscience*, *6*, 198–208.
- Brosch, T., Coppin, G., Schwartz, S., & Sander, D. (2012). The importance of actions and the worth of an object: Dissociable neural systems representing core value and economic value. *Social Cognitive and Affective Neuroscience*, *7*, 497–505.
- Brosch, T., Pourtois, G., & Sander, D. (2010). The perception and categorization of emotional stimuli: A review. *Cognition & Emotion*, *24*, 377–400.
- Brosch, T., Pourtois, G., Sander, D., & Vuilleumier, P. (2011). Additive effects of emotional, endogenous, and exogenous attention: Behavioral and electrophysiological evidence. *Neuropsychologia*, *49*, 1779–1787.
- Brosch, T., & van Bavel, J. J. (2012). The flexibility of emotional attention: Accessible social identities guide rapid attentional orienting. *Cognition*, *125*, 309–316.
- Brosch, T., & Wieser, M. J. (2011). The (non)automaticity of amygdala responses to threat: On the issue of fast signals and slow measures. *Journal of Neuroscience*, *31*, 14451–14452.
- Brown, M. W., & Bashir, Z. I. (2002). Evidence concerning how neurons of the perirhinal cortex may effect familiarity discrimination. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *357*, 1083–1095.
- Craig, A. D. (2009). How do you feel—now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*, 59–70.
- Cunningham, W. A., & Brosch, T. (2012). Motivational salience: Amygdala tuning from traits, needs, values, and goals. *Current Directions in Psychological Science*, *21*, 54–59.
- Cunningham, W. A., van Bavel, J. J., & Johnsen, I. R. (2008). Affective flexibility: Evaluative processing goals shape amygdala activity. *Psychological Science*, *19*, 152–160.
- Cunningham, W. A., & Zelazo, P. D. (2007). Attitudes and evaluations: A social cognitive neuroscience perspective. *Trends in Cognitive Sciences*, *11*, 97–104.
- Ellsworth, P. (2013). Appraisal theory: Old and new questions. *Emotion Review*, *5*, 125–131.
- Frijda, N. H. (2007). *The laws of emotion*. Mahwah, NJ: Erlbaum.
- Grandjean, D., & Scherer, K. R. (2008). Unpacking the cognitive architecture of emotion processes. *Emotion*, *8*, 341–351.
- Knoch, D., Pascual-Leone, A., Meyer, K., Treyer, V., & Fehr, E. (2006). Diminishing reciprocal fairness by disrupting the right prefrontal cortex. *Science*, *314*, 829–832.
- Kumaran, D., & Maguire, E. A. (2007). Which computational mechanisms operate in the hippocampus during novelty detection? *Hippocampus*, *17*, 735–748.
- LaBar, K. S., Gitelman, D. R., Parrish, T. B., Kim, Y. H., Nobre, A. C., & Mesulam, M. M. (2001). Hunger selectively modulates corticolimbic activation to food stimuli in humans. *Behavioral Neuroscience*, *115*, 493–500.
- Lindquist, K. A., Wager, T. D., Kober, H., Bliss-Moreau, E., & Barrett, L. F. (2012). The brain basis of emotion: A meta-analytic review. *Behavioral and Brain Sciences*, *35*, 121–143.
- Moors, A. (2013). On the causal role of appraisal in emotion. *Emotion Review*, *5*, 132–140.
- Moors, A., Ellsworth, P., Scherer, K. R., & Frijda, N. (2013). Appraisal theories of emotion: State of the art and future development. *Emotion Review*, *5*, 119–124.
- Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology*, *77*, 247–265.
- Oya, H., Kawasaki, H., Howard, M. A., III, & Adolphs, R. (2002). Electrophysiological responses in the human amygdala discriminate emotion categories of complex visual stimuli. *Journal of Neuroscience*, *22*, 9502–9512.
- Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews Neuroscience*, *9*, 148–158.
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a “low road” to “many roads” of evaluating biological significance. *Nature Reviews Neuroscience*, *11*, 773–783.
- Pourtois, G., Spinelli, L., Seeck, M., & Vuilleumier, P. (2010). Temporal precedence of emotion over attention modulations in the lateral amygdala: Intracranial ERP evidence from a patient with temporal lobe epilepsy. *Cognitive, Affective, & Behavioral Neuroscience*, *10*, 83–93.
- Ranganath, C., & Rainer, G. (2003). Neural mechanisms for detecting and remembering novel events. *Nature Reviews Neuroscience*, *4*, 193–202.
- Roseman, I. J. (2013). Appraisal in the emotion system: Coherence in strategies for coping. *Emotion Review*, *5*, 141–149.
- Roy, M., Shohamy, D., & Wager, T. D. (2012). Ventromedial prefrontal-subcortical systems and the generation of affective meaning. *Trends in Cognitive Sciences*, *16*, 147–156.
- Sander, D. (2009). The amygdala. In D. Sander & K. R. Scherer (Eds.), *The Oxford companion to emotion and the affective sciences* (pp. 28–32). New York, NY: Oxford University Press.
- Sander, D. (in press). Models of emotion: The affective neuroscience approach. In J. L. Armony & P. Vuilleumier (Eds.), *Handbook of human affective neuroscience*. Cambridge, UK: Cambridge University Press.
- Sander, D., Grafman, J., & Zalla, T. (2003). The human amygdala: An evolved system for relevance detection. *Reviews in the Neurosciences*, *14*, 303–316.
- Sander, D., Grandjean, D., Kaiser, S., Wehrle, T., & Scherer, K. R. (2007). Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. *European Journal of Cognitive Psychology*, *19*, 470–480.
- Sander, D., Grandjean, D., & Scherer, K. R. (2005). A systems approach to appraisal mechanisms in emotion. *Neural Networks*, *18*, 317–352.
- Scherer, K. R. (2013). The nature and dynamics of relevance and valence appraisals: Theoretical advances and recent evidence. *Emotion Review*, *5*, 150–162.
- Scherer, K. R., & Brosch, T. (2009). Culture-specific appraisal biases contribute to emotion dispositions. *European Journal of Personality*, *23*, 265–288.
- Schwartz, C. E., Wright, C. I., Shin, L. M., Kagan, J., Whalen, P. J., McMullin, K. G., & Rauch, S. L. (2003). Differential amygdalar response to novel versus newly familiar neutral faces: A functional MRI probe developed for studying inhibited temperament. *Biological Psychiatry*, *53*, 854–862.
- Seidel, E. M., Eickhoff, S. B., Kellermann, T., Schneider, F., Gur, R. C., Habel, U., & Derntl, B. (2010). Who is to blame? Neural correlates

- of causal attribution in social situations. *Social Neuroscience*, *5*, 335–350.
- Sperduti, M., Delaveau, P., Fossati, P., & Nadel, J. (2011). Different brain structures related to self- and external-agency attribution: A brief review and meta-analysis. *Brain Structure and Function*, *216*, 151–157.
- Tricomi, E., & Fiez, J. A. (2008). Feedback signals in the caudate reflect goal achievement on a declarative memory task. *Neuroimage*, *41*, 1154–1167.
- van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping*, *30*, 829–858.
- van Veen, V., & Carter, C. S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience*, *14*, 593–602.
- Zahn, R., Moll, J., Krueger, F., Huey, E. D., Garrido, G., & Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proceedings of the National Academy of Sciences*, *104*, 6430–6435.