

Précis on *The Cognitive-Emotional Brain*

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Abstract: In *The Cognitive-Emotional Brain* (Pessoa 2013), I describe the many ways that emotion and cognition interact and are integrated in the brain. The book summarizes five areas of research that support this integrative view and makes four arguments to organize each area. (1) Based on rodent and human data, I propose that the amygdala's functions go beyond emotion as traditionally conceived. Furthermore, the processing of emotion-laden information is capacity limited, thus not independent of attention and awareness. (2) Cognitive-emotional interactions in the human prefrontal cortex (PFC) assume diverse forms and are not limited to mutual suppression. Particularly, the lateral PFC is a focal point for cognitive-emotional interactions. (3) Interactions between motivation and cognition can be seen across a range of perceptual and cognitive tasks. Motivation shapes behavior in specific ways – for example, by reducing response conflict or via selective effects on working memory. Traditional accounts, by contrast, typically describe motivation as a global activation independent of particular control demands. (4) Perception and cognition are directly influenced by information with affective or motivational content in powerful ways. A dual competition model outlines a framework for such interactions at the perceptual and executive levels. A specific neural architecture is proposed that embeds emotional and motivational signals into perception and cognition through multiple channels. (5) A network perspective should supplant the strategy of understanding the brain in terms of individual regions. More broadly, in a network view of brain architecture, “emotion” and “cognition” may be used as labels of certain behaviors, but will not map cleanly into compartmentalized pieces of the brain.

Keywords: brain; cognition; emotion; integration; prefrontal cortex; motivation

1. Introduction

In *The Cognitive-Emotional Brain* (Pessoa 2013), I describe how emotion and cognition interact and are integrated in the brain. I believe that brain research has been ill-served by the dichotomization of large concepts like *cognition* and *emotion*. Further, strict a priori definitions of these concepts fuel dichotomization. We need a vocabulary that views concepts as complementary pairs that mutually define each other and, critically, do not exclude each other. As in the book, I will not define here terms such as *emotion*, *motivation*, and *cognition*; they will be used descriptively to refer to paradigms, task conditions, or “processes” that are closer to the traditional intended meanings of these terms. The book is aimed at students and investigators interested in the brain basis of emotion, especially those interested in understanding how perception and cognition reflect and embed affective/motivational significance. The book integrates findings from nonhuman animal research and human imaging research, the latter being the area my research focuses on.

The structure of this précis is as follows. Section 2 briefly reviews issues covered in chapters 2–4 of the book, which propose how to conceptualize amygdala function in broader terms than typically adopted in the field, and argue against the notion of the “automaticity of emotion.” Sections 3–6 focus on chapters 5–7 of the book, which describe how cognitive-emotional/motivational interactions and integration take place in the brain. Section 7 addresses the general issue of structure-function mapping in the brain. There, I argue for a “network” view of brain function

but also describe several problems with this view that are underappreciated in the literature. Potential tools to characterize complex structure-function mappings are described. Finally, in Section 8, I draw some conclusions of the network perspective to the understanding of emotion and the brain.

2. Amygdala and the automaticity of emotion

2.1. Amygdala

Chapter 2 discusses the ever-important amygdala and its role in brain function. Based on rodent and human data, I describe how the amygdala's functions go beyond

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emotion as traditionally conceived, reflecting a trend toward viewing this structure not simply in terms of “fear.”

A key function of the amygdala is to shape *selective information processing*. Selection of information for further analysis is, of course, a central problem that needs to be solved for effective behavior (Grossberg & Levine 1987). The amygdala is a core structure in a system involved in “What is it?” processing and thus contributes to highlighting what is of significance to the organism (Pribram & McGuinness 1975). However, the functions of the amygdala also involve “What’s to be done?” A key reason for this is that the amygdala participates in the representation of value (including positive value) and in decision making. For example, amygdala lesions impair behavior on the Iowa Gambling Task in humans and alter delay-based decision making in rats (e.g., they become more impulsive). The amygdala thus takes part in an impressive array of processes that far exceed some of its proposed functions, such as vigilance, arousal, salience detection, novelty detection, and relevance detection. “Information gathering” (Whalen 1998) better captures several of its functions but comes short, too. In the end, it is better simply to refrain from overly summarizing its functional repertoire so as to better appreciate the wide scope of the amygdala’s contributions to brain mechanisms and behavior.

2.2. Subcortical “low road” pathway and emotional processing

A purported division of labor between cortical and subcortical regions has been present from the time of the earliest *circuit models* of emotion (e.g., Papez 1937). Many versions of this type of dual processing model exist, including some variants that have captured the popular imagination, such as the “triumvir brain” (MacLean 1970; 1990).

In the case of vision, it has been suggested that a subcortical pathway from the retina to superior colliculus to pulvinar to amygdala that entirely bypasses cortex enables the processing of emotion-laden visual stimuli to be fast, automatic, and nonconscious. In chapter 3, I argue against this notion on several general grounds: (1) Affective visual information is not handled qualitatively faster than other visual information; (2) processing of affective visual stimuli involves both low- and high-spatial frequency information; and (3) the amygdala is not required for rapid, nonconscious detection of affective information. For these and many other reasons, Ralph Adolphs and I proposed the “multiple waves” model as an alternative to the low-road pathway scheme (Pessoa & Adolphs 2010). The model shifts the debate away from whether there is a unique subcortical pathway to whether a processing architecture exists that is capable of rapidly transmitting information via multiple pathways. The resulting multiple waves model emphasizes the role of the pulvinar in coordinating and regulating the flow of multimodal information, which is accomplished via a series of thalamo-cortical loops. In this role, the pulvinar moves from being a passive relay station of the “standard hypothesis” to being an active element of information processing.

2.3. What kind of unawareness matters?

The research literature is replete with paradigms such as backward masking and the attentional blink that challenge

the visual system so that awareness can be studied. At times, much is made about neuroimaging responses observed in the amygdala for very brief stimuli (e.g., 15–30 ms). In such cases, subjects may report not seeing them (“subjective unawareness”). In the book, I argue that this type of “subliminal” unawareness is not the most relevant one to understand the impact of affective content on behavior and on clinical conditions such as anxiety. A more important sense is associated with the idea of *unintentional* processing, which may prove to be more important to the understanding of human behavior. Whether the unintentional unconscious is sophisticated and flexible, as argued by social psychologists (see Bargh & Morsella 2008), is a matter of debate. But there can be no doubt that it is *qualitatively* different from the type of subliminal unconscious sometimes emphasized in the emotion literature (for evidence that the “subliminal unconscious” may be quite “dumb,” see Loftus & Klinger 1992 – if at all present; Pessoa 2005).

2.4. Why is the amygdala important?

In the broader neuroscience literature, the amygdala is viewed as a central node in emotional processing in part because of the “low-level” properties ascribed to the subcortical pathway. Defects in the amygdala system are said to underlie phobias, mood disorders, and post-traumatic stress syndrome, and variability in its functioning to reflect individual differences at the genotypic and personality level.

Although in chapter 3 I challenge many of the properties typically ascribed to the subcortical pathway, the amygdala is indeed important for behavior and mental health. First, together with the hypothalamus and medial PFC, the amygdala has extensive projections to downstream regions in the brainstem that are capable of mobilizing the body; indeed, its central nucleus is at times described as a “controller of the brainstem.” The autonomic and neuroendocrine connections of these brain regions are part of sympathetic and parasympathetic networks that coordinate bodily responses in the face of challenges to the organism. Second, the amygdala, hypothalamus, medial PFC, and related regions, being among the most extensively connected parts of the brain, are optimally positioned to influence information processing. As hubs through which evaluative signals are communicated, they are thought to have widespread effects on mental function and to play a significant role in affective and cognitive impairments observed in mood disorders. Metaphorically speaking, as one of these hubs, the amygdala is strategically positioned to “ignite” both body and brain.

2.5. Processing of emotion-laden information and automaticity

Shiffrin and Schneider (1977, pp. 155–156) defined an “automatic process ... as a sequence of nodes that nearly always becomes active in response to a particular input configuration.” Because automatic and controlled processes appear to be qualitatively opposed, it is natural to dichotomize mental phenomena into these two classes. But such a dichotomy has simply not held up in the face of data. Reports of automaticity have invariably been countered by reports of capacity limitation; behavioral effects

assumed to operate automatically are influenced in ways that belie that assumption.

The argument that I make in chapter 3 is that a better framework is one where performance is always considered *capacity limited* and described as a performance-resource function (Norman & Bobrow 1975). Some behaviors will exhibit shallower performance-resource relationships, where performance only rises slowly based on the mental effort exerted—these behaviors are hence “controlled.” Other behaviors exhibit steeper relationships, and ceiling performance is reached even when conditions are degraded (e.g., under short exposure)—these behaviors are hence “efficient.” Although the performance-resource function may seem to be an abstract construct when little is known about the task at hand, it forces researchers to consider a spectrum of scenarios when studying how a behavior depends on multiple factors that influence performance.

Why is a continuous framework better than a dichotomous one? For one thing, it fits the empirical data better: Researchers have repeatedly found capacity limitations for “automatic” phenomena (e.g., Pashler 1998). For another, the dichotomous framework is plagued by serious conceptual issues (Moors & De Houwer 2006). Another reason a continuous framework is better is that we still have an incipient understanding of *competition*—and, hence, of whether interference will result when multiple items are involved. The notion of competition, as accepted by most researchers, goes roughly as follows. Because processing capacity is limited, competition is proposed to “select” the most relevant information at any given time (Desimone & Duncan 1995; Grossberg 1980); when resources are not fully consumed, spare capacity is used to process task-irrelevant items (Lavie 1995). The problem is that we do not always know whether interference will occur in any given situation. Generally, multiple factors determine how information competes in visual cortex and beyond, including task difficulty, set size, spatial arrangement, cuing, and the like. Finally, a continuous framework demystifies the processing of certain complex features. For example, processes such as reading and the perception of elaborate emotional images are at times depicted as “automatic” in a sense that is almost magical (for a cogent in-depth discussion, see Pourtois et al. 2012). Indeed, the underlying mechanisms of abilities such as proficient reading and the perception of emotional scenes are remarkably fast. That we do not understand why they are so fast, however, simply means that we are still quite some way from a better mechanistic description of these processes.

2.6. Dual process models

The discussion of automatic versus controlled processes is also pertinent to *dual process* models. Common to these models is the strong assumption of the existence of two *qualitatively* different mental systems, for example, “intuition” and “reasoning” (see Keren and Schul 2009). A popular trend is to call the two components “system 1” and “system 2,” where the first is automatic/heuristic/reflexive and the second is controlled/analytic/reflective (Evans 2008). But as others have expressed in the past, the idea of a dual system model is both slippery and conceptually unclear (see Keren & Schul 2009). For one, nearly all dual process models have as a central component the

automatic versus controlled dichotomy, which as discussed above is not a viable distinction. In fact, as with the question of automatic versus controlled processing of emotion-laden stimuli, the question of whether there are two systems in dual process models is not an entirely empirical one. This is because no single critical experiment can provide a final, definitive answer. In the end, however irresistible dichotomies are to the human mind (Kelso & Engström 2006; Newell 1973), dichotomizing implies *oversimplifying* (Keren & Schul 2009; Kruglanski et al. 2006). A continuous framework is better, albeit more complex (Kruglanski et al. 2006).

3. Diverse forms of cognitive-emotional interactions are not limited to mutual suppression

Nauta (1971, p. 182) suggested that the PFC could be considered “the major—though not the only—neocortical representative of the limbic system.” Yet, most proposals in the literature portray the PFC’s core function as cognitive, or compartmentalize it into cognitive and affective regions (see Bush et al. 2000). In particular, the *lateral* PFC is still viewed as a quintessential cognitive region, especially the portion that is loosely referred to as the “*dorsal-lateral* PFC.” This section reviews human studies that have investigated cognitive and emotional processing in the human PFC (see also Dolcos et al. 2011) to explore how emotion and cognition, domains traditionally thought of as mutually antagonistic, interact there. The section does not discuss the part of the PFC called the orbitofrontal cortex, whose contributions to emotion are well accepted (Zald & Rauch 2007). In the ensuing discussion, it is useful to consider the regions outlined in Figure 1.

3.1. The “Classical” view: Emotion-cognition push-pull

In an important paper, Drevets and Raichle (1998) noted that regional blood flow during attentionally demanding cognitive tasks *decreased* in regions such as the amygdala, orbitofrontal cortex, and ventral-medial PFC, whereas blood flow *increased* in these regions during specific emotion-related tasks. Conversely, blood flow during experimentally induced and pathological emotional states (Mayberg et al. 1999) *decreased* in regions such as the dorsal-medial and dorsal-lateral PFC, whereas blood flow *increased* in these regions during cognitive tasks. These reciprocal patterns of activation suggested to Drevets & Raichle (1998) that emotion and cognition engage in *competitive* interactions.

This insight led to a wealth of studies pursuing the notion of a *dorsal-cognition versus ventral-emotion* axis of organization in the human brain. For example, Dolcos and colleagues investigated emotional distraction during working memory tasks (see also Anticevic & colleagues 2010). Subjects were shown sample stimuli that had to be remembered during a subsequent delay period during which they saw distracting stimuli, including neutral and emotional pictures. The findings of one of their studies (Dolcos & McCarthy 2006) are illustrated in Figure 2. During the delay period, responses in dorsal-lateral PFC (Fig. 2B) were highest for the “scrambled” (digitally scrambled versions of pictures), intermediate for neutral, and *lowest* for

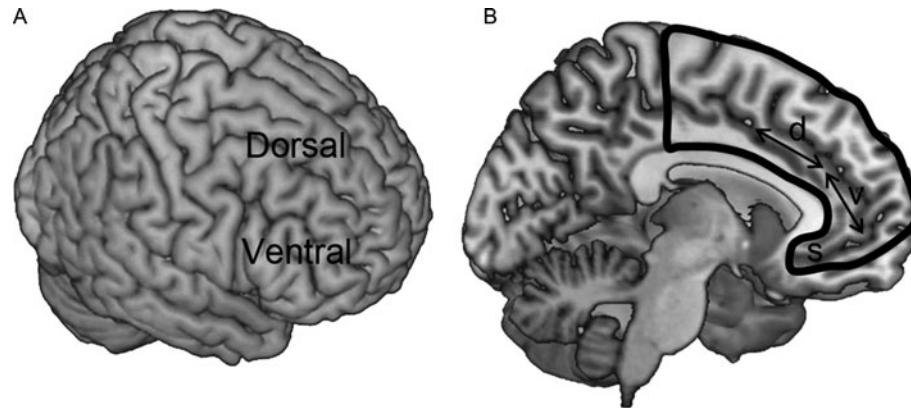


Figure 1. Frontal cortex anatomy. “Prefrontal cortex” refers to cortex “in front of motor areas,” typically anterior to Brodmann area 6. (A) Lateral surface of cortex, showing dorsal and ventral sectors. (B) Medial surface of cortex, outlined in black, showing approximate locations of dorsal (d) and ventral (v) sectors. In the paper, dorsal parts of medial prefrontal cortex also include parts posterior to the “d” arrow (such as presupplementary and supplementary motor areas). S, subgenual anterior cingulate cortex.

emotional distractors – a pattern of responses also observed in parietal cortex. Behavioral performance mirrored this and was *worst* for emotional distractors. Viewing emotional distractors during the delay period appeared to interfere with neural activity normally observed in these sites – activity that supports working memory performance (e.g., Pessoa et al. 2002). Responses in the ventral-lateral PFC (Fig. 2C) followed the opposite pattern, namely, the strongest responses were observed during the viewing of emotional distractors, suggesting that ventral-lateral PFC contributed to *inhibiting* the distracting effects of stimuli presented during the delay period. Overall, several studies are consistent with the *dorsal-cognition versus ventral-emotion* segregation (both along the lateral surface of the brain and its medial sector), including those probing emotional distraction, emotional conflict, and emotion regulation (Ch. 5).

The organization of the *medial* PFC, a complex brain region involved in diverse functions (Vogt 2008), has strongly fueled the dorsal versus ventral view of emotion and cognition organization in the brain, particularly following another influential paper (Bush et al. 2000; see also Devinsky et al. 1995). In the next section, I argue against the dorsal versus ventral framework in the medial PFC in

particular, and in the subsequent section against the dorsal versus ventral view in the PFC more generally.

3.2. Beyond the dorsal versus ventral-medial dichotomy in the prefrontal cortex

Results from several individual studies challenge the dichotomy. For example, Mobbs and colleagues (2010) examined how brain responses vary as a function of perceived threat proximity. In an unusual experimental manipulation, each participant inside the MRI scanner placed a foot into a custom-built box containing multiple compartments, while watching a video of a live tarantula placed into one of the compartments at varying distances from the foot (actually prerecorded). Increases in responses as a function of proximity were observed in several brain regions; notably in the dorsal-medial PFC.

The “attentional network” involves fronto-parietal regions, including the dorsal-medial PFC (Corbetta & Shulman 2002; Kastner & Ungerleider 2000). To assess brain regions that are sensitive to high levels of threat, I reviewed activation sites reported in aversive conditioning studies (Pessoa 2009). Surprisingly, activation was repeatedly reported not only in the amygdala but also in frontal

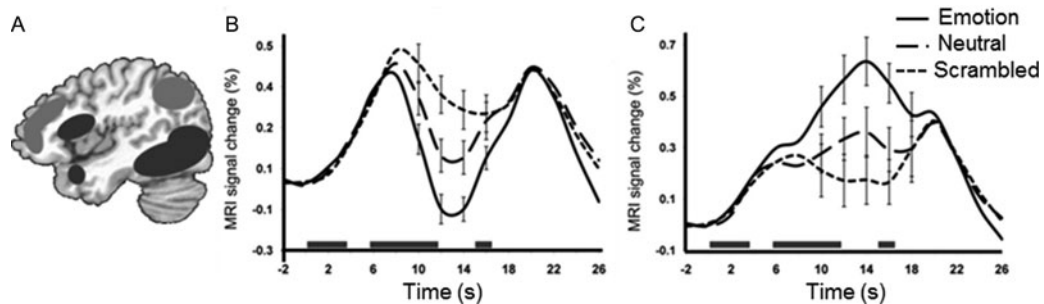


Figure 2. Emotional distraction during a working memory task. Subjects were shown scrambled, negative, or neutral distractor images during the delay period of the task. (A) Schematic representation of differential responses in brain. Regions where responses were stronger to scrambled than to emotional images are shown in light gray; regions where they were stronger to emotional than to scrambled images, in dark gray. (B) Time course data for dorsal-lateral prefrontal cortex. (C) Time course data for ventral-lateral prefrontal cortex. Horizontal bars in panels B and C correspond to onset and duration of sample stimuli, distractors, and probes, respectively. Time series plots kindly provided by Florin Dolcos, adapted with permission from Dolcos and McCarthy (2006).

sites overlapping with those in the attentional network, including the dorsal-medial PFC – consistent with findings from formal meta-analyses (Etkin & Wager 2007; Mechias et al. 2010). To understand the organization of the medial PFC and its role in emotion, Etkin and colleagues (2011) reviewed both the human and nonhuman animal literatures. They surmise that sites in *both* dorsal and ventral-medial PFC make prominent contributions to emotional processing. Finally, an extensive formal meta-analysis of human neuroimaging studies (Shackman et al. 2011) further demonstrates the considerable overlap of sites in the medial PFC engaged during negative affect and cognitive control (Fig. 3).

In summary, although it is still influential, the segregation model of medial PFC organization is no longer viable, as different research groups now argue (e.g., Etkin et al. 2011; Pessoa 2009; Shackman et al. 2011). Large portions of the PFC are engaged during emotional processing, including *both* dorsal and ventral portions of the medial PFC. Indeed, when large numbers of studies are considered jointly, the weight of their findings strongly favors an organization of the medial PFC that is *not* segregated into affective and cognitive compartments but instead is shared by cognitive and affective domains in a way that allows the medial PFC to support the *adaptive control* of complex behaviors (Pessoa 2008; Shackman et al. 2011).

3.3. Beyond push-pull: When emotion and cognition work together

Now, I will turn to the broader issue of the frequently held view of emotion-cognition organized as push-pull, or antagonistic, systems. Consider once more the study by Dolcos and McCarthy (2006) that showed that emotional distractors produced *decreased* responses in parts of the dorsal-lateral PFC that are important for cognitive tasks. This type of response, which favors the antagonistic organization, is far from universal, however. For example, also during conditions of emotional distraction, Erk et al. (2007) observed *increased* responses to emotional stimuli in the dorsal-lateral PFC. They also observed increased responses when they increased the load of a separate non-emotional working memory task. In other words, both the emotional and cognitive manipulations produced

enhanced responses in the dorsal-lateral PFC. Conversely, emotional manipulations do not always generate decreased responses in frontal-parietal areas that are recruited by effortful, cognitive tasks. For example, in one of our studies, when subjects viewed a “threat cue” that signaled a potential upcoming shock, *deactivation* was observed in emotion-related regions (Choi et al. 2012).

In all, cognitive-emotional interactions take diverse forms that go beyond a straightforward antagonistic relationship (Ch. 5). Instead, I suggest that lateral PFC, in particular, is a *convergence site* for cognitive and emotional signals where they are integrated.

3.3.1. The basic “direction” of brain responses and their interpretation. As discussed above, a key question during cognitive-emotional interactions is whether emotional information decreases or enhances a region’s responses during cognitive tasks – to decide if the relationship is push-pull. Unfortunately, the direction (increases vs. decreases) of brain responses does not uniquely determine their functional significance. Consider again the working memory study by Dolcos and McCarthy (2006), which showed *decreased* responses in dorsal-lateral PFC during emotional distraction. More important, this condition was linked with *impaired* task performance, matching the pattern of an antagonistic cognitive-emotional interaction. But how should we interpret these findings? Because it is unknown whether *increased* responses reflect greater capacity to utilize the region, neural inefficiency, or increased effort, the interpretation of the results is equivocal. The difficulty here is not about problems of interpreting functional MRI responses given their indirect relationship with neuronal activity. The same issues would arise with cell recordings, because disentangling, say, neural efficiency, increased effort, and so on, is again far from simple.

A potential strategy is to interpret response changes in terms of behavior *and* brain responses during *neutral* tasks. During working memory, we know that dorsal frontal and parietal regions are important from both monkey and human work. In these regions, response magnitude even tracks performance on a trial-by-trial basis (Pessoa et al. 2002). Thus, when emotional distractors lead to decreased responses in dorsal-lateral PFC *and* impaired task performance (Anticevic et al. 2010; Dolcos &

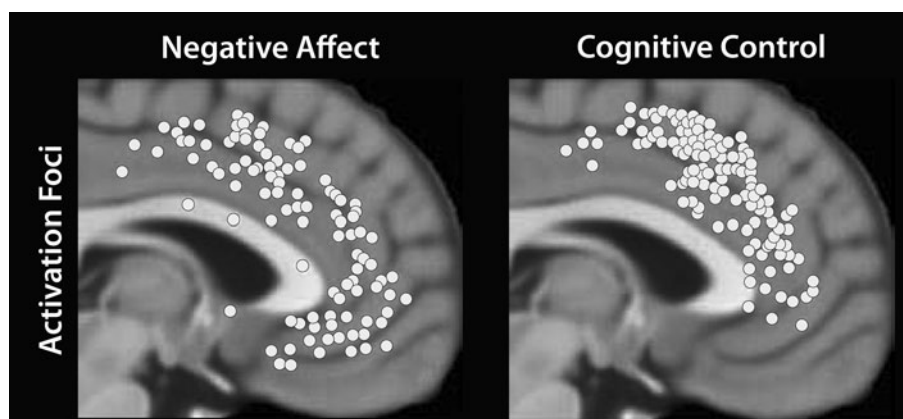


Figure 3. Cognition and emotion in medial frontal cortex. Foci of activation across studies of negative affect and cognitive control. Extensive overlap between emotion and cognition was observed in dorsal-medial prefrontal cortex. Figure kindly provided by Alex Shackman and adapted with permission from Shackman et al. (2011).

McCarthy 2006), it is possible to more strongly interpret the findings in terms of underlying antagonistic interactions. Although in this case the original interpretation holds, the example underscores the need to ground the responses during emotional manipulations by building on closer ties between a brain region's responses and associated behavior during nonemotional tasks.

3.3.2. Anxiety, executive function, and prefrontal cortex responses. A closely related issue arises in the context of studies of brain responses in anxious individuals: Are cognitive control areas in the PFC, including the dorsal-lateral PFC, *under-* or *overactivated* in these individuals? This question is relevant given the belief that anxiety is particularly associated with *reduced* processing efficiency. Thus, to maintain comparable levels of task performance, anxious individuals must exert greater cognitive effort (Eysenck et al. 2007), which is linked to *increased* responses in brain regions involved with cognitive control.

But some studies have reported that anxiety is associated with *underactivation* in cognitive control circuits (Bishop 2007; 2009; Bishop et al. 2004; see also Basten et al. 2011; for additional discussion, see Eysenck & Derakshan 2011). Examining under- or overutilization of a brain area, however, does not lead to an unequivocal interpretation of cognitive processing in anxious subjects, as argued by Fales and colleagues (2008). This is because either reduced or enhanced neural recruitment may reflect differences in a host of factors, including efficiency, motivation, effort, or the capacity to activate regions when needed. The difficulties surrounding the issue of under- versus overactivation are mirrored by those encountered in the human developmental literature, where changes in the responses of a brain region with age are hard to interpret (Somerville & Casey 2010).

The upshot of section 3 is as follows: The effects of emotion on cognition, and vice versa, are best viewed not as a simple push-pull mechanism, but as interactions that result in processes and signals that are neither purely cognitive nor emotional. Instead, their “cognitive” or “emotional” nature is blurred in a way that highlights the integration of these domains in the brain (Pessoa 2008).

4. Motivation: Interactions between motivation and cognition

According to traditional psychological models, motivation relies on a global, rather blunt *energization* factor to influence the vigor and frequency of behavioral output, though without specific effects (e.g., Duffy 1962; Hull 1943). Current progress in understanding the mechanisms of reward and motivation challenges this view, which has renewed interest in motivational effects on perception and cognition. Chapter 6 contains discussion of the *selective* ways motivation affects task performance, some of which I briefly review here.

Jan Engelmann and I investigated the impact of changes in incentive value on behavior during a difficult spatial localization task (Engelmann & Pessoa 2007). Participants performed the task under conditions in which they could earn extra monetary rewards, avoid losing money, or, during a baseline condition, neither gain nor lose. In theory, motivation could lead to indiscriminate responding increasing the number of both correct detections and false alarms.

Instead, detection performance improved as a function of absolute incentive value (gains and losses produced similar results) *independent* of unspecific influences, such as general activation (e.g., purely faster response times) or response bias (e.g., more conservative responses). We observed increases in visual sensitivity (d-prime) in both endogenous and exogenous attention tasks (see also Engelmann et al. 2009).

In an event-related potential (ERP) study, Hickey and colleagues (2010) sought to dissociate “strategic” (such as paying more attention) and “incidental” (such as undesired) effects of reward. To that end, they probed how reward in one trial affected visual processing in the next. Following a high-reward trial, the P1 ERP response component, which occurs approximately 100 ms after stimulus onset, was found to be stronger contralateral to targets of the same (task-irrelevant) color rewarded on the *previous* trial, revealing facilitated responses based on previous-trial reward. So-called N2pc responses were found to be stronger as well, indicating that target processing was enhanced. Notably, P1 and N2pc effects were observed on trials following high reward when a salient *distractor* was shown in the reward-paired color, showing that reward has an impact that can be *independent* of its role in establishing goal-driven attention (e.g., when a subject deliberately increases attention in anticipation of reward). In a related monkey cell-recording study, Peck and colleagues (2009) showed that cues signaling reward biased attention in a value-specific fashion, even though they were “maladaptive” (they interfered with the required behavior). They proposed that posterior parietal cortex in the monkey contains a visuospatial map—a *saliency* map—that takes into account reward expectations when guiding attention.

Does motivation influence the selection of information? To answer this question, Srikanth Padmala and I investigated the effects of reward during a response-conflict task (Fig. 4)

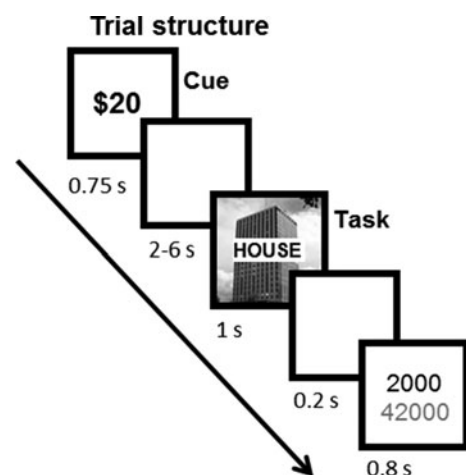


Figure 4. Response-conflict paradigm. In the reward condition shown here, a cue stimulus (“\$20”) signaled that subjects would be rewarded for fast and correct performance; in the control condition (not shown here), a cue stimulus (“\$00”) signaled that there would be no reward. During the target phase, a stimulus picture of a house or building was presented together with a task-irrelevant word (an incongruent condition is illustrated here). After the target stimulus, subjects were informed about the reward and about the total number of points accrued. Reproduced with permission from Padmala and Pessoa (2011).

(Padmala & Pessoa 2011). Based on previous studies, we anticipated that motivation would enhance engagement of fronto-parietal attentional regions and, consequently, that these regions would be better positioned to exert goal-directed control influencing visual processing (Fig. 5). Behaviorally, we observed response interference: Performance was slower on incongruent trials than on neutral ones. But reward reduced response interference. Given that reward also *decreased* response facilitation (i.e., the beneficial effect of a congruent task-irrelevant item), the results supported the inference that motivation enhanced *attentional filtering*, thereby reducing the influence of the task-irrelevant word item. Our brain imaging results revealed that, during the cue phase when subjects were told whether a reward was possible, responses in fronto-parietal regions were stronger with reward—consistent with increased attention. Notably, larger cue-related responses were associated with larger decreases in interference-related responses in the dorsal-medial PFC during the subsequent task phase. This suggested that upregulation of control during the cue phase led to decreased interference during the task phase.

We also observed responses to the cue in several subcortical sites that are engaged during reward-related processing, including the caudate and putamen in the dorsal striatum, nucleus accumbens in the ventral striatum, and midbrain. We reasoned that, if motivationally salient cues engage fronto-parietal regions more robustly during the cue phase, these regions should exhibit increased “coupling” with some of the above regions, which are sensitive to the motivational significance of the cues (Fig. 6A). Indeed, in the reward condition, we observed increased trial-by-trial functional connectivity between the intraparietal sulcus in parietal cortex and the putamen, caudate, and nucleus

accumbens (Fig. 6B; see also Harsay et al. 2011). More interestingly, the strength of the differential coupling (reward minus nonreward) between cortical and subcortical areas was linearly related to individual differences in reward sensitivity, showing that the functional interaction between these regions was stronger for subjects who scored higher in this dimension. See also Krebs et al. (2010; 2011).

Interactions between motivation and working memory have been the target of several neuroimaging studies (e.g., Beck et al. 2010; Gilbert & Fiez 2004; Jimura et al. 2010; Pochon et al. 2002; Taylor et al. 2004). In the study by Jimura and colleagues (2010), reward did not simply increase activation; it also shifted the timing of working memory responses (an effect that correlated with individual differences in reward sensitivity). They suggested that, in the reward condition, subjects may have adopted a more *proactive* control strategy to aid performance instead of a just-in-time *reactive* strategy—and thus increase their chance of reward (Braver 2012; Braver et al. 2007). Interactions between motivation and working memory have been studied in monkey cell-physiology studies, too. Not only do cells in the lateral PFC hold information of an object’s shape and location, but they are also modulated by reward expectancy (Watanabe 1990; 1996; see also Leon & Shadlen 1999). In fact, studies demonstrate that cognition and motivation signals are *integrated*. For example, during the delay period of a delayed-eye saccade task, some lateral prefrontal cells increased their firing if the monkey was initially cued to make a saccade to the preferred versus the opposite direction; these cells also exhibited increased firing during rewarded versus unrewarded trials (Kobayashi et al. 2002). Importantly, during rewarded trials of saccades to the preferred direction, there was an increase of the amount of transmitted *information* with respect to target position, as quantified by information theory; reward information increased the discriminability of target positions, leading to enhanced performance (see also Kobayashi et al. 2007).

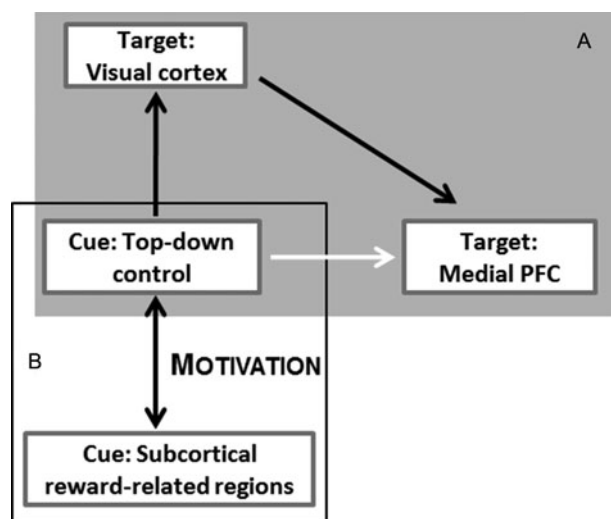


Figure 5. Hypothesized network interactions. (A) Predicted mediation by target/distractor processing in visual cortex of the relationship between attentional control implemented in fronto-parietal cortex during the cue phase and conflict-related activity in medial prefrontal cortex during the subsequent target phase (see white arrow). (B) Predicted effect of motivational context on functional interactions between fronto-parietal cortex and subcortical regions involved in reward processing. Reproduced with permission from Padmala and Pessoa (2011).

4.1. Energizing force versus selective effects

Traditional accounts describing motivation as a global activation independent of particular control demands have been echoed by a functional MRI study in which Kouneiher and colleagues (2009) argue that motivation and cognitive control can be regarded as two *separate* and *additive*—instead of *interactive*—factors. Although there is little question that motivation can have generalized, *activating* contributions to behavior (see Robbins & Everitt 2007; Salamone et al. 2009), current findings (Ch. 6) underscore the ability of motivation to shape behavior *selectively*, whether by reducing response conflict or task-switch costs, via selective effects on working memory, or by improving long-term memory (for the latter, see the work of Adcock and colleagues; e.g., Adcock et al. 2006). Another body of research demonstrating selective effects of motivation has investigated attentional effort, as described by Sarter and colleagues (e.g., Sarter et al. 2006).

5. Dual competition model

Here, I describe a framework in which both emotional and motivational signals are integrated with perception and cognition so as to effectively incorporate value into the

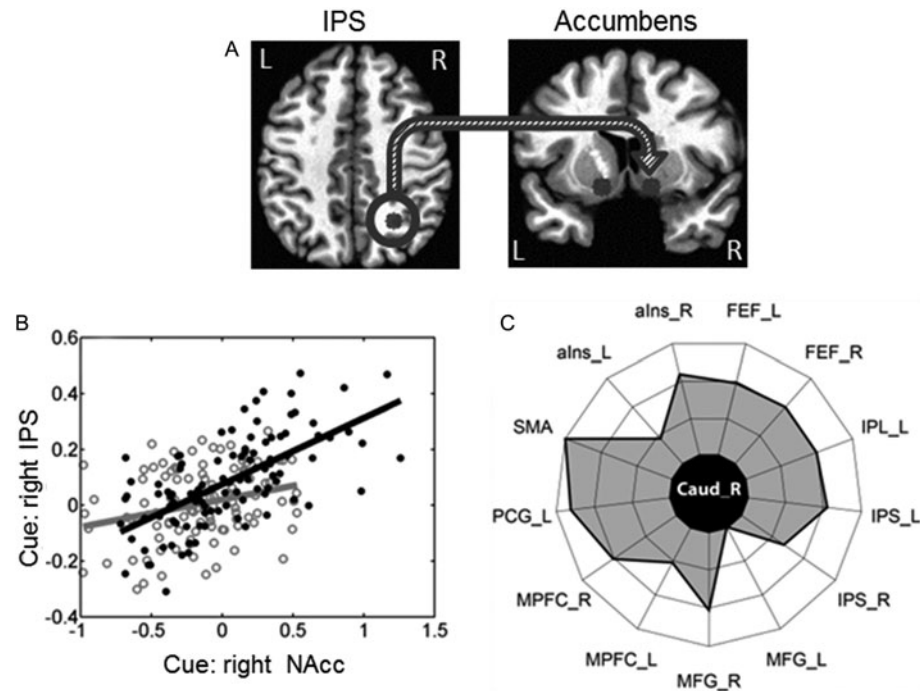


Figure 6. Functional connectivity during reward trials. (A) Regions exhibiting stronger functional connectivity with the right intraparietal sulcus (IPS) during the cue phase for reward trials. (B) Scatter plot showing the trial-by-trial relationship between right IPS and right nucleus accumbens (NAcc) signals during reward (black dots and line) and no-reward (gray dots and line) trials. Data are illustrated for a sample subject. (A-B) Reproduced with permission from Padmala and Pessoa 2011. (C) The polar plot shows increases in functional connectivity of the right caudate with nearly all regions belonging to the “other” community. Line lengths represent the relative strength of the functional connectivity between regions. Key: _L, left; _R, right; Caud, caudate; FEF, frontal eye field; IPL, inferior parietal lobe; aIns, anterior insula; IPS, intraparietal sulcus; PCG, precentral gyrus; MFG, middle frontal gyrus; MPFC, medial prefrontal cortex; SMA, supplementary motor area. (C) Reproduced with permission from Kinnison et al. (2012).

unfolding of behavior (Pessoa 2009; Pessoa & Engelmann 2010). To reflect the central idea that both emotion and motivation influence competition at both the perceptual and the executive levels, the framework is termed the dual competition model (thus “dual” spans both “emotion and motivation” and “perceptual and executive”). Following general remarks in the next paragraph, I will describe how the framework applies to emotion (sect. 5.1, focusing on emotion-laden negative stimuli) and then motivation (sect. 5.2, focusing on task manipulations involving reward).

Competition for neural resources exists in the sensory cortex (Grossberg 1980). To understand the flow of information processing more generally, we need to go beyond perceptual competition and explicitly incorporate the role of executive control. Behavioral research indicates that executive control is not unitary and that different functions have their own limited processing capacities, or resources. Neuropsychological research also supports the dissociation of cognitive operations, consistent with the “fractionation” of the central executive (Norman & Shallice 1986; Stuss & Knight 2002). Yet ample evidence also suggests at least some unity of executive functions—certain mechanisms are shared across functions (Duncan et al. 1996; Miyake et al. 2000). Capacity sharing has implications for information processing because it implies executive competition: Subcomponents of executive control are mutually interacting, such that multiple functions cannot be independently executed simultaneously. This competition can be cast in terms of resources. Accordingly, even though some executive processes rely on partly independent mechanisms, they

share a common pool of resources. Therefore, when a given function is needed, resources devoted to one operation will not be available for other operations, and behavioral interference will ensue.

5.1. Emotion

5.1.1. Perceptual competition. How does affective significance influence visual processing? Researchers have described a projection system emanating from the amygdala that reaches nearly all levels of the ventral visual system. Although this system is often highlighted as the sole modulatory mechanism for visual processing, I propose that at least five other mechanisms need to be investigated as well. These mechanisms, which include both cortical and subcortical structures, involve network interactions that sculpt how visual signals evolve in response to the behavioral and affective significance of sensory stimuli.

One mechanism through which emotion may affect perception involves other *valuation* regions, most notably orbitofrontal cortex (Barrett & Bar 2009) and possibly the insula. The orbitofrontal cortex is important for the evaluation of sensory stimuli (Zald & Rauch 2007) and is reciprocally interconnected with visual cortex, especially the more anterior portions of the ventral stream (Barbas 1995; Cavada et al. 2000; Rempel-Clower & Barbas 2000; Saleem et al. 2008). This region is thus capable of influencing responses in visual cortex based on affective value. A second mechanism involves the basal forebrain, whose terminals influence visual processing through the release of

acetylcholine. For example, cholinergic mechanisms affect the competition between attended and unattended stimuli (Furey et al. 2000; 2008). Several regions that participate in the evaluation of incoming inputs project to the basal forebrain, which is then able to modify information processing in visual cortex. Third, regions in lateral frontal cortex and parietal cortex are suggested to modulate visual processing according to an item's affective significance. In particular, both the frontal eye field and parietal cortex contain priority maps (Fecteau & Munoz 2006; Serences & Yantis 2006). To embed affective significance into priority maps, fronto-parietal regions work closely with regions such as the hypothalamus, amygdala, orbitofrontal cortex, and anterior insula, to prioritize processing based on the emotional value of a sensory stimulus (note that anatomical connectivity will not be direct in some cases; see Ch. 9). A fourth mechanism involves the pulvinar complex of the thalamus, whose importance for affective processing is a result not of its putative role as part of a subcortical pathway, but instead of its connectivity with other cortical regions (Pessoa & Adolphs 2010). I have proposed that the pulvinar amplifies responses to stimuli of potential value to the organism during challenging sensory conditions (Padmala et al. 2010). A fifth potential mechanism was recently reported by Zikopoulos and Barbas (2012), who described a pathway from the amygdala to the reticular nucleus of the thalamus and suggested that the connection is important for the capture of attention by emotion-laden stimuli. I anticipate that additional mechanisms beyond those described here will need to be considered, too.

5.2. Executive competition

Because emotion can either enhance or impair cognitive performance, to see how emotional content impacts executive control, we must consider at least two factors: the

strength or arousal of the stimulus (or manipulation) and task relevance (see also Mather & Sutherland 2011). When arousal is “low” and affective significance is task *irrelevant*, some interference with the main task may be observed and the behavioral effect will be typically small. When, however, arousal is “high” and the stimulus/manipulation is task irrelevant, resources are more fully diverted toward the processing of the emotional item and, because the mobilization of resources is more pronounced, the effects on behavior are greater (Lang et al. 2000; Panksepp 1998). For example, in our investigation of cognitive-emotional interactions, Choi, Padmala, and I (2012) observed that response conflict increased on trials with the possibility of shock, suggesting that the impact of emotion on behavior comes in part from the more vigorous recruitment of attentional/effortful control required to prioritize the processing of high-arousal items. Naturally, attentional/effortful control involves executive control resources and, because situations associated with high levels of arousal are expected to recruit some of these resources (see also Bishop 2007; Eysenck et al. 2007; Mathews & Mackintosh 1998), interference with executive functions will ensue (Fig. 7A). The impact of emotion on performance thus occurs because of limited processing capacity and competition for common-pool resources.

What about the situation when the emotional stimulus is task *relevant*? Here, two outcomes are possible. If the affective intensity is “low,” task performance might improve because control will be mobilized in the service of handling the task at hand, and the executive functions needed for task completion will more effectively compete for resources. In all, task performance will be enhanced. If, however, the affective intensity is sufficiently high, task performance might be compromised. Thus, in a study of response inhibition, my colleagues and I asked participants to perform a simple discrimination task but to withhold responding when they saw

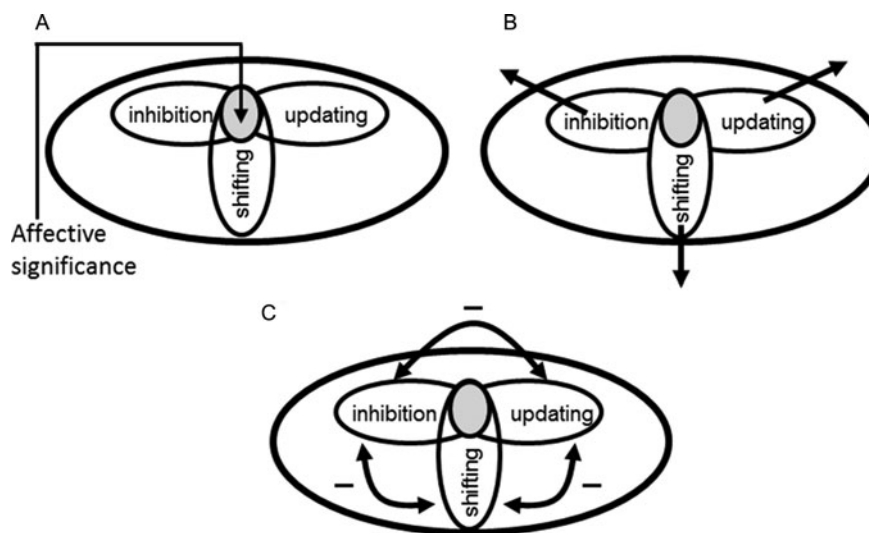


Figure 7. Executive control, competition, and processing resources. (A–C) Processes are proposed to share resources called “common-pool resources” (smaller ellipses in gray), such that the engagement of one will detract from the processing of the other. Common-pool resources are necessary for general functions of attentional/effortful control. (A) High-arousal emotional stimuli recruit common-pool resources that allow their processing to be prioritized, thus detracting from other mechanisms sharing those resources. (B) These stimuli also trigger executive functions, such as updating, shifting, and inhibition, to handle the challenges to the organism, as indicated by the arrows emanating from attentional/effortful control. (C) Competition for resources during cognitive and emotional manipulations can, at times, produce push-pull-like interactions. Reproduced with permission from Pessoa (2009).

a stop signal (Pessoa et al. 2012). We found that, when we used both fearful and happy faces as low-arousal stop signals, response inhibition was enhanced relative to neutral faces, but when we employed high-arousal emotional stimuli (previously paired with mild shock) as stop signals, response inhibition was impaired relative to neutral stimuli. Thus, inhibition performance was degraded even though emotional content was task relevant. We conjectured that processing the emotional stimulus consumed resources needed for inhibition.

5.3. Processing resources

Although the concept of resources invoked in accounts of the limits of information processing has been criticized in the past (e.g., Logan 1988; Navon 1984; Neisser 1976) and has not been mechanistically specified, further insight into it can be gained by examining brain regions sensitive to changes in task load, including the attentional network. Accordingly, researchers have probed attentional bottlenecks observed during tasks such as the attentional blink and the phenomenon known as the “psychological refractory period.” Based on these paradigms, Marois and colleagues have proposed the existence of a “unified” attentional bottleneck that involves several regions of the fronto-parietal attentional network (Tombu et al. 2011). If robust emotional manipulations indeed consume processing resources, then they should engage sites implicated as “bottleneck areas.” As described in section 3, a compilation of activation peaks in aversive conditioning functional MRI studies revealed sites throughout the lateral and medial PFC, in addition to the anterior insula (Pessoa 2009). Thus, attentional bottleneck regions are consistently recruited during emotion processing. If this recruitment prevents them from being adequately engaged when neutral task-related processing is required, we should expect to see behavioral impairments (see also Bishop et al. 2004).

5.4. Triggering additional functions

A distinct impact of emotion is the result of its influence on *specific* resources. Dealing with an emotional stimulus requires the types of behavioral adjustments that characterize executive functions. For example, to refresh the contents of working memory, to switch the current task set, and to cancel previously planned actions might require updating, shifting, and inhibition, respectively. Such adjustments recruit specific resources required for emotional processing (Fig. 7B) and, if these resources are temporarily unavailable for the task at hand, behavioral performance will be compromised—the more so, the stronger the emotional manipulation (see below). An example may help to illustrate. Suppose a subject is performing a cognitive task and a change in background color signals that she or he will receive a shock sometime in the next 30 seconds. The subject might update the contents of working memory to include the “shock possible” information, shift between the execution of the cognitive task and “monitoring for shock” every few seconds, and, if another cue indicated that the shock would be delivered in the next second, inhibit a response to the cognitive task to prepare for the shock. In other words, dealing with the emotional situation

necessitates the same types of executive functions that are considered to be the hallmark of cognition.

5.5. Cognitive-emotional interactions versus push-pull

The dual competition framework suggests that brain regions important for executive control are actively engaged by emotion. In contrast, push-pull studies have demonstrated *reduced* signals in some of these regions when emotional stimuli are shown. Hence, the two frameworks appear to make opposite predictions. The findings of Anticevic and colleagues (2010) provide a potential clue as to when we might expect antagonistic interactions. Whereas, relative to neutral, negative distractors decreased responses in the dorsal-lateral PFC during the delay period of the working memory task, *task-related* distractors (stimuli similar to items to be remembered) actually increased responses, in much the way increases in working memory demand would. What explains this difference?

Dealing with the negative stimuli during the delay period produced a momentary “neglect” of the memory maintenance (Anticevic et al. 2010). In contrast, because neutral task-related distractors were so similar to the to-be-remembered items, participants may in effect have also held them in memory so as to avoid matching the final probe stimulus to a distractor. Consequently, the distractors may actually have increased working memory load. I therefore suggest that cognitive-emotional push-pull interactions are related to a type of competition that directs processing *away* from the concurrently executed main task, thereby producing decreased activation (in relative terms) in some of the key frontal and parietal regions underlying the task at hand (Fig. 7C). Which is to say, deactivations are the result of competitive interactions between resources required for executive functions. As such, they should be understood not in terms of a mutually suppressive relationship between emotion and cognition, but in terms of executive competition.

5.6. Neural interactions

Cognitive-emotional interactions rely on the communication between “task networks” (e.g., the attentional network during attention tasks) and “valuation networks,” which involve both subcortical regions, such as hypothalamus and amygdala, and cortical ones, such as orbitofrontal cortex, anterior insula, and medial PFC. These interactions are suggested to take place via multiple forms of communication (Fig. 8).

First, direct pathways connect task and valuation networks. One example is the pathway between orbitofrontal and lateral PFC (Barbas & Pandya 1989). Other examples are the pathways between the extensively interconnected lateral surface of the PFC (including dorsal-lateral PFC) and all cingulate regions (Morecraft & Tanji 2009). A second type of communication relies on “hub” regions at the *intersection* of task and valuation networks—hubs are highly connected and central regions that play a key role in information communication between different parts of a network.

What are some of the hub regions? Dorsal-medial PFC plays a prominent role as “common node” of executive and emotional networks because of its participation in integrating inputs from diverse sources, notably cognitive and affective ones (e.g., Devinsky et al. 1995; Fig. 8). This

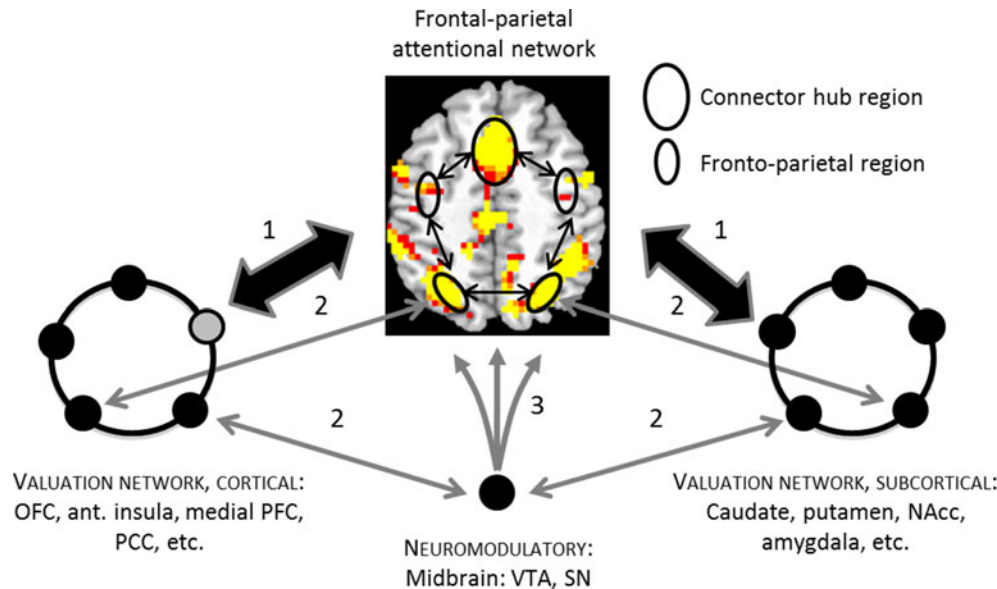


Figure 8. Modes of interaction between cognitive and emotion/motivation networks. (1) Interactions rely on hub regions, such as those in the dorsal-medial prefrontal cortex, which are part of both attentional and motivational networks (hub region in the slice and gray node in the cortical valuation network). (2) In addition, specific regions may link the two networks, either directly or via the thalamus. (3) Finally, motivational signals are further embedded within cognitive mechanisms through the action of diffuse neuromodulatory systems. Key: ant., anterior; NAcc, nucleus accumbens; OFC, orbitofrontal cortex; PCC, posterior cingulate cortex; PFC, prefrontal cortex; SN, substantia nigra; VTA, ventral tegmental area. Reproduced with permission from Pessoa and Engelmann (2010).

region is involved in multiple executive functions, such as conflict detection, error likelihood processing, and error monitoring (Alexander & Brown 2011). As reviewed in section 3, the dorsal-medial PFC is also reliably engaged during conditions involving negative affect (see Fig. 3), as are all sectors of the anterior-medial PFC.

A second hub region, the anterior insula, is important for interoception (Craig 2002; 2009). Moreover, threat, uncertainty, and risk are all factors that engage the anterior insula (Singer et al. 2009), which is also reliably recruited by cognitive processes (Craig 2009; Van Snellenberg & Wager 2010). Indeed, in a recent analysis of the functional diversity of brain regions (see sect. 7.4 and Fig. 14), the anterior insula emerged as one of the most diverse in the brain (Anderson et al. 2013; see also Uddin et al. 2013). In all, the dorsal-medial PFC and anterior insula provide substrates for ample cognitive-emotional integration that, in broad terms, include both bodily “input” and “output” signals (roughly, via anterior insula and dorsal-medial PFC, respectively). Of course, these regions do not work in isolation. During cognitive-emotional interactions, they interact with the lateral PFC and parietal cortex, for example (Fig. 8).

A third type of communication depends on the diffuse action of neuromodulatory systems, including the action of dopamine and norepinephrine. Widespread modulatory connections originating from these systems reach large portions of the cortical surface and multiple subcortical areas, from which they are able to rapidly influence brain responses during emotional situations (Arnsten 2009; Panksepp 1998).

6. Motivation

The framework of the dual competition model described thus far for the case of negative emotion also describes

how motivation influences perceptual and executive competition. This applies to situations in which individuals work for a potential reward, as well as paradigms in which an item acquires motivational significance by being paired with reward.

6.1. Perceptual competition

How does motivational significance influence sensory processing? Several of the circuits described in the context of emotion operate in the case of motivation, too. Notably, the interactions between valuation networks and fronto-parietal regions important for attentional control are engaged by both emotion and motivation. An illustration of the latter was described in the response-conflict study reviewed previously (see Fig. 4 and Fig. 5). One of the differences between emotion and motivation is that at times the interactions will involve *different* valuation regions, say, the amygdala in the case of emotion and the accumbens in the case of motivation. Yet, the general form of the interaction is similar. Which is to say, items of affective/motivational significance will redirect the flow of signals such that their processing is favored. I further propose that mechanisms involving the basal forebrain and the pulvinar operate for both emotion and motivation. More generally, despite the considerable differences between basal forebrain, pulvinar, and fronto-parietal mechanisms, each shapes, say, visual perception by altering competition in visual cortex. Thus, the idea is that their respective pathways may be engaged both during emotional and motivational conditions. Once they are engaged, the downstream effects on visual processing (and elsewhere) may be the same for both types of manipulation. A corollary of this notion is that priority maps (Awh et al. 2012; Baluch & Itti 2011; Fecteau & Munoz 2006; Serences & Yantis 2006; Wolfe 1994) – containing representations of

spatial locations that are behaviorally important – incorporate signals as a result of an item’s affective and motivational significance.

6.2. Executive competition

Motivation influences executive competition, too, and section 4 described examples during response-conflict, task switching, and working memory. Two effects of motivation on executive function are proposed here. First, motivation *sharpens* executive functions by enhancing them or by making them more efficient (Fig. 9). An illustration of this effect was the working memory study by Kobayashi and colleagues (2002) in which reward increased the amount of transmitted information regarding the item being maintained in memory. Second, motivation *reallocates* resources available to executive functions, increasing the likelihood of reward attainment by improving performance (Fig. 9). For example, in the study by Jimura and colleagues (2010) brain responses appeared to reflect a shift toward a proactive control strategy that was beneficial to performance. Motivation can thus be viewed, at times, as reallocating resources to prioritize implementation of the rewarded task component at the expense of unrewarded components (Fig. 7C) (which at times can lead to deleterious performance effects; Padmala & Pessoa 2010).

6.3. Neural interactions

The same general architecture for cognitive-emotional interactions is proposed to underlie cognitive-motivational interactions (Fig. 8). In particular, the interactions between valuation networks and fronto-parietal regions important for attention and executive control are suggested to be common to both emotion and motivation. Subcortical reward/valuation regions include the caudate (particularly more ventral portions), nucleus accumbens, midbrain, and the amygdala; and cortical regions include orbitofrontal cortex, anterior insula, medial PFC, and posterior cingulate cortex.

Hub regions also play a central function during interactions between cognition and motivation. For example, Mesulam and colleagues suggested that posterior cingulate cortex is important for the integration of motivational and spatial attention information (Mohanty et al. 2008; Small

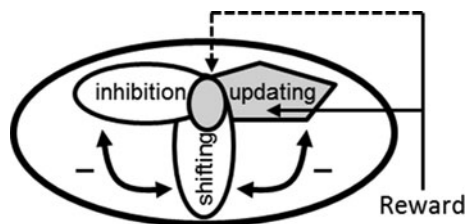


Figure 9. Executive control and reward. Motivation is proposed to have two key effects on executive function: first, it fine-tunes executive functions that are important for the task at hand (represented by the change of shape of the updating function; see solid arrow); and, second, it redistributes the allocation of common-pool resources (gray ellipse; see dashed arrow), and thus modulates how executive processes compete with each other. Reproduced with permission from Pessoa (2009).

et al. 2005; see also Platt & Huettel 2008). Another key hub region is medial the PFC (including the dorsal PFC), already discussed in the context of emotion. Indeed, multiple sources of evidence demonstrate that the medial PFC is a critical component of the motivational system (see Summerfield & Koechlin 2009; Vogt 2008; Walton et al. 2007). Shackman and colleagues (2011) proposed that the dorsal-medial PFC implements domain-general processes of adaptive control, based on the region’s extensive contributions to cognitive control, negative affect, and nociception. I suggest that the proposal should be extended to incorporate motivation as well, which is to say, that dorsal-medial prefrontal context implements *motivated adaptive control*—where “motivated” is understood to include emotional processing. The anterior insula has been repeatedly implicated during the processing of negative events (Paulus & Stein 2006; Simmons et al. 2006). But a growing number of studies implicate it during appetitive conditions (Liu et al. 2011a; Mizuhiki et al. 2012; Naqvi & Bechara 2009; Padmala & Pessoa 2011; Samanez-Larkin et al. 2007). Here, I propose that the anterior insula is a chief hub region for cognition-motivation interactions.

As in the case of emotion, a third mode of communication involves the widespread action of neuromodulatory signals, including those of dopamine and acetylcholine. It is possible that dopaminergic and cholinergic neuromodulation provide a key mechanism by which motivation sharpens executive control (and hence behavioral performance), for example, by improving the signal-to-noise ratio of relevant neurons (e.g., Goldman-Rakic et al. 1989). Motivation thus enhances processing efficiency in target cortical and subcortical regions.

6.4. “Resources”: Linking human and animal literatures

The dual competition model employs the admittedly vague concept of “resources.” One way in which a more mechanistic account can be formulated is to build on the extensive literature of motivation in nonhuman animals. Redgrave and colleagues (Redgrave & Gurney 2006; Redgrave et al. 1999) have proposed that dopamine-related circuits in the striatum facilitate the reallocation of limited processing capacity toward unexpected events of behavioral significance, including rewarding ones. Thus, instead of simply providing a “reward signal,” striatal activation drives the redistribution of available resources to salient events whose processing is then prioritized (see also Horvitz 2000; Zink et al. 2004). Furthermore, Sarter et al. (2006) propose that increased prefrontal cholinergic activity contributes to the recruitment of goal-driven mechanisms (see also Sarter et al. 2005), which depend on fronto-parietal regions, act to enhance sensory processing and to attenuate interference effects.

6.5. Mechanisms of motivational effects: Conceptual issues

Disentangling the contributions of cognition and motivation to neural signals is far from easy, especially when experiments involve goal-directed task manipulations. For example, in human studies, subjects may be instructed that a potential reward will result following a cue stimulus if their performance is both fast and accurate. In such

cases, increased brain signals may reflect enhanced attention because subjects are more likely to engage attention when a reward is at stake. But whether the increased signals *actually* reflect greater attention is another matter, an issue Maunsell described forcefully in the context of monkey physiology studies of attention:

When the effects of spatial attention are examined, subjects are motivated to direct attention to one location or another only by expectations about which location is more likely to be associated with a reward.... Such reward manipulations reliably lead to shifts in attention ... However, these experiments typically provide no basis for assigning changes preferentially to attention or to expectations about reward. In most cases, attention-related modulation could equally well be described in terms of expectation about rewards because the two are inextricably confounded. (Maunsell 2004, pp. 262–63)

Maunsell's point raises the broader issue of the relationship between motivation and cognition. One possibility is that motivation has effects that take place independently of cognition (Fig. 10A). A second is that motivation modulates behavior by engaging the same functions that are used by cognition, in which case, the impact of motivation on behavior could be described as “mediated by cognition” (Fig. 10B). This mediation could be partial only, such that both direct (motivation-to-behavior) and indirect (motivation-via-cognition-to-behavior) effects take place. A third possibility is that cognition and motivation are more intertwined, such that they *jointly* guide behavior (Fig. 10C), in which case, although certain processes could be described as “cognitive” and others as “motivational,” the interactions between them are sufficiently strong that their separation is more semantic than real. See Chelazzi et al. (2013) for a related discussion.

The situation Maunsell describes thus could be portrayed in terms of the mediation model (B): *Mechanistically*, effects of attention are obtained via “attentional circuits.” Whereas this relationship would presumably indicate that such motivational effects are less interesting, I argue that *how* motivation recruits “cognitive” circuits is as important as which circuits it recruits. Indeed, I suggest that the major issue is conceptual, and that by using separate boxes for “attention” and “motivation,” the models of Figure 10 describe motivation in an impoverished way. As in the case of emotion and cognition (Pessoa 2008), I propose that it is counterproductive to carve the brain into “attention” (or “cognition”) and “motivation.” Chapters 6 and 7 outline how motivational signals are *embedded* into cognition (and perception) through multiple mechanisms. In this manner, the “inextricably confounded” relationship described by Maunsell (2004) ceases to be a problem and

can be seen as a *property* of brain organization (see also sect. 7.2).

7. Network perspective on brain function

The type of embedding of emotional and motivational signals into perception and cognition (e.g., Grossberg 1982) necessitates a network perspective of brain organization. Thus, *the network itself is the unit*, not the brain region. Processes P that support behavior are not implemented by an individual area, but rather by the interaction of multiple areas, which are dynamically recruited into multiregion assemblies.

7.1. Overlapping networks

Commonly, networks are described in terms of unique, *nonoverlapping* sets of brain regions (Fig. 11A). But this assumes that brain areas compute a specific function, one that is perhaps elementary and needs other regions to be “actualized,” but nonetheless is well defined. I propose that networks contain overlapping regions, such that specific areas will belong to several intersecting networks (Mesulam 1990). In this manner, the processes carried out by an area will depend on its network affiliation at a given time. What determines a region's affiliation? For this, the importance of the *context* within which a brain region is operating must be considered (McIntosh 2000). For example, in Figure 11B, region A_n will be part of network N_1 during a certain context C_k , but will be part of network N_2 during another context C_l . The existence of context-dependent, overlapping networks also means that from the perspective of structure-function mappings summarized in Figure 11B, a given region will participate in multiple processes. In addition, the importance of context emphasizes the need to consider *dynamic* aspects of structure-function relationships. A network needs to be understood in terms of the interactions between multiple brain regions as they unfold temporally. In the extreme, two networks may involve the exact same regions interacting with each other in distinct ways across time.

Though simple, the “multiple affiliation” point is sufficiently important to merit an example. Consider the case of the amygdala. Even a simplified view of its anatomical connectivity shows that, minimally, it belongs to three networks. The first is a “visual network,” as the amygdala receives fibers from anterior parts of temporal cortex. The amygdala, by its turn, influences visual processing via a set of projections that reach most of ventral occipito-temporal cortex. The second is the well-known “autonomic

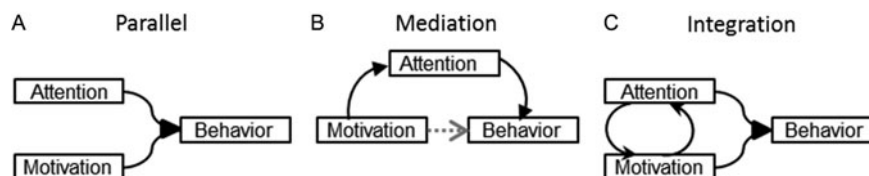


Figure 10. Three models of the relationships between attention and motivation. (A) In the parallel model, attention and motivation have independent effects on behavior. (B) In the mediation model, the influence of motivation on behavior is mediated via attentional systems. (C) In the integration model, attentional and motivational systems interact so strongly they cannot be decomposed. Adapted with permission from Pessoa and Engelmann (2010).

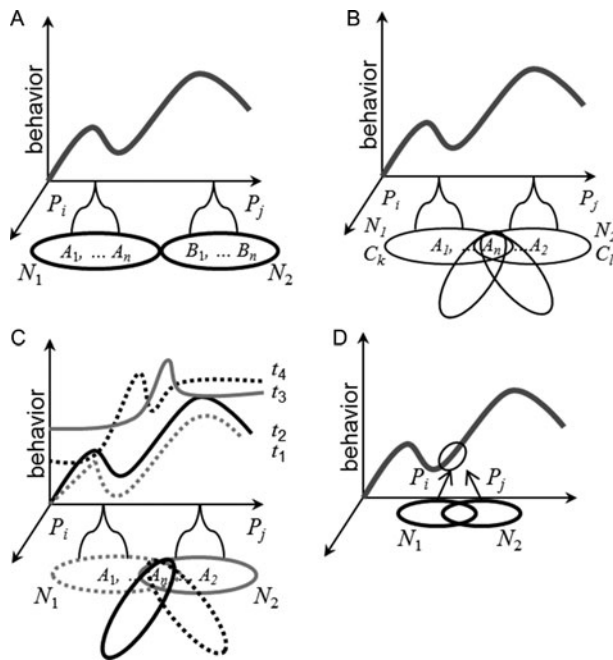


Figure 11. Structure-function mapping and networks. (A) The “landscape of behavior” depicts the multidimensional space of behaviors. $A_1, A_2, A_n, B_1,$ and B_n =brain regions; N_1 and N_2 =networks; P_i and P_j =processes. (B) Intersecting networks. The networks C_k and C_l (and the additional ones) intersect at node A_n . (C) Dynamic aspects. Because region A_n will have network affiliations that vary as a function of time, the processes carried out by the emerging networks will evolve across time and lead to dynamic “landscapes of behavior.” The four time points represented are such t_1 is close to t_2 but far from t_3 and t_4 , which are close to each other. (D) Structure-function mappings in the case of networks. Two networks may instantiate similar processes, a case of many-to-one mapping. The reverse relationship is also suggested to apply to networks, namely, one-to-many mappings. Reproduced with permission from Pessoa (2013).

network,” as evidenced by connectivity with subcortical structures such as the hypothalamus and periaqueductal gray, among others. Via this network, the amygdala participates in the coordination of many complex autonomic mechanisms. The third is a “value network,” as evidenced by its connectivity with the orbitofrontal cortex and medial PFC. In total, the amygdala affiliates with different sets of regions (“networks”) in a highly flexible and context-dependent manner. Many other examples of this *dynamic affiliation* idea exist, including the fronto-parietal cortex, whose regions affiliate with others based on task demands (Cole et al. 2013).

Two issues deserve further consideration here. First, when describing networks, the term *process* is preferable to *function*. One reason is that a process emerges from the interactions between regions—it is thus an *emergent property* (see Bressler & Menon 2010). Furthermore, a process is viewed as a useful external description of the operation of the network, and not necessarily as a fixed internal computation implemented by the network (Thompson 2007; Thompson & Varela 2001; Varela et al. 1992; cf. Lindquist & Barrett 2012).

A second—and critical—issue is whether utilizing networks solves the many-to-many mapping problem we face

when considering regions as the unit of interest. In other words, does a description of structure-function relationships in terms of networks allow for a one-to-one mapping? For example, in the context of the salience network, Menon, Uddin, and colleagues note that “to determine whether this network indeed specifically performs this function will require testing and validation of a sequence of putative network mechanisms” (Bressler & Menon 2010, p. 285; see also Moussa et al. 2011). The prospect of simpler structure-function relationships (hence *less* context dependent) is discussed by Buckner and colleagues when describing regions of high connectivity: “An alternative possibility is that the hubs reflect a stable property of cortical architecture that arises because of monosynaptic and polysynaptic connectivity. Within this alternative possibility, the same hubs would be expected to be *present all of the time*, independent of task state” (Buckner et al. 2009 pp. 1867–68; emphasis mine).

Unfortunately, the attempt to map structure to function in a one-to-one manner in terms of networks will be fraught with some of the difficulties encountered when considering individual brain regions (Ch. 8). To be true, the problem is ameliorated, but the mapping is still highly complex. For example, two distinct networks may generate similar behavioral profiles (Fig. 9D; many-to-one); a given network will also participate in several behaviors (one-to-many). Broadly speaking, a network’s operation will depend on several more global variables, namely an extended context that includes the state of several “neurotransmitter systems,” arousal, slow wave potentials, and so forth. In other words, a network that is solely defined as a “collection of regions” is insufficient to eliminate the one-to-many problem. What if we extend the concept of a network with these additional variables? For example, Cacioppo and Tassinary (1990) suggest that psychological events can be mapped to physiological ones in a more regular manner by considering a spatiotemporal pattern of physiological events. The notion of a network is thus extended to incorporate other physiological events, for example, the state of a given neurotransmitter (as in the elegant work by Marder and colleagues; see Marder & Goaillard 2006). How extensive does this state need to be? Clearly, the usefulness of this strategy in reducing the difficulties entailed by many-to-many mappings will depend on how broad the context must be (Thompson 2007).

7.2. An example: Cognitive-motivation interactions

Graph-theoretical analysis of functional neuroimaging data has focused almost exclusively on characterizing the large-scale properties of resting-state data (Bullmore & Sporns 2009; Wang et al. 2010). In a recent study, we sought instead to understand the network properties of a focused set of brain regions during task conditions engaging them (Kinnison et al. 2012). In particular, we analyzed the data of the response-conflict task discussed previously (Fig. 4 and Fig. 5; Padmala & Pessoa 2011). At the network level, *global efficiency* (a measure of integration) increased and *decomposability* (a measure of how easily a network can be divided in terms of smaller subnetworks or “communities”) decreased (Fig. 12). In other words, the network became less segregated with reward, revealing that one way in which a reward cue affects brain responses is by increasing functional connections across brain regions.

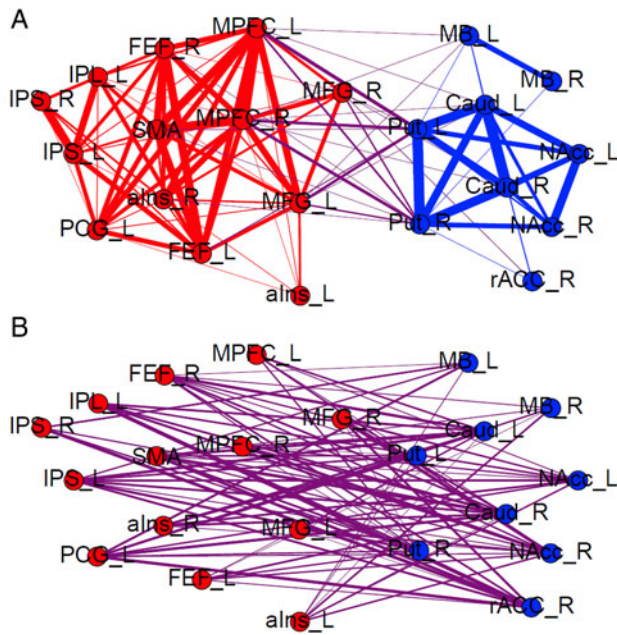


Figure 12. Network structure and reward. (A) Community detection was applied to the set of brain regions that responded more strongly to reward than to no-reward context at the cue phase. Two communities were detected. (B) Comparison of the pattern of connectivity between reward and no-reward contexts revealed increases during the former, mostly between the two communities, reflecting increased integration with reward. Adapted with permission from Anderson et al. (2013).

From the vantage point of a single region, the changes in functional connectivity can be quite broad and can be characterized via a functional connectivity *fingerprint* (see Passingham et al. 2002). For example, the caudate (Fig. 6C) and the nucleus accumbens showed increases in functional connectivity to nearly all cortical regions that were driven by reward, reinforcing the notion of “embedding” described earlier. Finally, this example underscores the need to move beyond simple pairwise relationships between regions to a multivariate representation of the changes in functional connectivity that underlie network reorganization.

7.3. Issues when considering networks

If we are to use networks to understand structure-function mappings, then we must consider several issues. I briefly describe them here (see also Pessoa 2014).

7.3.1. “Importance”: Structural and functional embedding.

A network framework moves the unit of analysis away from brain regions and distributes it *across* them. This does not mean that regions provide equal contribution to specific behaviors, of course. That being the case, devising ways to characterize a region’s *importance* is of great interest. This section builds on a recent discussion by Vlachos and colleagues (2012), who considered this question in the context of neurons.

What determines the *importance* of a region to a given computation? One strategy is to consider its degree of *structural embeddedness* and *functional embeddedness*. The former refers to the way elements are physically

embedded in their surrounding; the latter is the influence elements have on the activity of other elements, which depends on structural embeddedness, in addition to other synaptic and cellular properties, ongoing activity, neuromodulators, and so forth. Regions (that is, nodes) with high connectivity (that is, high degree) have the potential to be influential, particularly if they function like connector hubs (Guimera & Nunes Amaral 2005). Counterintuitively, however, in some circumstances the most highly connected nodes of a network are not the most influential (Kitsak et al. 2010; see also Liu et al. 2011b). Instead, the most prominent nodes are those located within the *core* of the network. In other words, they belong to a *topologically central* subnetwork. Hence, one way to measure embeddedness is to determine nodes that exhibit the property of *centrality* (Newman 2010). In general, however, no single measure will perfectly capture *influence* or *importance* because different measures will convey different aspects of network organization. Indeed, multiple measures of centrality have been proposed (Rubinov & Sporns 2010) and generate different results (Zuo et al. 2012). Therefore, a combination of different metrics will provide a better measure of embeddedness and, better still, how a node affects network properties (Liu et al. 2011b; Modha & Singh 2010; Vlachos et al. 2012); see also Power et al. (2013).

A further issue relates to *communicability* in complex networks (Estrada & Hatano 2008). Many important measures that characterize networks are based on the shortest paths connecting two nodes, including the determination of communities. Counterintuitively, as described by Estrada and Hatano (2008), “information” can in fact spread along paths that are not the shortest (see also Borgatti 2005; Newman 2005). This has implications for the understanding of brain networks because direct anatomical connectivity is frequently emphasized as the chief mode of communication between brain regions. The notion that communicability does not necessarily rely on shortest paths reminds us of the need to obtain network-level properties in describing the flow of signals in neural networks. It also highlights the need to characterize functional connectivity between regions, which does *not* uniquely depend on direct anatomical connections (see Adachi et al. 2012).

7.3.2. The importance of weak connections. Here, I critique another component of the “standard” network view, which can be summarized as follows: Network states depend on strong structural connections; conversely, weak connections have a relatively minor impact on brain states.

Schneidman and colleagues (2006) recorded simultaneously from 40 cells in the salamander retina. Although some pairs of cells had very strong correlations, most correlations were weak. Importantly, the findings demonstrated that *weak pairwise correlations* are capable of generating *strongly correlated network states*. The lesson learned here is that weak connections cannot be disregarded when the goal is to understand network states. Now consider that most studies of large-scale networks based on structural and functional data disregard weak connections. In fact, in resting-state functional connectivity studies, researchers typically assign connections with weak correlations (say <.3) a value of zero (no connection) (e.g., Meunier et al. 2009). Although more studies are evidently needed

to examine the implications of weaker connections to brain architecture, their importance is unlikely to be restricted to cells in the salamander retina. For example, Bassett and colleagues (2011) studied the dynamic reconfiguration of human brain networks during learning and uncovered several clusters of brain regions that remained integrated with one another by a complex pattern of weak functional interconnections.

7.4. Understanding a region's function via multidimensional profiles

If brain regions are engaged in many processes based on the networks they are affiliated with in particular contexts, they should be engaged by a range of tasks. Although this introduces outstanding problems, the availability of data repositories containing the results of thousands of neuroimaging studies provides novel opportunities for the investigation of human brain function (Yarkoni et al. 2010).

Like others (e.g., Robinson et al. 2012), my colleagues and I recently employed a data-driven approach to investigate the functional repertoire of brain regions based on a large set of human functional MRI studies (Anderson et al. 2013). We characterized the function of brain regions in a multidimensional manner via their *functional fingerprint* (Passingham et al. 2002), namely, the relative

degree of engagement of the region across a range of task domains (Fig. 13, top); the approach was extended to networks, too (Fig. 13, bottom). Based on the fingerprints, we calculated a *diversity index* to summarize the degree of *functional diversity*; a brain region with high diversity would be one engaged by tasks in many domains, whereas a low-diversity region would be engaged by a few domains. We found that diversity varied considerably across the brain (Fig. 14).

Our findings suggest that brain regions are very diverse functionally, in line with the points raised by Poldrack (2006; 2011). Beyond the descriptive aspects of the approach, it outlines a framework in which a region's function is viewed as inherently *multidimensional*: A vector defines the fingerprint of a region in the context of a specific domain structure. Although the domain that we explored used a task classification scheme from an existing database, it was not the only one possible. How should one define the domain structure? One hope is that cognitive ontologies can be defined that meaningfully carve the “mental” into stable categories (Bilder et al. 2009; Price & Friston 2005). I contend, however, that *no* single ontology will be sufficient. Instead, it is better to conceive of several task domains that are useful and complementary in characterizing brain function and/or behavior. Thus, a region's functional fingerprint needs to be understood in terms of a

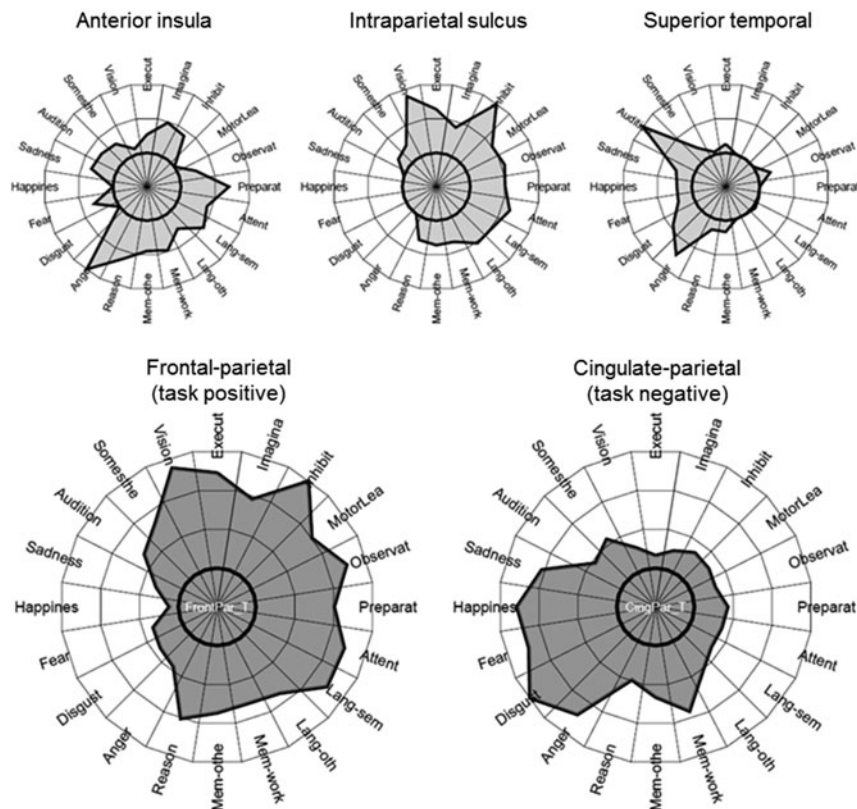


Figure 13. Functional fingerprints of regions and networks. (Top) Polar plots illustrate the fingerprints of three brain regions. Each vertex corresponds to one of the domains investigated. Both the left anterior insula and the left intraparietal sulcus exhibited diverse functional profiles. The superior temporal gyrus in the vicinity of auditory cortex was less diverse, although the fingerprint revealed its involvement in emotional processing, in addition to audition. (Bottom) Polar plots illustrate the fingerprints of two brain networks, which were defined by Toro and colleagues (2008) based on a meta-analysis of task activation data. The frontal-parietal “attention” network was a task-positive network generated by “seeding” the left intraparietal sulcus. The cingulate-parietal “resting-state” network was a task-negative network generated by “seeding” ventral-anterior medial prefrontal cortex. Although both networks are quite diverse, the analysis revealed that they are fairly complementary to one another. Adapted with permission from Anderson et al. (2013).

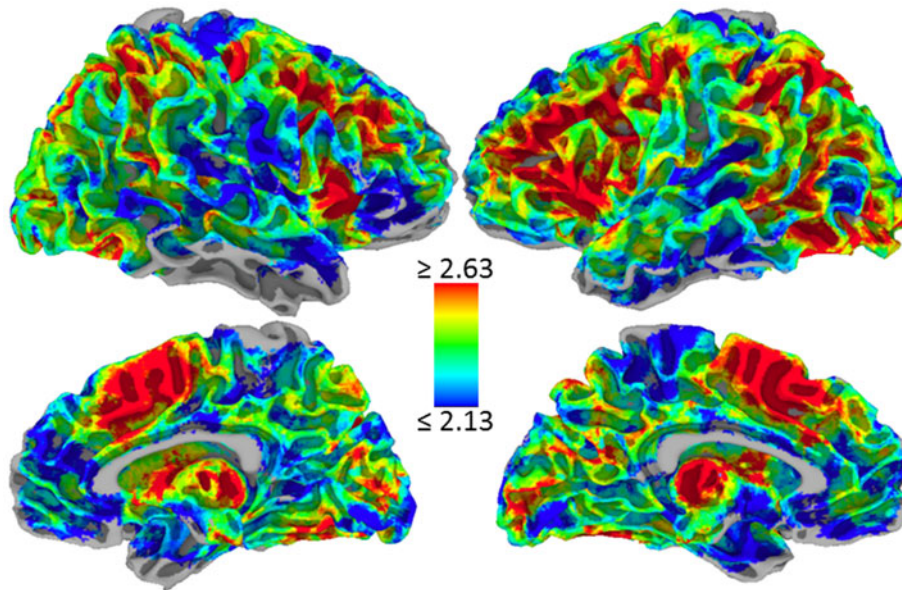


Figure 14. Functional diversity map. Areas of higher functional diversity are shown in warm colors, and areas of lower diversity are shown in cool colors (color bar represents diversity Shannon entropy values). Locations without colors did not have sufficient findings for the estimation of diversity. Adapted with permission from Anderson et al. (2013).

family of (possibly related) domains. Finally, the framework can be extended to networks, provides a way to compare them as described next, and to advance our understanding of the properties of constituent nodes (see Anderson et al. 2013).

7.5. Comparing brain networks

In several instances, investigators have proposed closely related networks (for example, “dorsal attention” and “executive control”), raising the possibility that they could be closely related, or possibly the same except for a change in label. Thus, developing tools that help characterize and understand brain networks is of great relevance and could help reveal principles of organization.

With this in mind, we asked the following question (Anderson et al. 2013): What is the relationship of the functions of regions belonging to a given network? One approach is to evaluate how homogeneous fingerprints are in a network. In other words, are fingerprints from the regions of network *X* more similar to each other than to those of regions from network *Y*? In our investigation, we chose to not investigate a unique set of networks, but instead considered possibly related (or even closely related) networks defined by different research groups and approaches, including meta-analysis, resting-state, and task-based approaches. To contrast brain networks to each other in terms of the functional fingerprints of the component regions, we employed a multivariate test based on “statistical energy” (Aslan & Zech 2005). Interestingly, several network pairs were found to be only modestly distinct (e.g., dorsal and ventral attention networks). Moreover, some of the networks that have been distinguished from one another in the past were not strongly distinct (e.g., the fronto-parietal “adjust control” network and the cingulo-opercular

“maintain task set” network described by Dosenbach and colleagues 2008).

We also evaluated the *assortativity* of the regions within networks, where assortativity refers to the tendency of “like to connect with like” (e.g., Christakis & Fowler 2007). Functional fingerprints within an assortative network would be relatively similar to each other and relatively dissimilar to fingerprints from other networks. Interestingly, we observed several levels of assortativity, suggesting that existing networks are composed of nodes whose functional repertoire varies in their homogeneity. In fact, one version of the task-negative network tended to be *disassortative*, namely, its regions tended to be more *dissimilar* to each other than to those of other networks, consistent with the notion that task-negative networks are relatively heterogeneous (Andrews-Hanna et al. 2010).

8. Conclusions

As I reflect on the network perspective described in chapter 8, five significant implications come to mind. First, given the extensive interactions between brain territories, emphasis shifts from attempting to understand the brain a region at a time to characterizing how coalitions of regions support the mind-brain. And because brain regions are not the unit of interest, they should not be viewed as “cognitive” or “emotional.” This stands in sharp contrast to the traditional view, which sees regions whose function involves homeostatic processes or bodily representations as emotional, and those less aligned with such operations as cognitive.

Second, considered from the network perspective, the architectural features of the brain provide *massive* opportunity for cognitive-emotional integration, encompassing *all* brain territories. For example, extensive communication between the amygdala and visual cortex exists. Thus, visual processing takes place within a context that is defined by

signals occurring in the amygdala and related brain regions (e.g., orbitofrontal cortex), including those linked to affective significance. In this sense, vision is never *pure*, but only *affective* vision. A similar point can be made for other sensory modalities. Cognitive-emotional interactions also abound in the PFC, which is commonly described with reference to abstract processes. More generally, given inter-region interactivity, and the fact that networks intermingle signals of diverse origin, although a characterization of brain function in terms of networks is still needed, the networks themselves are best thought of as neither “cognitive” nor “emotional.”

Third, regions traditionally viewed as central for affective processing appear to be extremely well connected (Ch. 9), which suggests that they have at times important “near-global” roles and that this may be a central feature of their class. But they are not the only regions with high connectivity: We encounter highly connected regions throughout the brain, including occipital, temporal, parietal, and frontal lobes, in addition to insula, cingulate, thalamus, and other regions at the base of the brain.

Fourth, the network perspective reminds us that emphasizing only interactions between brain regions that are connected by direct, robust structural connections is misleading. The strength of functional connectivity is equally important and at times (frequently?) will deviate from the strength of the structural connection. Architectural features guarantee the rapid integration of information even when strong structural connections are not present – and support functional interactions that will vary based on context. A case in point is illustrated by the “one-step” property of amygdala–PFC connectivity (i.e., amygdala signals reach nearly all prefrontal regions within a single connectivity step in the PFC), which allows the amygdala to engage in functional interactions with lateral PFC regions not heavily connected to it (see Averbeck & Seo 2008).

And, fifth, the insights gained from adopting a network perspective suggest that the mind-brain is *not* decomposable in terms of emotion (or motivation) and cognition. In other words, the neural basis of emotion and cognition should be seen as governed less by properties that are intrinsic to specific sites and more by interactions among multiple brain regions. In this sense, emotion and cognition are *functionally integrated systems*, namely, they continuously impact each other’s operations.

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Open Peer Commentary

Cognition as the tip of the emotional iceberg: A neuro-evolutionary perspective

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Abstract: We emphasize the importance of a neuroevolutionary perspective in moving beyond the cognition-emotion dichotomy. Cognitive behavior depends on cortical structures firmly rooted in the emotional brain from which they have evolved. As such, there cannot be cognition without emotion. Endocrine regulation of amygdala connectivity, a neural “switch” between impulsivity and deliberation, further underscores the phylogenetic impossibility of a cognition-emotion dichotomy.

In *The Cognitive-Emotional Brain*, Pessoa (2013) confronts the reader with the richness of what human neurosciences have achieved in the past decades and what these achievements imply for our understanding of human behavior and its neural underpinnings. A central aim of his book is to show that the often-applied conceptual dichotomy between “emotional” and “cognitive” brain regions is an incorrect view of how the brain is organized. Pessoa brings forth an abundance of studies showing that the neural substrates of cognition, on the one hand, and emotion, on the other hand, are largely shared, and by no means mutually exclusive. According to Pessoa, the brain should be understood from a network perspective: The function of the brain depends on its intrinsic connections rather than on specified brain modules. As such, Pessoa’s view concurs with previous critiques of a modular brain (Panksepp & Panksepp 2000; Prinz 2006b) and with the currently popular idea that, more so than brain regions alone, it is the neural connections between these regions that are of main interest (Seung 2012; Sporns 2010). Although we appreciate the breath of research addressed by Pessoa to convince his audience (and he surely convinced us), we were surprised to find that the book lacks a neuroevolutionary approach in describing brain function. We think this is a missed opportunity because a neuroevolutionary perspective illustrates why the distinction between emotion and cognition lacks theoretic ground and, thus, explanatory value.

In the human lineage, the most striking neural development is the vast increase in size of the neocortex. Evolved from the frontal part of the forebrain, the neocortex overlays the brainstem and limbic system, which consists of a set of brain regions (e.g., the amygdala and hypothalamus) shared by all mammalian species (MacLean 1990). The development of the anterior and dorsal part of the prefrontal cortex enabled people to mentally represent abstract information and to inhibit prepotent action tendencies, which gave rise to cognitive capacities such as foresight, planning, and selection of different behavioral responses. Together with increased linguistic capacities, this cortical development opened the door to modern culture (Munakata et al. 2011; Wilson 1998). However, the vast majority of the human cerebral cortex remains involved in unconscious processing of information from the environment and the viscera, which, through constant communication with phylogenetically older regions of the brain, can change our behavior without conscious deliberation (Damasio 2010). The neocortical expansion thus facilitated highly complex capacities often termed “cognitive,” but these capacities are still firmly rooted in the largely unconscious emotional brain. As such, cognition can be seen as the tip of the emotional iceberg. By definition, evolution builds on what is already there and is incapable of fundamental design changes in complex organisms. Thus, from a neuroevolutionary perspective there is not only no cognition without emotion, but this insight also provides the theoretical grounding for a network organization, instead of modular organization, of the brain.

A neural substrate that intriguingly exemplifies this mechanism of cumulative adaptation is the amygdala. The amygdala has often

been regarded as a single subcortical structure, but animal work and recent advances in neuroimaging techniques show this view to be incorrect. In fact, the amygdala consists of many nuclei that resemble either subcortical (central and medial amygdala nuclei, CMA) or cortical (lateral and basolateral amygdala nuclei, BLA) cytoarchitecture. Considering the amygdala's location and structure, we believe it is the perfect candidate to integrate what Pessoa describes as "cognition" and "emotion." Although Pessoa elaborates on the amygdala's heterogeneity, he seems to struggle to incorporate this feature in his network perspective of the brain. We believe that a neuroevolutionary view on amygdala functions will remedy this issue.

In terms of motivated behavior, two major amygdala network models can be identified. The first is a parallel model in which the cortical (BLA) and subcortical (CMA) amygdala respectively drive instrumental and impulsive goal-directed behavior through their projections to striatal and prefrontal structures (Balleine & Killcross 2006; Phillips et al. 2003). Second is a serial model in which information flows from BLA to hypothalamus and brain stem via CMA regions, which drives reflexive vigilance and fight-or-flight behavior (Whalen & Phelps 2009). Recent evidence also indicates that the BLA not only feeds the CMA's initiation of vigilance but also exerts opposite influence that can reduce innate fear (Macedo et al. 2006; 2007; Tye et al. 2011). Functional and structural MRI studies confirm these distributed networks of amygdala subregions in humans (e.g., Bickart et al. 2012). Recent studies also confirmed the models' behavioral consequences, demonstrating that humans with focal damage to the BLA show increased fear vigilance (Terburg et al. 2012b) and more impulsive socioeconomic choices (van Honk et al. 2013). Hence, a view emerges where the "cortical" amygdala (BLA) drives instrumental behavior and the "subcortical" amygdala (CMA) drives impulsive behavior. Thus, when combining the neuroevolution of the amygdala with recent evidence on its function and connectivity, the amygdala can be considered a key component of Pessoa's network perspective as a neural switch between impulsivity and deliberation. In this view, behavior cannot be considered distinctly "cognitive" or "emotional," but will always be a cognitive-emotional synergy given the evolutionary organization of the brain.

This view of the amygdala as a neural "switch" extends even further when considering the endocrine regulation of amygdala function and connectivity (Bos et al. 2012). For example, the steroid hormone testosterone and the neuropeptide oxytocin have opposite effects on amygdala output. When people are under direct social threat, testosterone decreases amygdala-cortical connectivity patterns and upregulates amygdala-subcortical routes (van Honk et al. 2011b; Terburg & van Honk 2013), whereas oxytocin reduces amygdala output to the brainstem (Stoop 2012) and increases amygdala-cortical coupling (Riem et al. 2011). Moreover, both hormones have been involved in sexual and reproductive behavior in animal species living as long as 450 million years ago (Bryan et al. 2008; Goodson & Bass 2001), and these functions have been conserved in humans. In line with the evolutionary development of the amygdala and the neuroendocrine system, the behavioral impact of these hormones has extended to more diverse human behavioral repertoires. Following evidence that testosterone promotes social, but not predatory, aggression (Archer 2006), recent testosterone studies have focused on human dominance behavior. Being the leader of the pack provides evolutionary advantages by increasing chances of survival, and testosterone indeed not only promotes emotional-reflexive (Terburg et al. 2012a) but also cognitive-strategic (Eisenegger et al. 2010; van Honk et al. 2012) dominance behavior. In addition, testosterone in humans has recently been shown to affect even more complex social behaviors; for example, it reduces interpersonal trust (Bos et al. 2010), reduces cognitive empathy (van Honk et al. 2011a), and promotes utilitarian decision making (Montoya et al. 2013). As predicted based on its opposite effects on amygdala function, oxytocin has opposite effects

to those of testosterone; it increases interpersonal trust (Kosfeld et al. 2005) and increases cognitive empathy (Domes et al. 2007). Thus, the neuroendocrine messengers that have evolved to serve basic emotional processes throughout the animal kingdom have come to serve complex, allegedly "cognitive," functions in humans. They do so by acting on ancient brain "hubs" and "switches," thereby leaving no brain areas unaffected.

In agreement with Pessoa, this literature highlights the difficulties, if not impossibility, of defending a view in which parts of the brain are discussed in terms of their unique functions. We suggest that a neuroevolutionary approach in discussing brain function provides for a theoretic reason for rejecting the "emotion-cognition" dichotomy and also provides a theoretical grounding for a network organization, instead of a modular organization, of the brain. In addition, Pessoa (2013) notes that "more than making the case *against* dissociating [emotion and cognition], one of my goals in this book is to move beyond the debate and to illustrate the many ways in which emotion and cognition interact and in fact are integrated" (p. 3). We fully agree with Pessoa that the emotion-cognition dichotomy is one in need of revision, but we wonder if Pessoa's focus on cognition-emotion interactions might inadvertently keep the false dichotomy alive. We believe that a neuroevolutionary perspective, which sees cognition as the tip of the emotional iceberg, provides a solution to definitely move beyond this debate and allows us to focus on explaining *how* the brain brings forth behavior, *irrespective* of the terminology that is used to describe this behavior.

On emotion-cognition integration: The effect of happy and sad moods on language comprehension

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Abstract: I comment on Pessoa's (2013) idea that the interaction between emotion and cognition cannot be reduced to mutual interference. As an example that bolsters Pessoa's position, I discuss the effects of happy and sad moods on discourse and sentence comprehension. I distinguish between the effects of moods elicited without participants' knowledge (incidental) and moods elicited with participants' contribution (constructed).

In *The Cognitive-Emotional Brain*, Pessoa (2013) effectively argues against the traditional view on which interactions between emotion and cognition in the brain are interpreted exclusively in antagonistic terms. According to this traditional view, emotional and cognitive brain systems are distinct; they compete for processing resources and lead to mutual suppression. Pessoa argues that this view is restrictive and does not capture the many possible ways in which emotion and cognition actually interact in producing behavior. His view, based on accumulating evidence that emotion and cognition share brain systems (especially those identified as informational hubs, e.g., amygdala, medial prefrontal cortex, anterior insula), is that emotion and cognition can interact in ways that result in more efficient behavior.

I agree with the gist of this argument. My aim here is to relate this account to complementary research on affective states and cognitive processes that are not considered in the book and that can strengthen Pessoa's position. One interesting case, for example, lies in the effect of mood on language comprehension, especially at the discourse and sentence level.

Pessoa's account is based mainly on research about processing emotional stimuli, focusing primarily on visual perception and executive functions and touching upon trait anxiety and depression. The cases Pessoa considers are therefore those in which emotion has a strong, rapid bottom-up effect (emotional stimuli) or has a persistent and prolonged top-down effect (trait anxiety and depression). Research on the effects of experimentally induced happy and sad moods on cognitive processes has shown that moods can influence performance when they are *preexisting* and *unrelated to the task at hand* and, most importantly, when people are *unaware of experiencing them* (for a review, see Martin & Clore 2001). These features put mood in the position to exert an influence on cognitive processes for longer periods than the emotions elicited by experimental stimuli (such as a shock or a disgusting picture). Mood's effect also differs from that of emotional stimuli in that it is top-down. At the same time, it differs also from the top-down effect of trait anxiety and clinical depression: Because mood waxes and wanes easily in everyday life, it has less extreme and persistent effects on cognition. We discuss here research on the effects of mild happiness and mild sadness, as examples of moods that listeners and readers may be experiencing during language comprehension.

Experimentally induced moods can have a strong effect on a wide range of high-level cognitive functions (e.g., judgment, memory, executive functions; for reviews, see Clore & Huntsinger 2007; Martin & Clore 2001). The fact that mood can influence integration processes during discourse comprehension is a recent finding; language has been usually studied as one of the cognitive functions most impermeable to affect, at least at the sentence and discourse level.

Recent research has found that incidental mood can have a strong and rapid influence on the way discourse is understood. Incidental mood is elicited with a procedure of which participants are not aware and that results in mild affective changes escaping participants' awareness (e.g., Koch et al. 2013; Matovic et al. 2014). Behavioral evidence has shown that readers induced into a happy or sad incidental mood judge a positive or a negative story ending as more surprising when its valence mismatches that of the mood (Egidi & Gerrig 2009). This is seen not only in explicit behavioral evaluations after reading, but also in neural responses during listening to the story endings (Egidi & Nusbaum 2012). Mood interacts with linguistic content as early as 400 ms after the presentation of a critical word. The study by Egidi and Nusbaum (2012) examined the effect of happy, sad, and neutral moods on the comprehension of a positive and negative ending that concluded a very short story. Mood modulated the auditory N400 effect, with a pattern of increased N400 for story endings mismatching the valence of the mood (for consistent results; see also Chung et al. 1996). The N400 pattern for the happy and sad group further differed from that of the neutral mood group. Importantly, the effect of mood in evaluations and N400 effect occurred when positive and negative endings were equally consistent and plausible (Egidi & Gerrig 2009; Egidi & Nusbaum 2012). A study by van Berkum and colleagues (2013) further found a reduced N400 for sad mood (vs. happy mood) after verbs that create an implicit causality bias (e.g., *Carice annoyed Tom because he/she repeatedly had to correct her mistakes*). At the sentence level, Federmeier et al. (2001) also examined the effects of positive and neutral moods on semantic organization by using sentence pairs. In this study, positive mood, as compared to neutral mood, was associated with a decrease in N400 amplitude between unexpected items of different categories (e.g., *They wanted the hotel to look more like a tropical resort. So along the driveway they planted rows of pines/tulips*).

Taken together, these results highlight a very direct effect of mood on cognition, with no intentional component. In these cases, the effect of mood cannot therefore be attributed to motivational or attentional differences. Consistent with Pessoa's position, the influence of incidental mood suggests that the concepts of selection and competition for resources cannot

easily explain the interaction between emotion and cognition, and that low arousal is not necessarily linked to decrement in performance. Instead, the impact of mood may be that of adjustment, as in the case of responding to positive and negative endings as more or less consistent depending on mood (Egidi & Gerrig 2009; Egidi & Nusbaum 2012). However, general interference cannot be completely ruled out: Results such as the mood-dependent reduced sensitivity to implicit causality (van Berkum et al. 2013) suggest that interference is a possible effect of mood on language.

At the sentence level, recent behavioral research has shown that incidental moods influence participants' ability to discriminate between ambiguous and unambiguous sentences (Matovic et al. 2014). Other studies have also found evidence of mood modulations of linguistic processes that typically elicit N400 and P600. These studies have capitalized on a known tendency of happy and sad moods to promote different processing strategies. Several behavioral studies of social judgment and memory have in fact found that happy mood promotes a more global, top-down and heuristics-based type of processing, whereas sad mood promotes more local, bottom-up, and analytic type of processing (e.g., Bless 2000; Clore & Huntsinger 2007; Fiedler 2001). Importantly, however, this effect is more often obtained when participants are induced to experience a certain mood by taking active part in changing the way they feel and maintaining it over time. Typically, participants are presented with a happy or sad stimulus (or are asked to think of something happy and sad) and are instructed to allow the stimulus to put them in a certain mood and to maintain that mood throughout the experiment (e.g., Chwilla et al. 2011; Vissers et al. 2010; 2013). In this way, mood is voluntarily constructed and therefore likely to influence cognition through a different avenue than incidental mood. Mediating factors such as (1) awareness of being in a certain mood, (2) the strategies participants adopt to maintain a certain mood, (3) the potentially different ease with which different moods can be maintained, and (4) the constant attention participants pay to how they feel may result more easily in the adoption of different processing strategies than does incidental mood.

In the literature on sentence processing, this indirect effect of mood has been studied on the consistency effect elicited by reading high and low cloze-probability sentences (e.g., *the pillows are stuffed with feathers/books*; Chwilla et al. 2011). It was found that the N400 effect was differently distributed depending on participants' mood. Vissers and colleagues (2010; 2013) also found that the effect of constructed mood can modulate syntactic processing, as seen by a different amplitude and scalp distribution of the P600 in reading subject-verb disagreements and apparent syntactic anomalies (as a result of unusual semantic context: e.g., *the fox the poachers hunts/hunt*). Interestingly, no effects of mood on syntactic anomalies was found when a less explicit mood manipulation was used (van Berkum et al. 2013), thus suggesting that some aspects of linguistic processing may be permeable to mood only when participants are made consciously aware of their mood via mediating factors (such as those mentioned above). In general, motivational and attentional explanations of the kind discussed by Pessoa are definitely applicable to the research on the effect of constructed mood on language.

With respect to the neural architecture underlying the effect of mood on discourse and sentence comprehension, there is only one study on this issue: an fMRI experiment examining the effects of incidental happy and sad mood on consistent and inconsistent story endings (Egidi & Caramazza 2014). The study's results are consistent with the notion that mood and language interact to create emergent activation patterns rather than attenuating or increasing activity in fixed networks. Specifically, a contrast between story endings that were consistent or inconsistent with prior context showed that happy and sad mood moderated inconsistency detection, but did so in different networks. For example, happy mood increased sensitivity to inconsistency in regions often linked to language comprehension, whereas sad mood increased

sensitivity to inconsistency in other networks, less frequently linked to language processing. With respect to Pessoa's position, these results show that incidental mood can fundamentally alter the baseline functioning of linguistic processes, by restructuring the brain networks that perform that function. In this sense, these results are consistent with Pessoa's view of emotion-cognition relation as integration.

To conclude, research on the effects of mood on discourse and sentence comprehension shows that mood does not only interact with language processing in terms of interference or enhancement of function, but that it also fundamentally alters how linguistic processes are performed. This is especially seen in modulations of fast ERP responses to inconsistencies and linguistic anomalies and in mood-dependent reorganizations of the brain networks that perform linguistic functions. These results constitute a constructive addition to Pessoa's account, as they both increase its scope and highlight an additional way of emotion-cognition interaction that is not mentioned in the book.

Surprise as an ideal case for the interplay of cognition and emotion

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Abstract: The target article is a timely exposition on the impact of how emotion and cognition interact, a specifically important issue in surprise research. Psychologists debate whether disconfirmed expectations or sense-making processes determine surprise levels experienced for an event. We posit that, in surprise, cognition and emotion are intertwined, making it an interesting test case for the proposals in this article.

In *The Cognitive-Emotional Brain*, Pessoa (2013) highlights the interplay of emotion and cognition in the brain. When one considers the panoply of human emotions, the emotion and cognition in surprise seems an ideal test case for this interplay.

Surprise has been intensively researched since Darwin's time, perhaps because it involves this interesting mixture of emotion and cognition. Although originally conceived of as a "basic emotion" (e.g., Darwin 1872; Ekman & Friesen 1971; Izard 1977; Plutchik 1991; Tomkins 1962), more recently surprise has been reappraised more as a cognitive state because, unlike most emotions, it can either be positively or negatively valenced (Ortony & Turner 1990). Surprise clearly involves an emotional reaction (often accompanied by a startle response), but it also seems to service a strategic, cognitive goal, as it directs attention to explain why the surprising event occurred and learn for the future (e.g., Foster & Keane 2013; Macedo 2010; Maguire et al. 2011; Ranganath & Rainer 2003).

Attentional models of learning suggest that when events are surprising, they collect and focus neural resources that enhance the processing of the event and drive learning (as in, for example, the Pearce-Hall model; Pearce & Hall 1980; see also Hayden et al. 2011; Roesch et al. 2012). In neural models of surprise in learning and novelty, it is predominantly suggested that surprise arises from comparative processes between what was expected to occur and what actually occurs (e.g., Hayden et al. 2011; Roesch et al. 2012; Wessel et al. 2012). Many cognitive theories of surprise take a similar view – that surprising events are low probability events in the context of the event sequence, that are schema discrepant, or conflicting with previous expectations (e.g., Meyer et al. 1997; Reisenzein & Studtmann 2007; Schützwohl &

Reisenzein 1999; Teigen & Keren 2002; 2003). However, recent theories of surprise have placed a greater emphasis on the "sense-making" aspects of surprise (e.g., Foster & Keane 2013; Kahneman & Miller 1986; Maguire & Keane 2006; Maguire et al. 2011; Pezzo 2003). These sense-making theories argue that surprise is fundamentally about understanding an abnormal event, about finding an explanation for the event's occurrence. For example, the recently developed metacognitive explanation-based theory of surprise (Foster & Keane, under review), proposes that the difficulty of explaining an event informs the emotional feeling of surprise.

As Pessoa discusses at a more general level, the dichotomising of systems into a dual-process model with separable mental systems consisting of automatic versus controlled processes is questionable, whereas a continuous framework seems optimal. In the phenomenon of surprise, this continuous framework is consistent with sense-making accounts that emphasise understanding, involving the mechanism of explanation, with the feeling of surprise arising from the ease/difficulty of this understanding process. Traditionally, explanation is seen as playing a role in building causal models or predictive schemas to deal with future events (Heider 1958; Lombrozo & Carey 2006). Apart from having a predictive role when a new situation is initially encountered, however, explanation may also serve to help people decide how information should be weighted or how attention should be allocated, even as an event is occurring (Keil 2006; see also Foster & Keane 2013). So, for this cognitive emotion, there is a true interaction between cognition and emotion, which seem to be intrinsically linked in the experience of surprise.

This focus on the more cognitive, explanation-based treatment of surprise has yet to be fully explored at a neurological level. However, Pessoa's suggestion that the amygdala is involved in much more than "fear," that it has novelty, salience detection, and information gathering functions, identifies it as a candidate structure playing a role in surprise. In surprise research, it has been found that functioning of the amygdala central nucleus is important in learning (e.g., Belova et al. 2007; Lin & Nicolelis 2008), but it seems that the functioning of the amygdala may only be critical at the time that the surprise is initially experienced, whereas functioning of other areas, such as the cholinergic neurons in the subthalamic substantia innominata/nucleus basalis magnocellularis, are critical when that enhanced associability gained from surprise is seen in more rapid learning (Holland & Gallagher 2006).

Indeed, further hints about the importance of an interplay between cognition and emotion in surprise can be gleaned from studies of two neural mechanisms involved in processes that have been linked to surprise. These are the P300, a positive-going wave in the human ERP appearing 250–500 milliseconds after a stimulus, which is thought to respond to contextual novelty, and the N400, a negative-going wave in the human ERP which peaks around 400 milliseconds post-stimulus, and which is associated with the processing of meaningful stimuli (Coulson & Kutas 2001), particularly to words and pseudowords. The N400 is additionally thought to respond to stimulus novelty (for a review, see Ranganath & Rainer 2003) and is especially large in response to semantic violations. It should be noted that the P300 is sometimes split into two components, P3a and P3b; of these, the P3b appears to be more linked to surprise (e.g., Kopp & Lange 2013). As an example of this interplay in surprise, P300 amplitude, although responsive to contextual novelty, is also thought to be associated with "significance" (Donchin 1981), "information value" (Sutton et al. 1965), and "meaning" (Johnson 1986), all of which are encompassed by the proposal that it is a manifestation of "context-updating" or "understanding" during interaction with the environment (Ferrari et al. 2010). Motivationally significant stimuli, including emotionally valent stimuli, are associated with larger P300s than motivationally insignificant or emotionally neutral stimuli (Keil et al. 2002), and studies involving feedback stimuli about monetary gains or losses have shown that the P300 is sensitive to the absolute magnitude of the feedback

outcome, for both gains and losses (e.g., Yeung & Sanfey 2004). These effects of subjective probability and motivational significance on P300 amplitude are modulated by the amount of attention paid to the stimulus, particularly if the subject is engaged in a secondary task that poses increasing perceptual demands (cf. Kok 2001). So, findings for the P300 seem to reflect that it is influenced by both cognitive and emotional components.

A reduction in N400 amplitude appears to reflect ease of processing, or ease of integration after-the-fact; more colloquially, “easier understanding” (e.g., Coulson & Kutas 2001; Eddy et al. 2006; Kutas & Federmeier 2000). It has been suggested that the N400 is larger when integration is relatively more difficult (Eddy et al. 2006). Consistent with our approach, which encompasses both the emotional and cognitive aspects of surprise as arising from a process of attempting to explain the event, it has been suggested that in joke processing, positivities (which have been argued to reflect the more emotional surprise component) and sustained negativity of the N400 (which has been proposed to index a more cognitive reinterpretation of information) can all occur within the same time window (Coulson & Kutas 2001). So, again, the N400 seems to be influenced by emotional factors as well as cognitive factors, during the same time frame, reflecting the interplay of these aspects in surprise.

The target article thus opens up exciting possibilities for future work on surprise. Neuroscientific research assessing the impact of surprise still tends to treat it as merely the disconfirmation of expectations, whereas recent theories suggest that this traditional treatment is too simplistic and that surprise should instead be conceptualised more as a feeling that arises from cognitive difficulty in explaining why an event occurred (see Foster & Keane 2013; under review). More specifically for this article, we feel that surprise could be an interesting test case for many of Pessoa’s proposals, such as his discussion of the differential possibilities of the relationship between cognition and motivation, and, more generally, for his position that cognition and emotion are fundamentally linked, as we feel the interaction between the intrinsic motivational, cognitive, and emotional components may guide our behaviour both during and in response to surprising events.

Enactive neuroscience, the direct perception hypothesis, and the socially extended mind

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Abstract: Pessoa’s *The Cognitive-Emotional Brain* (2013) is an integrative approach to neuroscience that complements other developments in cognitive science, especially enactivism. Both accept complexity as essential to mind; both tightly integrate perception, cognition, and emotion, which enactivism unifies in its foundational concept of sense-making; and both emphasize that the spatial extension of mental processes is not reducible to specific brain regions and neuroanatomical connectivity. An enactive neuroscience is emerging.

Enactivism has been gaining in popularity in a variety of disciplines over the last couple of decades (Di Paolo & Thompson 2014). Its discourse is centered on a cluster of concepts – autonomy, sense-making, emergence, embodiment, and experience (Di Paolo et al. 2010). Briefly, *mind* is defined as meaningful activity in the world; it is an autonomous process of sense-making embodied in self-sustaining neural, bodily, and sensorimotor dynamics under precarious far-from-equilibrium conditions. Speculations

about internal mental representations are rejected in favor of investigations of the complex dynamics that structure a subject’s lived (phenomenological) and living (biological, i.e., both neural and bodily) existence (Thompson 2007).

Nevertheless, a specifically enactive neuroscience is still outstanding. To be sure, some of its key concepts can be traced to the neuroscientific research done by Maturana and Varela in the 1960s and 70s. And after the first comprehensive statement of the enactive approach (Varela et al. 1991), Varela continued to promote a systems approach to neuroscience (e.g., Varela et al. 2001). Moreover, Varela’s proposal of integrating this approach with a disciplined study of first-person experience turned into one of its core methods: neurophenomenology (Gallagher 2009). Such methodological recommendations are valuable, but they are not an enactive theory of the brain.

This striking omission has not gone unnoticed. For example, proponents of the predictive processing framework, which aspires to a unified theory of the brain (Friston 2010), are taking advantage of this lacuna by attempting to subsume enactivism under its way of thinking (e.g., Clark 2012; Seth 2014). Although this takeover move is resisted by some enactivists (Froese & Ikegami 2013; Roesch et al. 2012), as yet there is no clear alternative proposal.

I suggest that Pessoa’s (2013) integrative approach provides much needed steps in the right direction. He avoids two undesirable extremes that typically characterize other approaches. He rejects the tendency, prevalent in neuroimaging research, to reduce aspects of mind to specific brain regions (pp. 194–95). And neither does he reduce the workings of the brain to one general abstract principle (e.g., a free-energy principle). Instead, Pessoa emphasizes that there is a diversity of neural structures and processes at play; that structure and function are mutually dissociable; and that mental processes are realizable in multiple ways by distributed networks and unavoidably context dependent. This middle way between the extremes of anatomical specificity and computational generality matches with enactivism’s insistence on a systems theoretic approach that nevertheless remains grounded in the concreteness of the living organism. And Pessoa is in favor of developing stronger links between neuroscientific data and subjective experience (p. 116). I am also intrigued by several more specific convergences between his approach and the enactive approach.

Pessoa interprets the findings of cognitive neuroscience as demonstrating that perception, cognition, emotion, and motivation do not refer to essentially distinct categories. Instead, they are overlapping aspects of a complex network of mental processes in which one aspect can temporarily become more expressed than the others depending on the circumstances, but in which none can be completely isolated from the others. The enactive approach has come to the same conclusion on the basis of theoretical considerations stemming from the philosophy of the organism and phenomenology of the body, which is why the notion of sense-making has become one of its core concepts (Thompson 2007). Briefly, sense-making refers to the process by which an organism enacts a meaningful point of view on the world, which always contains a mixture of sensation, pre-reflective interpretation, and valuation. Accordingly, every organism is situated in what von Uexküll (1934/1957) once called an *Umwelt*: a concrete context of significance defined by affordances for interaction, which are shaped by the environment but also by each organism’s embodiment, knowledge, and motivations (goals, needs, desires). This supports Pessoa’s contention that “vision is never *pure*, but only *affective*, vision. A similar point can be made for other sensory modalities” (p. 257).

As Colombetti (2014) has argued extensively, an important implication of the enactive theory of sense-making is that affectivity is an essential aspect of mind, and that this primordial affectivity provides the foundation for the origins of more specific emotions, moods, and values. In the words of Varela and Depraz (2005, p. 61): “emotions cannot be seen as a mere ‘coloration’ of the

cognitive agent, understood as a formal or un-affected self, but are immanent and inextricable from every mental act.” Enactivism therefore provides a suitable interpretative framework—for example, for explaining the finding that emotional networks are among the most widely connected in the brain (Pessoa 2013, p. 229). In addition, the substantial connections from brain regions implicated in cognitive and emotional processing to even the earliest sensory regions, such as projections from the amygdala and the pulvinar to visual cortex, are to be expected if we primarily live in a meaningful world, and not in some abstract model consisting of meaningless physical facts, as assumed by classical cognitive science. Enactive theory may therefore help us to better understand the role of “nonstandard” pathways to visual perception (Pessoa 2013, pp. 244–46).

This convergence also provides an opportunity for neuroscience to help resolve a puzzle that has emerged for enactive theory. In short, if sense-making is the default mode of being in the world, such that an organism’s point of view is saturated with affordances that are meaningful in terms of its potential actions, then how do we explain the emergence of the detached observer’s stance and dispassionate reflection, that is, precisely the hallmarks of higher-level cognition (Cappuccio & Froese 2014)? The problem is no longer just to understand how perception, cognition, and emotion are integrated, but likewise under what conditions they can become temporarily separated. This task becomes especially pressing when it comes to explaining the unusual requirements of sense-making in the context of symbolic culture.

For example, when we see a representation of a pipe, as in Magritte’s famous painting, what we perceive is a presentation of an imagined pipe that is in fact objectively absent (Seth 2014). But from the point of view of most animals (as long as they have not been enculturated), such a representation is experienced differently: either the presented is taken as objectively present (i.e., a pipe is seen, as a result of a failure of veridical perception), or the presented is not even recognized as such. Phenomenologically, to experience a representation *as* a representation, one has to detach from one’s immediate preoccupations with the world so as to bring the underlying material substrate of the potential representation to attention, while neutralizing any preexisting affordances of that medium, in order to then imbue it with renewed meaning in accordance with cultural norms. The revolutionary human abilities based on symbolic cognition, particularly language and writing, are only achievable with this tight yet flexible integration of perceptual, cognitive, and emotional processes. Pessoa (2013) did not systematically review species-specific differences of neural integration, but we can hypothesize that in humans these processes are more flexibly integrated. Findings worthy of a closer look include the malleable relationship between prefrontal cortex and the amygdala (p. 115) and the relative isolation of prefrontal cortex from sensory stimuli (pp. 233–34; 255–56).

Pessoa’s work also nicely complements the enactive approach to social cognition, which includes the phenomenological claim that we normally directly perceive aspects of others’ minds in their bodily expressions; for example, happiness in another’s smile. This “direct perception hypothesis” (Froese & Leavens 2014) stands in contrast to standard theory of mind accounts, which start from the assumption that others’ subjective states are perceptually inaccessible and must therefore be inferred (or simulated) based on perception of purely objective surface behavior. Unless we are referring to the abnormal social experience of certain people with schizophrenia and autism spectrum disorder, standard approaches are not phenomenologically convincing (Froese et al. 2013). But it is easy to see how they theoretically made sense when combined with the premise that perception, cognition, and emotion are distinct modules: perception could only ever deliver neutral physical facts, such that cognition then has to figure out what is going on, after which it can evoke an emotional response. However, if perception, cognition, and emotion are tightly integrated, as Pessoa asserts, then there is no longer

any reason to assume that perception cannot directly present us with others’ states of minds in their meaningful bodily expressions. Conversely, the direct perception hypothesis helps us to better understand the role of cognitive-emotional feedback to early sensory regions: it is required to constitute such a meaningful perceptual world.

Pessoa’s proposal also productively relates to another controversial theory of the enactive approach—namely that bodily and environmental (including social) activity can form a genuine part of mental processes (De Jaegher et al. 2010; Thompson 2007). On this view, the brain is conceived of as a “mediating organ” (Fuchs 2011) of embodied activity in the world rather than as its sole basis (Gallagher et al. 2013). Returning to an issue raised earlier, one criticism of recent attempts to formulate a predictive processing account of enactive perception is that the former is committed to the classical cognitivist assumption of brain-centered internalism (Di Paolo 2014; Froese 2014), which in the social domain equates with individualism. Admittedly, it is difficult to investigate a distributed view of the mind with the current tools of neuroscience, and even neurophenomenology has not always managed to avoid internalism (Beaton 2013). However, a more embodied and socially situated neurophenomenology seems possible (Desmidt et al. 2014; Froese et al. 2014).

Pessoa does not take an explicit stand with regard to the limits of mind, but I suspect that he might be sympathetic to this highly contextualized enactive view (see, e.g., p. 202). Crucially, he allows that functional connectivity can play a role in neural processes even in the absence of direct anatomical connectivity (pp. 148–49). It is only a small additional step to extend this concession to include some kinds of extra-neural processes as another type of functional connectivity. For example, there does not seem to be any principled reason for excluding bodily and environmental dynamics from neuroscientific explanations, because externally mediated activity can functionally connect effectors and sensors into a coherent sensorimotor system (Fig. 1).

Relatedly, it has been debated whether the direct perception hypothesis should be cashed out solely in terms of individuals, or whether social interaction can play a constitutive role as well. For example, when we share an intimate moment with a loved one, may we actually be sharing one experience co-constituted by networks distributed across two brains? Several authors have argued that the underlying dynamics of emotional episodes can span two or more individuals (Colombetti 2014, pp. 66–70), and Pessoa’s approach is consistent with this possibility. According to the enactive approach, not every kind of interaction is sufficient. Individuals must co-regulate their activities such that the

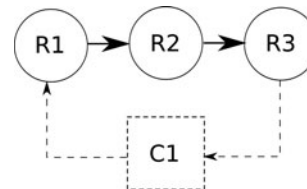


Figure 1 (Froese). Two indirect relationships between function and anatomical structure. According to Pessoa (2013, pp. 207–12), a functional relationship between two regions of the brain (R1 and R3) does not necessarily have to be supported by direct structural connectivity (solid arrows), because their functional connectivity can be mediated via structural connectivity through another region (R2). But other forms of mediation are conceivable, including dynamical routes via extra-neural context C1 (dashed arrows). Most straightforwardly, we can think of region R3 as the motor system, region R1 as the sensor system, and context C1 as the body situated in an environment. R1 and R3 are then also functionally connected by sensorimotor interactions.

conditions of success of their actions cannot be reduced to one individual (Froese et al. 2014), and the effects are further enhanced by emotional engagement (Schilbach et al. 2013). This is reminiscent of Pessoa's thinking about degrees of isolability and decomposability in neural networks (pp. 196–97); for example, that strong integration requires coupled systems that are strongly interacting. Moreover, measures of functional connectivity are considerably strengthened in affective versus neutral contexts (pp. 209–11). Thus, unless there is a principled reason for rejecting the application of Pessoa's approach to inter-brain integration, we can genuinely participate in each other's sense-making.

Integration of cognition and emotion in physical and mental actions in musical and other behaviors

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Abstract: Integration of cognition and emotion, discussed by Pessoa in *The Cognitive-Emotional Brain* (2013), is further illustrated by music. In music, I argue, this integration begins during mental control of the actions by which musical sounds are produced. Many emotional reactions to the music we hear are also strongly related to the actions by which musical sounds are produced. Studies involving music can further illuminate the integration of emotion and control of action throughout behavior.

The experience that music creates as we play it or listen to it (Dewey 1934/1980) has strong emotional components. How our brains connect music to emotion is less well understood (Juslin & Vastfjall 2008; Lindquist et al. 2012). But the pleasure that making music gives children can help to explain why they will work to develop music-making skills—skills whose learning can also affect broader skill development (Gardiner et al. 1996; 2000; 2003; 2008a; 2008c; Zuk et al. 2014).

Facial expressions (Ekman 1992) that communicate genuine emotion depend on direct involvement of emotion in the control of the expressive action (Damasio 2010). Music-making acts should be viewed in a similar way.

As I discussed previously (Gardiner 2012), Damasio's theory concerning emotion (1994/2005; 1999; 2010) seems especially relevant to the relationship of music and emotion. Damasio integrates evidence from James and Lange (1922) and Cannon (1929) with extensive, more-recent research to propose that emotion is deeply related to ongoing moment-to-moment activation and restoration adjustments of physiology responding to changing demands on body and brain. If one adds secondary and background emotions and mixtures that defy verbal classification to primary emotions such as fear and joy, normal experience shows no break, only changes, in emotion. *Feelings* make us aware of major features of our physiological emotional adjustments in ways that interact with our longer-term behavioral choices and even decision making and reasoning (Damasio 1999).

I will begin with several examples where activities of making music create emotional experience, then discuss emotional experiences while listening to music. Some of these examples will be more familiar than others.

Music making typically involves *rhythm* and always involves *tempo*, and these both affect emotional experience. The behavioral uses of rhythm in locomotion are especially relevant here. Reiterations within rhythmic forms can help an individual to coordinate muscular activities with more general physiological activation and recovery. Such integrated physiological coordination

can aid individual capability to continue rhythmic behavior over time. Relationship between music and locomotion was important to ancient Greeks (Sachs 1953). Putnam Aldrich taught that to the ancient Greeks, *rhythm* was verb: a way of moving through time (Aldrich 1958). The feelings we experience when walking rhythmically at *andante* rhythmic tempo, or playing music with such rhythmic tempo, include an awareness of the associated, unhurried and calm physiology of our body (Gardiner 2012). Slowing or increasing the tempo in rhythmical locomotion or in music can cause related changes in the emotional experience and a related sense of absence or presence of haste.

A more subtle change in experience related to rhythm can also be experienced in both locomotion and music making. In my daily walks, my progress seems less and less hurried as I change thinking of my individual stepping acts to mentally grouping them into sets of two, then three, then four. I notice my breathing slowing and presume that my heart rate changes as well, as my sense of haste decreases. Something analogous happens when I group the individual acts in music making into higher-order groupings, for example when called upon by rhythmic notation involving so-called *cut time* in the last movements of sonatas by Haydn, Mozart, or Beethoven. The decreased sense of haste experienced is useful in helping to more easily produce music that moves forward rapidly.

These examples only introduce the many ways in which rhythm has been developed to interact with emotion in music making.

A second type of contribution to emotional experience as music is produced comes from reaction to the specific sounds individually and in combination that are chosen to be used for musical purposes. I will focus here on sounds used most frequently within Western music. These either convey a transient percussive quality (e.g., as produced by clapping or by striking a drum) or, following a start transient, produce a continuing rhythmic vibration so rapid that individual vibrations do not reach awareness. But we perceive changes in main frequency of vibration as involving changes in perception of *pitch*. Other induced modes of vibration related to perceived *overtones* also affect the auditory experience. The percussive or pitch-bearing sounds have been produced vocally or by instruments in many different ways (Geiringer 1978; Sachs 1940/2006; 1943/2008) that can affect emotions differently. Here I will focus on choices of pitches for sounds from which music is built. The ratios of frequency between sounds when presented in sequence (during *melody*) affect a sense of direction of movement within the music, and also a sense of musical distance within perceived musical motion. These ratios of frequency also affect the quality and degree of *harmony* or *dissonance* as two or more sounds with the same or different pitches are presented at the same time. *Modes* and *scales* identify those pitch relationships that are allowed. The difference in emotional experience produced by combinations of musical pitches taken from a *major scale* and from a *minor scale* can be striking—major typically conveying most easily positive; minor, negative emotion. Hence, the first movement of Mozart's Piano Sonata KV 310 in A minor, written at the time of his mother's death, can convey anger and grief when played with the particular pitches of the A minor scale. But if the pitch values of only a few notes are changed slightly, as if the piece were written in A major, it would be essentially impossible to convey the same emotions available in A minor.

That music making depends on specific choices of sounds, and specific plans for organizing the production of these sounds over time is of course well understood. But emotions developed as music is performed do not come only from such basic features. As or still more importantly, they come from other details of the creational acts by which musical sounds are produced. Two performances of the same piece can express emotion very differently depending upon such other details.

In work begun in the 1970s and continued, Manfred Clynes has opened an extremely important window on the relationship of such details of music making to emotion (Clynes 1977; Clynes

& Nettheim 1982; Clynes & Walker 1982). Here, I can only introduce this work and discuss musical implications of his earliest observations.

Clynes developed a scientific instrument to study and compare the vertical and horizontal pressures as an individual produced a pushing gesture with the finger. He compared gestures produced with no specific emotion in mind with those made when subjects were asked to express a specific emotion through the action. He compared expressions of anger, hate, grief, joy, love, sex, and reverence. And he reported that as individuals indicated they were indeed experiencing and thus expressing the emotions through the pressing acts, the nature of records they produced took on characteristic shapes. The shapes were sufficiently different across emotions but similar across subjects that the associated emotion could be established from the records themselves. Clynes also recorded muscular activities and other measures of physiology.

A detailed discussion of these initial experiments is not possible here. But they support and provide new opportunity to study scientifically how music-making acts relate to emotional experiences the acts express.

A few examples may help to clarify the implications I see in these observations.

Joy, Clynes (1977, pp. 39–40) tells us, was expressed on his device by a brief strong downward gesture, then an upward rebound with overshoot, leading to a feeling of “floating” that continued until a new gesture was started. If the song “Mary Had a Little Lamb” is sung joyfully, this seems to me to involve gestures of producing and jumping off each note in a way similar to what Clynes reports, and I am aware of a slight sense of floating briefly between the notes. Children typically sing it in this way. This organization of gestures seems to me to be associated with a feeling of joy more strongly than if the notes are sung or played with more connection between them. This type of production at the piano seems related also to the joy that can be conveyed by many last movements of Haydn sonatas. It may be noted that a smile also involves upward movement and a sense of facial lightening.

Love, by contrast, Clynes reports (1977, pp. 37–38), though also a positive emotion, is expressed quite differently in a prolonged smooth curve. Such a form of action could, and typically would, need phrasing over several notes, as in the love theme from “Tristan and Isolde” by Wagner. The Andante movement of Mozart’s KV 311 Piano Sonata, now in F major, seems to express love more strongly with musical gestures connected as Clynes’s observation implies, rather than with the greater detachment associated with joy just discussed. It is plausible that Mozart intended to express love for his mother with this second movement that follows on the anger and pain expressed in the first movement.

Turning now to listening to music (Gardiner 2008b), I propose that emotions experienced are most frequently closely related to those developed as music is created. The growing research concerning mirror neurons (Rizzolatti & Craighero 2004), and the insight this work gives into empathy (Damasio 2010), provides support for this proposition.

An obvious potential problem with this hypothesis is that many listeners who respond to music’s emotions do so even before they have developed the skills needed to produce the music with the emotional values they experience. The ways we have been discussing in which the person or people producing music specifically generate emotional experience addresses this difficulty.

Emotions related to rhythmic movement within music build upon the experience and foundation we all have regarding locomotion.

Reactions to particular musical sounds chosen for music can be especially strong when we produce the sounds ourselves and experience related physiological reactions. But for reasons still not adequately understood, the sounds chosen for music also have a potential individually and in combination to develop emotion in a

listener. This has been noticed and exploited in many different ways throughout human history. Emotions related to harmony and dissonance to tension and its release, seem to have been especially important to the choice of sounds used musically (Gardiner 2012).

And as I have discussed and the work of Clynes helps to demonstrate, the ways in which emotion and action may interact in music making may well not be specific to music alone. It is notable that children who cannot develop their cerebral cortex as a result of early brain damage nevertheless show emotional reactions to music (Damasio 2010).

Music, then, as reviewed here, demonstrates a number of ways emotion can be integrated with the cognitive development and expression of physical acts. The integration of emotion with control of action that music exploits seems widespread throughout behavior. The varieties within spoken verbal expression and touch provide familiar examples. Musical expression can provide many opportunities to study this integration.

It is also of interest that music making involves skill (Gardiner 2008a; 2008c; 2011). The study of relationship of emotion to this example of skillful behavior may provide useful insight into how interactions between emotions and actions affect skillful behavior more generally.

How arousal influences neural competition: What dual competition does not explain

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Abstract: We argue that although the “dual competition” model is useful when considering interactions between emotional and neutral stimuli, it fails to account for the influence of emotional arousal on perceptual or goal-directed behavior involving neutral stimuli. We present the “arousal-biased competition” framework as an alternative that accounts for both scenarios.

In chapter 7 of *The Cognitive-Emotional Brain*, Pessoa (2013) presents his dual competition model to explain how emotion-cognition interactions determine the flow of information processing in the brain. A significant limitation of the dual competition model is that it focuses exclusively on the competition between processing emotional versus nonemotional information and ignores the question of how emotional arousal influences competition processes more generally in the brain. In our commentary, we contrast Pessoa’s “dual competition” framework to another recent emotion-cognition framework, “arousal-biased competition” (Mather & Sutherland 2011), which posits that not only do emotional stimuli compete with nonemotional stimuli, but that emotional arousal influences how nonemotional stimuli compete with each other for neural representation.

Pessoa’s framework is dual natured in that it emphasizes competition in both *perceptual* and *executive* processing. Although Pessoa notes that these two systems interact, he discusses them largely independently of one another in the book. The dual competition framework accounts for how *emotionally significant objects* compete with other information, winning greater attention and memory or impairing goal-directed behavior. Certainly, emotionally arousing things like guns or naked bodies draw attention and compete with other stimuli for both perceptual (e.g., Amtong et al. 2010) and executive resources (e.g., Choi et al. 2012). Pessoa does an excellent job detailing the neural pathways

and networks that are potentially involved in these competitive processes. But how does an *emotionally aroused state* influence the processing of otherwise benign information? For example, why do most people recall where they were, or who they were with, when they first heard about the 9/11 attacks, despite the nonemotional nature of such information? This type of enhanced memory of neutral details of arousing events is not predicted by the dual competition framework.

Critically, where Pessoa's dual competition framework, as well as most other theories of emotion-cognition interactions, comes up short is when having to account for how emotionally arousing stimuli sometimes enhance, rather than suppress, perception and memory for the *neutral* things that happen *nearby* in space or time. For example, fear-related cues have been shown to enhance both the perception of (Phelps et al. 2006), and the neural response for (Padmala & Pessoa 2008), simple visual features such as Gabor patches. Additionally, the presence of a task-irrelevant emotionally evocative image during encoding can produce either retrograde amnesia (Strange et al. 2003) or retrograde enhancement (Anderson et al. 2006) of neutral images. The dual competition framework can account for cases in which the processing of neutral stimuli is impaired by arousing stimuli (e.g., Amting et al. 2010), or when emotional distracters impair goal-directed behavior (e.g., Dolcos & McCarthy 2006). It does not account for cases in which arousing stimuli enhance perceptual processing of neutral stimuli (e.g., Padmala & Pessoa 2008; Phelps, et al. 2006). Nor does it account for cases in which emotional arousal facilitates executive processes (e.g., Knight & Mather 2009). In contrast, the arousal-biased competition model accounts for both arousal's enhancement and impairment effects by positing that arousal increases the gain on biased competition processes. Stimulus representations with high priority, either because of top-down goals or bottom-up salience, are further activated under arousal, while representations of competing, lower-priority stimuli, are further suppressed (Lee et al. 2014; Sutherland & Mather 2012).

In terms of perceptual competition, Pessoa reviews findings that demonstrate the competitive advantage held by emotionally significant objects, like emotional faces. However, recent findings indicate that emotional arousal also increases the gain on competition between nonemotional stimuli (Lee et al. 2014; Sutherland & Mather 2012). For example, on each trial in their study, Sutherland and Mather (2012) presented participants with a sound that was emotionally arousing or a neutral sound, and then 750 to 3000 ms later, briefly flashed eight letters on a white background and asked participants to report as many of the letters as they could. Some of the letters were light gray and some dark gray. Everyone reported a greater number of the more salient dark gray letters than the light gray letters, but this advantage for the salient letters was significantly greater after hearing emotionally arousing sounds. A similar pattern has been observed in the brain when participants were shown one salient stimulus next to a less salient stimulus, preceded by a tone previously conditioned to predict shock or a neutral tone (Lee et al. 2014). Lee et al. (2014) found that while neural activity in the fusiform face area (FFA) corresponding to the perceptually salient face images was enhanced, activity in the parahippocampal place area (PPA) corresponding to the nonsalient item was attenuated on fear-induced arousal trials. This enhancement of processing salient stimuli and inhibition of processing competing less salient stimuli exemplifies the type of interaction of emotional arousal and perceptual priority accounted for by arousal-biased competition.

When Pessoa considers "executive competition," he reviews findings in which a task-irrelevant emotional stimulus produces impairments in executive behavior and neural inhibition. However, his dual competition perspective cannot account for other findings demonstrating that the presence of a low-priority emotionally arousing stimulus can facilitate goal-directed (or executive) behavior (Anderson et al. 2006; Knight & Mather 2009; Steidl et al. 2006). For example, recently Sakaki et al. (2014)

found that when participants' goal was to encode items preceding a potentially emotional oddball item (i.e., oddball-1 items), memory was greater for goal-relevant items on emotional oddball trials compared to nonemotional oddball trials. This observation of retrograde enhancement demonstrates that task-irrelevant emotional arousal can facilitate the execution of task-relevant behavior, which is contrary to the predictions made by the dual competition framework. Additionally, when participants' goal was to encode the oddball item itself, the presence of an emotional oddball led to worse memory for oddball-1 items than the presence of an emotionally neutral oddball. Together, these findings demonstrate that emotional arousal can either *enhance* or *impair* memory for neutral items depending on how goal-relevant information is prioritized.

In conclusion, although Pessoa provides an informative take on how emotional stimuli influence resource competition within the brain, his dual competition model addresses only one subclass of how emotion influences neural competition. To understand how emotion influences cognition more generally, one must consider how emotional arousal can either enhance or impair processing of stimuli that are not inherently emotionally arousing. We argue that emotion influences competitive processes in the brain in general, regardless of whether the mental representations in competition are themselves inherently arousing.

The cognitive-emotional brain is an embodied and social brain

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Abstract: Pessoa (2013) makes a compelling case for conceiving of emotion and cognition as deeply integrated processes in the brain. We will begin our commentary by asking what implications this view of the brain has for an ontology of cognition – a theory of what cognition is and what cognitive processes exist. We will suggest that Pessoa's book, *The Cognitive-Emotional Brain*, provides strong support for an *embodied* theory of cognition. We end our commentary by offering some speculation about how Pessoa's arguments naturally extend to social cognition.

In the conclusions to *The Cognitive-Emotional Brain*, Pessoa (2013) suggests that the mapping of cognition and emotion onto the brain is best characterized in terms of "integration," rather than "segregation" (p. 251). At the beginning of the book, he tells us that he thinks of emotion and cognition as "complementary pairs that mutually define each other" (p. 5). Pessoa amasses a wealth of evidence that suggests the categories of cognition and emotion are not distinct categories. In chapter 2, for example, he elaborates his view of the amygdala as functioning as part of a larger system for relevance detection. This perspective calls into question theories in neuroscience that would divide the processing of emotion-laden visual stimuli into a subcortical low-road, and a cortical high-road. Pessoa mostly focuses his argument on his own field of cognitive neuroscience, but we suggest, however, that the implications go well beyond cognitive neuroscience. We suggest they are best interpreted as concerned with "cognitive ontology" – the debate over the right taxonomy to be used for understanding cognition (Anderson 2010; 2015; Poldrack 2006; 2008; 2010; Price & Friston 2005). Pessoa shows how neuroscience (by which we mean the combination of neuroimaging, behavioural and animal research that Pessoa reviews) should lead cognitive

scientists in general to reexamine the categories it employs to understand cognition. We suggest in particular it should lead cognitive scientists to embrace what we will call an *embodied* theory of cognitive processes.

Let us begin by justifying the claim that is implicit in this argument: that neuroscience can provide a constraint on theorizing about cognition in cognitive science. We take such a conclusion to be a consequence of the network perspective that Pessoa develops in his book. Such a perspective upsets any project of localizing function to specific anatomical brain regions. (For specific arguments to this effect, see chapters 8 and 9). There can be no one-to-one mapping of psychological function to anatomical regions or structures, because brain regions and structures are pluripotent and degenerate. *Pluripotency* refers to the well-established finding that one and the same region (e.g., Broca's area) can be involved in the performance of multiple functions (e.g., language processing, movement preparation, imitation, and imagery related tasks (see Anderson 2010 for discussion of this and other examples of pluripotency). Degeneracy refers to the finding that different neural structures can perform one and the same function (Edelman & Gally 2001; Figdor 2010; Friston & Price 2003). Taken together these findings suggest a *many-to-many* mapping of structure to function. There are a number of possible reactions one might have to this result. One might, for example, attempt to preserve the current theoretical framework we have for carving up cognitive processes and look for theories and models that map cognition more cleanly onto neural structures. A more radical response, however, is to question our current ways of functionally decomposing a complex cognitive process into more basic cognitive operations. We suggest that this more radical response is the one Pessoa recommends. The reason why we are not able to map function cleanly to the brain may lie with the categories, theories, and models we are using to define cognitive operations. In Pessoa's view, it lies with the antagonistic and separatist conception of the relation between emotion and cognition. We need a different set of conceptual tools for carving up the cognitive if we are to correctly model the cognitive operations that map onto the brain.

How, then, do we determine what functional contribution an individual brain region is making when we find it activated in a neuroimaging experiment? We cannot assume that whenever we find a brain region active it is being used to do the same thing (Poldrack 2006). The same brain region can be active in many different networks, and the contribution it makes to each network may vary over time based on the number, strength, and topology of its connections (Anderson 2010; Pessoa 2013, ch.8; Price & Friston 2005). Nor can we just focus on this type of anatomical or structural connectivity: brain regions that are not directly structurally connected may nevertheless be functionally connected, and vice versa (pp. 207–12). What we can do, however, is compare the different domains in which a region or network is systematically engaged. On the basis of these comparisons, Pessoa suggests one “hope is that cognitive ontologies can be defined that meaningfully carve the ‘mental’ into stable categories” (p. 226).

We suggest there is a cognitive ontology that can be extracted from Pessoa's book, and it is one that strongly supports an embodied theory of cognition. The core idea of “embodiment” as we shall understand is that cognitive processes are dynamically entangled with the bodily processes involved in sensorimotor interactions with the environment (see Kiverstein 2012; Kiverstein & Miller, under review). We will let some themes from Pessoa's book serve as an illustration of what we mean. The early chapters of his book establish that because of the extensive communication between the amygdala and visual cortex, vision is always laden with affective significance. We do not wait to see before we feel—instead our fast affective reactions to the environment inform and constitute our perceptual experiences (cf. Barrett & Barr 2009). Pessoa shows how areas of the brain that process emotional information (e.g., hypothalamus, insula, medial prefrontal

cortex) function as hubs that because of their extensive connections are optimally placed to have a “near global effect” on brain function. The function of these extensively connected affective brain regions is to evaluate what is significant for the organism and to mobilize the body for action on the basis of these evaluations. Putting these ideas together, we get the following big picture. Evaluations of affective significance that mobilize the body for action have a “near global effect” on cognition. We find it hard to imagine a better statement of what it means to claim that cognition is embodied.

Pessoa goes on to develop a picture of information-processing in the brain in which there is a constant competition for the efficient use of limited processing resources. He shows how “frontal-parietal regions work closely with regions such as the hypothalamus, amygdala, orbitofrontal cortex, and anterior insula to prioritize processing based on the emotional value of a sensory stimulus” (sect. 5.1.1, para. 2) He develops a model of attentional and executive control (the “dual competition model”) that shows how classically cognitive functions in the brain are in fact informed by representations emotional value, again supporting an embodied theory of attentional and executive control.

We will end our commentary by arguing that the argument we have begun to sketch for an embodied perspective on cognition naturally extends to the social brain. We will focus our argument on work in social cognitive neuroscience concerned with empathic responses to pain. This work has established that parts of the pain matrix are activated both when a subject is in pain and when another individual is perceived to be in pain (Singer & Lamm 2009). When, for example, we perceive a loved one being injected with a needle, there is activity in the same network of brain areas (specifically bilateral anterior insula; dorsal anterior cingulate cortex; and parts of the cerebellum and brainstem) that are active when we ourselves are injected (Decety & Lamm 2006; Singer & Leiberg 2009). Similar results have been found for empathetic experiences of touch (Bufalieri et al. 2007; Cheng et al. 2007; Lamm et al. 2007), disgust (Wicker et al. 2003), and joy (Jabbi et al. 2007).

This type of mirroring activity has however been shown to be modulated by contextual factors such as past experience, prior beliefs, and group membership (Avenanti et al. 2010; Azevedo et al. 2013; Lamm et al. 2007; Singer et al. 2006; Singer & de Vignemont 2006). These findings have led to a proposal to distinguish two separate systems in the brain for affective and cognitive empathy for pain (Jacob and de Vignemont 2012). This is in keeping with a more general distinction that is made between emotional contagion, in which I undergo a self-oriented emotion (I feel distressed because you are distressed), and cognitive empathy, in which I imaginatively recreate the pain you are undergoing. What should we make of this distinction between affective and cognitive empathy in the light of Pessoa's work on the cognitive-emotional brain?

We suggest it needs rethinking. Pessoa's work challenges dual process theories of cognition in general by calling into question divisions of cognition into automatic and cognitively controlled processes. He proposes replacing this dichotomy with “a continuous framework” that covers a spectrum of cases in which there is more or less demand on the brain's processing resources. What would the distinction between cognitive and emotional empathy look like within this continuous framework? We suggest such a distinction is a candidate for conceptual revision in the light of what Pessoa tells us about neural networks.

There are very likely some cases of empathy that require more or less expenditure of cognitive effort and control. However, it would be a mistake to treat these cases as different in kind from cases of emotional contagion that seem to be less demanding in the processing resources they consume. It would be a mistake to assume, for example, that the processing required for emotional contagion is resource independent and hence capacity unlimited just because contagion occurs unintentionally, and unconsciously. Based on Pessoa's discussion of emotion and attention in chapter

4, we suggest that one of the factors that decides whether limited processes resources are given over to empathy is whether the other person's emotions matter to us or not. (Also relevant will be the other demands on our attention [p. 85–89].) Consider in this light the findings that mirroring activity is context-sensitive. Azevedo et al. (2013) found, for example, that bilateral anterior insula activity and autonomic reactivity were greater when seeing a hand being painfully injected belonging to a person of one's own race as contrasted with a hand belonging to a member of an out-group. Whether or not we feel what the other is feeling seems to depend on the care one has for the other, a finding that is naturally explained using the ideas we just sketched from Pessoa's book.

A second point we want to briefly note is how Pessoa's network perspective requires us to rethink standard ways of understanding the human social brain. Uta and Chris Frith have suggested that the social brain in humans "has a 'theory of mind,' which enables us to predict what others are going to do on the basis of their beliefs and desires. It also has a 'mirror system' which enables us to understand others' goal and intentions and to empathise with their emotions by a mechanism of motor resonance" (Frith & Frith 2010, p. 165). Both systems are, however, conceptualized as made up of brain regions that compute specific functions. Pessoa suggests by contrast that the processes a brain region carries out will depend on the "network affiliation" it has at a particular time. Networks continuously dissolve and reform in ways that depend on the contexts in which they are functioning. If all of this is right, it is mistake to say that some set of brain regions are for mentalising or mirroring. There are networks that the brain uses in the context of social interactions, and the processing that takes place in these networks is deeply informed by what is of affective significance for the person (Schilbach et al. 2012). Sharing emotion with the other is important because it imbues our perception of the other person with affective significance.

Behavioral evidence for a continuous approach to the perception of emotionally valenced stimuli

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Abstract: Pessoa's (2013) dual competition model outlines a framework for how cognition and emotion interact at the perceptual levels and provides evidence within the field of neuroscience to support this new perspective. Here, I discuss how behavioral work fares with this new model and how visual detection is influenced by information with affective or motivational content.

Theories separating emotion from cognition are decades, maybe even centuries, old. Classic views of emotion have long proposed that each discrete emotion has dedicated neural circuitry that is activated automatically, without conscious awareness (e.g., Ekman & Cordaro 2011; Izard 2007; Panksepp 2007). More continuous, multicomponent models of emotion that allow for interactions between cognitive and affective systems have received recent attention in the literature (e.g., Coan 2010; Cunningham & Zelazo 2009; Lewis & Douglas 1998). In his Précis of *The Cognitive-Emotional Brain*, Pessoa presents a new approach to how cognition and emotion are integrated in the brain that is similar to these newer multicomponent models. His dual competition model outlines a framework for such interactions at the perceptual levels; here, I will discuss the specific aspects of his proposal that

address how perception is directly influenced by information with affective or motivational content and how behavioral data might speak to his new model.

According to what Pessoa calls the "standard hypothesis," the processing of emotionally valenced stimuli occurs rapidly, automatically, and nonconsciously, independent of attention and awareness. In terms of the brain, the processing of these stimuli takes the "low-road," or a subcortical route. He presents an alternative to the standard hypothesis – the multiple waves model – suggesting that emotional stimuli engage *multiple* regions of the brain, activating both cortical and noncortical channels. Thus, the processing of emotionally valenced stimuli cannot necessarily be accounted for by one specific mechanism, and there are multiple pathways for the perception of these stimuli.

Pessoa thoroughly evaluates neuroscience research that supports both the standard hypothesis and his new model, but given that the focus of *The Cognitive-Emotional Brain* (Pessoa 2013) is indeed on the *brain*, there is very little discussion of how behavioral work can also speak to these perspectives. There is in fact a large body of work on visual attention to emotional stimuli that researchers use to debate the standard hypothesis versus alternative accounts. Countless studies have reported that both adults and more recently, preschool children, detect negative or threat-relevant stimuli, such as snakes and spiders, more quickly than a variety of neutral stimuli, such as flowers, mushrooms, frogs, and cockroaches (Flykt 2005; 2006; Hayakawa et al. 2011; Lipp 2006; Lipp & Derakshan 2005; Lipp et al. 2004; Lipp & Waters 2007; LoBue 2010; LoBue & DeLoache 2008; 2011; Masataka & Shibasaki 2012; Öhman et al. 2001a; Purkis & Lipp 2007; Soares et al. 2012; Tipples et al. 2002b). They also detect threatening or angry faces more quickly than happy, neutral, or even sad faces (Calvo et al. 2006; Eastwood et al. 2001; Esteves 1999; Fox et al. 2000; Hansen & Hansen 1988; LoBue 2009; Lundqvist & Öhman 2005; Öhman et al. 2001b; Schubo et al. 2006; Tipples et al. 2002a; Williams et al. 2005). Similar findings have been reported with human infants (LoBue & DeLoache 2010; Rakison & Derringer 2008) and non-human primates (Shibasaki & Kawai 2009), providing compelling evidence that humans have a perceptual bias for the rapid detection of emotional (and specifically negative or threat-relevant) stimuli.

Consistent with the standard hypothesis, many researchers have explained perceptual biases for threat via automatic, pre-attentive, or nonconscious processes, as opposed to controlled, conscious, or cognitively mediated processes. Evidence for the automaticity account comes from data suggesting that the detection of threat-relevant targets (snakes, spiders, angry faces) does not vary based on the number of distracters present in an array. In other words, whereas the detection of nonthreatening stimuli slows when the number of distracters increases from four to nine, detection of threat-relevant stimuli remains equally efficient regardless of the number of distracters present in a matrix (e.g., Eastwood & Smilek 2005; Fox et al. 2000; Öhman et al. 2001a). This suggests that individuals use parallel, or automatic search mechanisms to detect threatening stimuli, and that they use serial, or conscious search strategies to detect nonthreatening stimuli.

However, despite several studies demonstrating evidence for automatic detection of threat, others present evidence against automatic search, either by failing to demonstrate set size effects for threat-relevant stimuli or by reporting detection latencies that are too slow to represent automatic search (for a review, see Becker et al. 2011a; Horstmann & Bauland 2006). Other studies demonstrate that the advantage for threat-relevant stimuli may have nothing to do with emotional valence at all and is, instead, driven by low-level features of the targets. Indeed, specific geometric shapes, such as the "V" shaped brow characteristic of angry faces or simple curvilinear figures common to snakes are sufficient in eliciting rapid detection (Larson et al. 2007; LoBue & DeLoache 2011; LoBue & Larson 2010). Further, presenting

participants with specific features of angry faces in non-face-like configurations maintains the advantage (Coelho et al. 2011; Horstmann et al. 2006), and removing or manipulating these important features eliminates it (Becker et al. 2011b).

While the controversy rages on about whether automatic versus controlled search mechanisms drive the rapid perception of emotional stimuli, most researchers acknowledge that *both* automatic and controlled processes likely play a role in threat detection (e.g. Frischen et al. 2008; Wolfe 1998). Further, research on visual attention to emotional stimuli is usually designed to test the standard hypothesis and does not allow for the study of multiple interacting pathways for rapid detection. This leaves us with the same old dichotomy that Pessoa's theory is aimed at revising—subcortical versus cortical routes, parallel versus serial search, nonconscious versus conscious processing—instead of leaving room for a continuous, more integrated explanation.

Very recent behavioral work that explicitly examines multiple pathways for the rapid detection of emotional stimuli indeed suggests that there is no single factor that effectively drives the phenomenon. In one recent study, for example, researchers attempted to examine the unique and potentially interacting roles of low-level perceptual cues, cognitive factors, and emotional state on rapid visual detection of threat. Across studies, adult participants were asked to detect low-level perceptual features of a commonly studied threat-relevant stimulus—snakes. They were asked to detect simple curvilinear (snake-like) versus equally simple rectilinear shapes in a visual search task in the absence of any threat-relevant cues. In Experiment 2, the same procedure was used, except that threat-relevant or non-threat-relevant *labels*—calling the simple shapes “snakes” or “caterpillars”—were applied to the curvilinear and rectilinear stimuli in order to examine the added role of cognition (or knowing the identity of a stimulus) in detection. Finally, in Experiment 3, a fearful or neutral emotional induction was administered to participants before they completed the visual detection task with curvilinear and rectilinear targets to examine the role that emotional state might play in rapid detection.

The results were compelling, implicating all three factors. Across all three studies, adults detected simple curvilinear shapes more quickly than simple rectilinear shapes in the absence of any threat-relevant cues, suggesting a perceptual bias for curvilinearity. Further, threat-relevant labels and a fearful emotional induction facilitated detection even further, potentially playing an additive role in rapid detection (LoBue 2014). This study—specifically designed to examine a more continuous hypothesis about the roles of perception, cognition, and emotion on rapid detection—suggests that multiple factors can lead to a bias for emotionally valenced stimuli.

Another recent study using eye-tracking technology further supports this perspective, demonstrating that the advantage for threat-relevant stimuli in visual search tasks cannot be accounted for by either bottom-up or top-down processing biases alone. In the study, researchers replicated a classic threat-detection paradigm with an eye-tracker. Adults were presented with 2×2 and 3×3 matrices of images and were told to press one button if all of the images were from a single category, and a second button if there was a discrepant image (target) in each matrix. The targets were threat-relevant (snakes and spiders) or non-threat-relevant (flowers and mushrooms)—the same photographs and procedure used in a classic, widely cited study by Öhman et al. (2001a). The results replicated previous work, demonstrating that adults detected discrepant snakes and spiders more quickly than discrepant flowers and mushrooms. Most importantly, the fixation data further suggested that a single mechanism was not solely responsible for the results.

There was indeed an advantage for snakes and spiders in perception; participants were faster to first fixate threat-relevant versus non-threat-relevant targets, suggesting (consistent with previous literature) that bottom-up processes lead to an advantage for the threat-relevant stimuli. However, there was also an

advantage for snakes and spiders in behavioral responding—participants were faster to decide that discrepant threat-relevant stimuli were present after first fixating them, demonstrating that there is also a top-down advantage for threatening stimuli in detection tasks. Together, this work suggests that a bias for threat-relevant stimuli is driven by an advantage in both bottom-up and top-down processing (LoBue et al. 2014).

Together, this behavioral work adds to the body of literature reviewed by Pessoa, suggesting that the processing of emotional stimuli cannot necessarily be accounted for by one specific mechanism and that there are *multiple pathways* for the perception of emotionally valenced stimuli. As he puts it, “the fate of a biologically relevant stimulus should not be understood in terms of a ‘low road’ versus a ‘high road,’ but in terms of the ‘multiple roads’ that lead to the expression of observed behaviors” (Pessoa 2013, p. 79). Although some of the newer behavioral work reviewed here supports a more continuous model of emotional perception, most behavioral work to date has sought to support or refute the standard hypothesis and does not necessarily allow for multiple interacting factors in their experimental designs. Ultimately, the consideration of newer, more continuous models of emotional perception might take us further in understanding the development of emotional behavior than traditional views that promote a fundamental separation between affect and cognition.

United we stand, divided we fall: Cognition, emotion, and the *moral link* between them

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Abstract: Contrary to Greene's dual-process theory of moral judgment (Greene 2013), this commentary suggests that the network view of the brain proposed by Pessoa, in which emotion and cognition may be used as labels in the context of certain behaviors, but will not map clearly into compartmentalized pieces of the brain, could represent a better explanation of the *rationale* behind people's moral behavior.

After *revealing* the *error* of Descartes (Damasio 1994), neurosciences seem to have taken two different paths in the study of brain organization during the past two decades. On the one hand, some researchers have tried to emphasize the deep interactions between cognition and emotion by postulating an integration of the brain's networks, none of which should be intended as specifically emotional or cognitive (Feldman Barret et al. 2007; Ochsner & Gross 2005; Pessoa 2008). But, on the other hand, there has been an escalation of *manichean* points of view, according to which there are *separate systems* for emotion and cognition that seem to subtend different *modules* in the brain (Keren & Schul 2009). Specifically, in the domain of moral decision making, the *dualism* between emotion and cognition has led to a *dual-process brain* framework that has received considerable attention due to the neuroimaging works of Joshua Greene (Greene et al. 2001; 2004; for a review, see Greene 2013). The main point of Greene's theory is that, when we make moral decisions (deciding whether an act would be right or wrong), we can be automatic, fast, and *emotional*, or controlled, slow, and *rational*. In an attempt to establish a bridge between neuroimaging data and moral philosophy, Greene proposes that deontological judgments arise from areas of the brain more associated with *emotional reactions*, whereas utilitarian judgments arise from areas of the brain more associated with *cognitive control*. In this sense, deontology is an emotionally (strong) based theory that may, in some cases,

pull us away from a clear deliberation about the significant characteristics of a moral situation. But, in some circumstances, we can transcend this visceral reaction by adopting a more rational and utilitarian point of view in order to override it, as well as constitute a more reliable moral guide because it is ineluctably cognitive. What emerges is a *dual-process (moral) theory* in which the deontological-utilitarian conflict (conflict that mirrors the emotional-cognitive conflict) should be understood in terms of a mutually suppressive relationship (Greene 2008).

In his interesting *The Cognitive-Emotional Brain*, Pessoa (2013) proposes a different framework of brain organization in which cognitive control and emotion are not competitive mechanisms but integrated processes. The book's main claim is that emotion and cognition are *functionally integrated systems* that continuously impact each other's operation. Although Pessoa never speaks about moral judgments, I am very sympathetic with the main claim, and I think that the framework proposed by the author may also have important echoes in the context of moral decision making. Specifically, the *network perspective* of brain organization (e.g., behavioral processes are not implemented by a single brain area, but rather by the interaction of multiple areas), accompanied by the integrative view of cognition and emotion that emerges from Pessoa's book, permits us to reconsider the *conflict* between utilitarian (cognitive) and deontological (emotional) ethics in moral decision making, as suggested by Greene (2013), and to "transform" this moral conflict through a *process of integrating* a set of different moral considerations. Here, I will focus on two aspects of Pessoa's proposal.

A "conflict" between reason and emotion do not require the existence of two systems. As noted by Keren and Schul (2009), to prove the existence of two systems, we need a strong argument regarding how the dichotomy emotion/cognition is arranged, allowing one system to be characterized by one attribute and the other by its complement. The arrangement chosen by Greene (2013) is that emotions are *automatic* processes and, on the contrary, reason involves the *conscious* application of decision rules. Furthermore, Greene identifies the ventromedial area of the prefrontal cortex (vmPFC) as deputed to emotional processes and the dorsolateral prefrontal cortex (dlPFC) as a clearly cognitive area that is dedicated to cognitive control. When people are faced with the *trolley dilemma*, they apply a utilitarian perspective using the dlPFC that favors hitting the switch to maximize the number of lives saved. Conversely, when people are faced with the *footbridge dilemma*, they experience a strong emotional response enabled by the vmPFC. As a result, most people judge that the action is wrong by adopting a deontological perspective. Instead, for those few people who endorse a utilitarian perspective in the footbridge dilemma, they have to override the negative reaction to pushing innocent people off the footbridge in order to perform an extremely affectively difficult action. By combining these ideas, we have a dual-process theory of moral judgment.

But this "alleged" conflict between cognition and emotion really requires two mutually suppressing systems, and is it really a conflict between utilitarianism and deontology?

Pessoa argued that the theories that posit a *push-pull* antagonistic organization in the prefrontal cortex involved in cognition and emotion, although still influential, are no longer tenable. In fact, there are a large number of studies that strongly favor organization of the prefrontal cortex not as a simple push-pull mechanism, but as interactions that result in processes that are neither purely cognitive nor emotional (Ochsner & Gross 2005; Pessoa 2008). Specifically, the dlPFC is seen as a focal point for cognitive-emotional interactions, which have been observed across a wide range of cognitive tasks. This means that brain regions that are important for executive control are actively engaged by emotion. Emotion can either enhance or impair cognitive performance, and the *dual competition* framework proposed by Pessoa, in which emotion and cognition interact with/compete for the resources required for the tasks, permits us to explain how

emotional content impacts executive control. Pessoa suggests that these interactions between emotion and cognition do not fit into a simple push-pull relationship; thus, a continuous framework seems better than a dichotomous one. The theory of moral judgment proposed by Moll et al. (2007; 2008b) in which moral decision making is implemented by a single set of brain areas could represent a valid alternative to Greene's dual-process theory. In this *single-process theory* of moral judgment, emotions act as a *guide* to the salience of situational information or as an input to the reasoning process. In that sense, the conflict between emotional and cognitive mechanisms is replaced by a process that integrates a set of different considerations. For these reasons, as it is conceivable (and possible) to develop a continuous model that maps the interaction between emotion and cognition, I think that it is also conceivable (and possible) to develop a continuous model that captures the interactions between deontology and utilitarianism as compatible and reinforcing theories without considering them mutually exclusive (Gray & Schein 2012).

Beyond the conflict between deontology and utilitarianism. In Manfrinati et al. (2013), we developed an experimental paradigm in which participants were explicitly required to choose between two possible resolutions of a moral dilemma, one deontological and the other utilitarian. Furthermore, we asked participants to rate their emotional experience during moral decision making, collecting valence and arousal ratings throughout the process of resolving the dilemma. In this way, we can assess whether, and to what extent, conscious emotion is engaged during the process of decision that will lead to the choice of one of the two resolutions. The results showed that cognitive and emotional processes participate in both deontological and utilitarian moral judgments. In particular, we found that, if the utilitarian judgment involves controlled reasoning processes to construct a set of practical principles for our moral behavior, then the whole process might have a high emotional cost. In fact, when people choose a utilitarian resolution, they might consider the consequences of an act as relevant in determining its morality, but they most likely feel that this resolution could undermine their moral integrity, thus evoking a harsh emotional feeling.

Furthermore, and contrary to Greene's (2008) prediction, according to which there is an asymmetry between utilitarian and deontological judgments, with the former driven by controlled cognitive processes and the latter driven by more automatic processes, we found that controlled reasoning is required to account not only for utilitarian judgments, but also for deontological judgments. In fact, our participants showed slower response times in choosing the deontological resolution of the dilemma than the utilitarian one. Given that these results showed an *integrative* pattern of emotional and cognitive processes in moral judgment, I think that this integrative pattern could also be applied to account for the relation between deontology and utilitarianism. Specifically, if the network perspective proposed by Pessoa suggests that the mind-brain is not decomposable in terms of emotion and cognition because they are functionally integrated systems, then we could hypothesize that moral cognition cannot be decomposed in deontology and utilitarianism. As claimed by Gray and Schein (2012), the *normative* conflict between deontology and utilitarianism seems to lose significance when we consider the *psychological* aspects of moral decision making. Indeed, when we investigate these psychological aspects, we realize that, many times, the acts of the moral agent are linked with their consequences, which suggests that people simultaneously care about deontological and utilitarian perspectives. Therefore, we might consider the relationship between deontology and utilitarianism as a *continuum* that "mirrors" the continuous framework between emotion and cognition highlighted by Pessoa.

To sum up, in this commentary, I have tried to point out that the network view of the brain proposed by Pessoa, in which emotion and cognition may be used as labels in the context of certain behaviors, but will not map clearly into compartmentalized pieces of the brain, may represent a significant *rationale* for the

investigations of moral behavior. In accordance with Pessoa's claim that the effects of emotion on cognition, and *vice versa*, are best viewed not as a simple push-pull mechanism, but as interactions that result in processes that are neither purely cognitive nor emotional, it no longer makes sense – in the field of moral decision making – to engage in debate over whether moral judgment is accomplished exclusively by reason or by emotion. Rather, moral judgment is the product of complex integrations/interactions between emotional and cognitive mechanisms.

Models for cognition and emotion: Evolutionary and linguistic considerations

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Abstract: A central claim in Luiz Pessoa's (2013) book is that the terms "emotion" and "cognition" can be useful in characterizing behaviors but will not be cleanly mapped into brain regions. In order to be verified, this claim requires models for the integration and interfacing of emotion and cognition; yet, such models remain problematic.

As Luiz Pessoa (2013) acknowledges in the preface of his insightful book, *The Cognitive-Emotional Brain*, the modeling of function-structure mappings for cognition and emotion has received very little attention in the literature, particularly when compared with the abundance of empirical findings confirming the interaction between cognition and emotion. Pessoa devotes an entire chapter to the problem of function-structure mappings and emphasizes its importance throughout the book with admirable clarity. His efforts to close this theoretical gap constitute a signal contribution to the literature. Because of the crucial role that function-structure mappings will play in future debates on emotion and cognition, this review focuses on Pessoa's proposals on how to model their integration.

An overview of the current state of the literature concerning models for cognition and emotion demonstrates the pressing need for developing theoretical approaches that systematize current findings. Pessoa forcefully argues that the "network perspective" he favors is particularly helpful in fulfilling this task. More specifically, the dual competition model (or DCM) that Pessoa offers receives substantial support from a vast array of findings in neuroscience, across species, which Pessoa documents in great detail. These findings strongly suggest that emotion and cognition are not isolated and, more important, that they are not discretely instantiated in neatly localized regions of the brain. Indeed, in many cases cognition interacts with emotion producing no systematically located activations. Pessoa's impressive analysis of these findings concerns attention-filtering processes in which emotion plays a decisive role in modulating cognitive processing. He thereby illuminates the larger issue of how emotion shapes cognition and vice versa, a topic that has been of central importance in neuroscience (e.g., LeDoux 1996).

Precisely because of the strong support that the DCM receives from the empirical findings, it is essential to analyze its theoretical underpinnings. A central tenet of Pessoa's integrative approach is that although "emotion" and "cognition" may be useful terms to characterize behaviors, they do not neatly map onto brain regions. To know if those conceptualize a unified network in the brain, one needs to know how the activations of this network instantiate the guiding characteristics and semantic contents underlying emotional and cognitive behaviors. Even if the DCM adequately models this network, and even if the function and structure of

the emotion cognition interface is best understood in terms of integrated networks (rather than brain regions), one still needs to explain how emotion and cognition map to each other in processes of perceptual attention and conscious awareness.

Here, one confronts two questions: (a) what is the role of attention and consciousness (including self-awareness) in the integration of cognition and emotion? and (b) what degree of complexity of the semantic information is required for the integration of cognition and emotion? Any answer to these questions – to create a satisfactory model for the integration of cognition and emotion – must involve evolution and language. With respect to evolution: How to identify automatic and unintended processes, as opposed to more recent forms of cognitive or emotional responses that require self-awareness? With respect to language, which Pessoa scarcely mentions: Can there be cognitive and emotional responses that are fundamentally dependent on the language capacity? These two questions are obviously related, and the potential implications of answering these questions with respect to the independence of emotion from cognition are not explicitly addressed by Pessoa's model, opening the possibility of a form of dissociation between emotion and cognition that may challenge his model.

These questions must be answered in order to define the fundamental aspects regarding the mapping between cognition and emotion. For example, although many forms of emotion seem to be quite basic or "dumb" as Pessoa argues (p. 247), cognition seems at least implicitly to require inferential and conceptual capacities. Presumably, many of those capacities are associated with the language capacity in humans. Complex cognitive and inferentially based reasoning appear to be a recent development in the evolution of the emotion and cognition network. Their recent development suggests at least some degree of independence between emotion and cognition in instances of *conscious* inference and perceptual attention because some emotional processes may occur unconsciously or independently from interactions with inferentially and semantically based cognition. Thus, considerations about evolution question the plausibility of a highly integrated network for emotion and cognition, in the sense that the automatic system may not map neatly to any of the more consciously effortful and inferentially mediated system.

The DCM hypothesizes that emotional and motivational signals are systematically integrated with perception and cognition. In order to distinguish between automatic and voluntary processes, however, it is fundamental first to specify how "emotion" and "cognition" are being understood. Pessoa (2005) correctly remarks that recent findings have challenged the view that emotion happens automatically and independently of attention and awareness. He proposes that current research should focus on how attention and awareness modulate emotion in perception. Yet, there are many forms of attention (including effortful, effortless, and unconscious attention). What is more, there may be more than one form of conscious awareness as argued in Montemayor and Haladjian (2015). The distinction between *awareness* and *self-awareness* is of particular relevance. For example, it has been argued that self-awareness is fundamental for many forms of emotional behavior and for conscious forms of cognition (Damasio 2010).

With respect to attention modulation and emotion, both selective attention and basic emotional reactions appear to be early evolutionary adaptations that require neither linguistic capacities nor self-awareness. By contrast, consciously aware emotion may necessitate capacities for identifying the mental states of conspecifics (or having a theory of mind) and language (see Carruthers 2000; Dennett 1969; 2005). Language may itself be a spandrel and a uniquely human capacity (Fitch et al. 2005), which strongly suggests its recent evolution. If conscious awareness is required for higher forms of attention that depend on semantic and conceptual content, then it becomes more difficult to maintain an integration model for emotion and cognition: the independence of many kinds of emotional processes from cognitive ones would have to be a central feature of any model of their interaction.

Furthermore, conceptual content seems to be deeply associated with language capacity because of its compositional and generative characteristics (Fodor 1998). Conceptual content is also associated with the more complex activities of imagination and metaphorical reasoning (Lakoff & Johnson 1980). All theories of conceptual content relate it to either the language capacity or the capacity to form the beliefs that support inferential reasoning. For these reasons, conceptual attention seems to be a recent, perhaps uniquely human, phenomenon (assuming that language and inferential reasoning are recent phenomena in the evolution of our species). Emotional reactions seem to be less dependent on imagination and metaphor. Still, it is very likely that at least some of the consciously aware emotional reactions are less automatic than others, for which there may be numerous explanations, including the autonomy of the “old” emotional system. Crucially, emotion and cognition could really be independent from one another in humans, even if they *interact* systematically. Culture and social cues could be a further complication (Tomasello 1999), in the sense that the semantic and inferential enrichments of emotional responses that characterize human emotional behavior may not only be independent from cognitive processing, but also fundamentally dependent on social cues and interactions.

Considerations regarding the necessity of a linguistic format for motivation, conceptualized in terms of the first-person perspective in humans, complicate the interaction between emotion and cognition even more. Some theorists argue that language is required for structuring self-consciousness (Baker 2013; Dewart 1989; Neuman & Nave 2010). As mentioned, language is scarcely mentioned by Pessoa, but it may be fundamental to understand the DCM, because some format must be responsible for the mapping between cognition and emotion, and language is ideally suited to perform this role. A model that explicitly addresses the role of language in relation to emotion and cognition is desirable and perhaps necessary, because of the probable linguistic underpinnings of self-awareness.

It is undoubtedly true that the dichotomization of concepts such as “emotion” and “cognition” can be simplistic. Pessoa’s model proposes that “emotion” and “cognition” do not exclude each other, but how exactly? It could be the case that the brain dynamics of oscillations are such that signals for emotion and cognition are indeed systematically coupled and always *interacting*, but this is compatible with their dissociation at the level of cognitive integration. At that level, they may play systematically distinct roles and never be *integrated*. For example, working memory and the kind of attention that is broadcasted cross-modally may systematically correlate with certain unified signals, but this need not be the case for automatic forms of emotion and cognition.

Finally, regarding the structure and function of cognitive and emotional processing, it is important to emphasize that there are patent discrepancies between their *normative* or behavior guiding role. The intensity and moral or aesthetic aspects of a set of emotions do not seem to depend on the integration of fact-based or perceptual aspects of stimuli. In particular, emotional intensity does not seem to depend on the conjunction of perceptual features. Rather, it appears dependent on a much more integrative process that generates a unique conscious experience, which is strongly unified and independent of any specific set of perceptual features. Emotional intensity also seems to be independent of the accuracy or inaccuracy of cognitive information, such as the epistemic consequences of an argument or the knowledge of features related to attention in perceptual processes. The structure and normative function of emotional and cognitive behavior may, therefore, be different. Likewise, measures for the intensity and structure of emotions may shed no light on the cognitive functions that interact with them and vice versa. The incommensurability between these different functions suggests that there is a deep kind of dissociation between emotion and cognition (a normative kind of dissociation).

For these reasons, one of Pessoa’s central arguments, which infers integration from the interaction of cognitive and emotional

signals, is problematic. The problem is reminiscent of arguments that invalidly infer causal explanation from systematic correlation. The book as a whole, however, demonstrates that new and more integrative approaches to the study of emotion and cognition are justified and urgently needed, and this is an aspect of the book that deserves praise and notice. Pessoa’s book is certainly an important step in the right direction – toward a conclusive and rigorous model for the interaction between emotion and cognition.

On theory integration: Toward developing affective components within cognitive architectures

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Abstract: In *The Cognitive-Emotional Brain*, Pessoa (2013) suggests that cognition and emotion should not be considered separately. We agree with this and argue that cognitive architectures can provide steady ground for this kind of theory integration and for investigating interactions among underlying cognitive processes. We briefly explore how affective components can be implemented and how neuroimaging measures can help validate models and influence theory development.

Like Pessoa (2013), many authors (e.g., Anderson 2007; Newell 1990; Reisenzein et al. 2013) have called for theory integration within psychological science. Indeed, the importance of integrating disparate theories of human behavior together is unlikely to be disputed. However, the path toward theory integration, on the other hand, can be quite thorny. Between research literatures, differences often arise concerning language, assumptions, and methodologies. For example, Pessoa discusses how the role of the amygdala reaches far beyond its typical description as a “fear center” for processing negative information. Similarly, within the book Pessoa describes numerous research findings that reveal (1) overlapping patterns of activation in brain structures previously considered specific to “cognitive” or “emotional” processing and (2) relevant interactions between affective states and cognitive tasks. Indeed, we applaud Pessoa for exploring the often rugged territory between established fields of research and for building a strong case in favor of an integrative approach.

Yet, we also challenge Pessoa on the grounds of defining an approach to theory integration. In what follows, we make three points. First, we suggest that *cognitive architectures* can provide steady ground for integrating theories of emotion and cognition, as well as for describing interactions among underlying processes of behavior. A cognitive architecture is a broad psychological theory implemented as a formal (e.g., computer) model that incorporates multiple facets of behavior, such as perception and memory, and that, ideally, can account for many different behavioral tasks, ranging from, for example, low-level eye movement behavior (e.g., Salvucci 2001) to deliberate problem solving (e.g., Anderson 2005). Second, we provide examples of how affective components have previously been (Cochran et al. 2006; Ritter et al. 2007) and might potentially be (e.g., Reisenzein et al. 2013) implemented within cognitive architectures. Third, we also briefly describe how neuroimaging data can potentially be incorporated into these types of models, as well as into the process of theory development.

Although the book offers a strong “why” for theory integration between the study of cognitive and affective aspects of behavior, we suggest that one promising avenue for “how” to accomplish this theory integration is by way of developing affective features

within formalized cognitive architectures. Pioneering artificial intelligence and cognitive science researcher Alan Newell, argued (e.g., 1973; 1990) that psychological science would benefit by moving beyond mere verbal (qualitative) hypotheses, such as simple dichotomies (e.g., nature vs. nurture), toward formalized (quantitative) hypotheses. Additionally, he suggested that one path toward a unified theory of mind is by developing cognitive architectures. A number of cognitive architectures have been developed, such as Soar (Newell 1990), EPIC (Meyer & Kieras 1997) and ACT-R (Anderson & Lebiere 1998; see Langley et al. 2008 for a review of different architectures). Take ACT-R, for example (see Anderson 2007 for details). This model incorporates decades of research to describe a full range of cognitive processes, from perception to action, and can provide fine-grained predictions about reaction times, neuroimaging measurements, eye-tracking data, as well as behavioral responses. In our view, it is quite stunning that, thus far, there have been relatively few attempts to incorporate affective components into architectural models of cognition and behavior. For the purpose of this commentary, the most noteworthy aspect of cognitive architectures relates to understanding and hypothesizing about interactions between different perceptual, motor, and cognitive components that naturally arise while modeling behavioral tasks. Within Pessoa's book and elsewhere (e.g., McGaugh 2000), affective aspects of behavior such as stress, motivation, and arousal have been shown to modulate cognitive processes such as attention and memory, and we believe that developing these affective components within cognitive architectures can afford researchers the ability to precisely define how and where these types of interactions may take place within a human system. Additionally, when one or more aspects of cognition are qualified based on an affective state and a possible system-wide chain of interactions occurs, cognitive architectures may be the best tool for dealing with the high level of complexity.

How can affective components be implemented within cognitive architectures? The approach that several authors have called for or begun working with is to define how affective states might modulate the underlying cognitive processes (e.g., attention, working memory) within the architecture (e.g., Belavkin 2001; Cochran et al. 2006; Dancy et al. 2013; Hudlicka 2004; Ritter et al. 2007; see also Gunzelmann et al. 2009 for similar work related to fatigue). This can translate to adjusting certain parameters within existing architectures. For example, Cochran et al. (2006) provide a relatively simple demonstration of this approach, in which they model the effect of one aspect of emotion (arousal) within one cognitive module of ACT-R (declarative memory). Cochran et al. (2006) point out that the standard ACT-R model is not able to predict the results of the classic study by Kleinsmith and Kaplan (1964), which found that study of high emotional arousal stimuli led to short-term forgetting and long-term remembering compared with low emotional arousal stimuli. To implement this impact of arousal on memory within ACT-R, Cochran et al. (2006) redefined and expanded certain parameters (specifically, within the declarative memory module) to produce a pattern similar to the behavioral data. Similarly, in another paper, Ritter et al. (2007) developed a model within ACT-R to predict performance on a serial subtraction task, in which certain cognitive mechanisms within the architecture (e.g., attention, working memory) were modified to represent the impact of stress. Much more, we suspect that it would be worthwhile to explore how the findings and theories presented within Pessoa's book can be modeled within cognitive architectures in similar ways.

Many cognitive architectures (ACT-R in particular) not only attempt to model the processes underlying human behavior, but they also incorporate neuroimaging findings to develop a brain-like system of structures and processes (e.g., Anderson 2007; Just & Varma 2007). Indeed, within ACT-R different cognitive modules are associated with certain brain structures. Because of this design approach, (1) neuropsychological findings can be

used to guide and constrain model development, and (2) neuroimaging data (such as fMRI) can be used in conjunction with behavioral measurements to help validate models (e.g., Borst & Anderson 2014). Because ACT-R provides latency information for different cognitive processes (e.g., visually encoding a stimulus, retrieving information from memory, producing a motor response), this pattern of activity can be translated into predictions for neuroimaging data in correspondence with the brain areas associated with the different cognitive modules. We suspect that this facet of cognitive architectures may be especially compelling for the development of affective components because, as Pessoa describes, certain brain structures (such as the amygdala) are associated with a variety of processes. These types of neuropsychological research findings can be taken into account when exploring how affective aspects might modulate particular processes within an architecture.

There is, perhaps, no better way to conclude this short commentary than by turning to one of the conceptual founders of integrative approaches to behavior and cognition. In many ways, Pessoa's book echoes Newell's (1990) argument that, "A single system (mind) produces all aspects of behavior. It is one mind that minds them all. Even if the mind has parts, modules, components, or whatever, they all mesh together to produce behavior.... If a theory covers only one part or component, it flirts with trouble from the start" (p. 17). In short, Pessoa contends that, given the high level of overlap between aspects of cognition and emotion, the two should not be considered separately. We agree with this and believe that the ideal research approach for pursuing this integration of theories includes cognitive architectures.

Neuropsychology still needs to model organismic processes "from within"

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Abstract: Four issues are discussed: (1) differences between cognition and emotion; (2) affect, emotion, and motivation differentials, including a neuropsychological model of motivation; (3) mental attention (working memory) as a resource neither affective nor cognitive, but applicable to both; and (4) explication of neuropsychological scheme units, which have neuronal circuits as functional infrastructure, thus helping to clarify the semantics of functional connectivity.

Pessoa's *The Cognitive-Emotional Brain* (2013) is important because it attempts to clarify in broad detail neuroscience relations among cognition, emotion, and motivation. Pessoa sees these constructs as intertwined in the brain networks but does not make apparent how cognition, emotion, and motivation *functionally* complement each other as different modes of processing.

A number of important issues remain unanswered. Do Pessoa's multiple waves and dual competition models (pp. 70–72, and Chapter 7 of his book) imply that performance is *overdetermined*—as Freud would have said—by many actively self-propelling, often connected brain processes? How are external "contexts" and related internal processes expressed in the brain?

Are they “passive” representations or *coordinated sets* of here-and-now-activated multiple circuits (heretofore called *schemes*)? A better neuropsychology should examine these and other topics, adopting a processing attitude “from within” – a perspective called *metasubjective* to contrast it to an external observers’ perspective (Pascual-Leone 2013). We illustrate this point by discussing four issues.

The first issue addresses subjective differences between emotion and cognition. Contrary to Pessoa’s belief (p. 4 of his book), capturing functional differences between psychology constructs is essential to understand their expression in the brain. Cognition assigns a *truth value* to experience – that is, asserting whether (present, past, or future) experiences are *true* or valid vis-à-vis *future outcomes*. In contrast, emotion processes assign a *vital value*, evaluating the importance of experience in situations for one’s life and living (done by *specific*, positive or negative, affect systems – love, mastery-seeking, guilt, joy, fear, etc.). These two sorts of value (truth vs. vital) complement one another and are *compatible but not interchangeable*. Because they are compatible, *some* circuits or networks carry both sorts of value together: fully and simultaneously *cognitive and affective*, as Pessoa claims. Some researchers call these sorts of hybrid processes *emotions* (Damasio 1999; 2010; Greenberg 2002), restricting the terms *feeling*, affect, *affective* (versus cognitive) to processes where vital value *predominates*. As Panksepp and Biven (2012) have reemphasized, *primary* “pure” affects have innate-instinctual (evolutionary) roots, each with a distinct sort of affective “flavor” – roots whose number is estimated as high as seven or nine primary affects (positive or negative). The existence of these innate roots is a major argument for differentiating between affects and emotions, because the latter always embody *situation-bound* cognitions that cannot be innate.

Neural networks differ relatively, *not absolutely*, on the sort of value they carry (truth/cognitive vs. vital/affective), often modulated by tasks/situations. We talk of cognition when the pragmatically *predominant* value is concerned with truth (e.g., lateral/dorsal prefrontal areas, lateral parietal). It is similarly useful to talk of affective or emotional when vital value dominates (e.g., periaqueductal gray area, anterior insula, orbitofrontal, medial prefrontal, posterior medial cortex). Affect and cognition, as complementary modes of processing, are in continuous *dialectical interrelation* (Pascual-Leone 2012; 2014; see Pessoa, p. 249) at the service of goal-directed activity: *activation of one mode tends to inhibit the other, although they are jointly needed to fully analyze external or mental experience*. Indeed, as Pessoa’s data show, when affect/emotion and pure cognition modes occur together *within the same task*, negative-affect activation may increase the use of mental-attentional effort as a result of the implicit executive-processing demand created by need to control the negative affect. Hence, truth value characterizes cognition and vital value affect; emotion involves co-existence of both values.

The second issue concerns organismic functional distinction among affect, emotion, and motivation. Affect and motivation are related, but they differ markedly (Pascual-Leone & Johnson 2004). Pessoa equates motivation with external reward (p. 135). However, a view “from within” the subject (i.e., metasubjective) shows it differently. Motivation has three conjoint characteristics: (a) *Affective motivation* is an implicit *conative* (i.e., purpose-seeking, quasi-volitional) *tendency* to convert conscious or unconscious *affective goals* into conscious or unconscious *cognitive goals*; (b) the *strength* or energy (magnitude of activation) *of this tendency is high*; (c) well-learned, purely cognitive schemes tend to apply, because schemes are self-propelling (Piaget’s *assimilation tendency* – with its *intrinsic cognitive-motivation strength*). Cognitive goals are dispositions to do something that is known, or believed, to be congruent with one’s affective goals. Affective goals are dispositions towards the future that seek certain vital outcomes or consequences (escape with fear, approach with love, attack with anger, etc.).

There is reason to believe that anterior and posterior cingulate gyri, albeit different, are interconnected sites where motivation

emerges (e.g., Beckman et al. 2009; Cromheeke & Mueller 2014; Pessoa, p. 237; Small et al. 2003; Torta et al. 2013). However, the network enabling affective motivation is much more complex. Without attempting a final formulation, our hypothesis is as follows (connections described here are often bidirectional, enabling loops). Once an instinctual-affect reaction in the midbrain occurs (perhaps in hypothalamus and periaqueductal gray area; Panksepp & Biven 2012), activation may spread to anterior insula (which may dynamically express organismic, interoceptive needs and costs) and to orbitofrontal cortex (which expresses current vital sensorial values, or external priorities, of the organism), among others. Then amygdala, one of the most connected context-and-situation sensitive sites for affect/emotion, synthesizes an *affective criterion of relevance* (Sander et al. 2003); it provides an implicit, current ranking of affective-organismic priorities for vigilance and attention. Hence, relative to appropriate threshold and in comparison to a baseline/control condition, low or nil activation of amygdala means low or nil *affective relevance* (*although a purely cognitive relevance of goals – Piaget’s assimilation tendency – might still exist*). Finally, we propose that affective/emotion information is transferred to anterior and posterior cingulate (ACC and PCC), where context-sensitive conversion of (here-and-now dominant) affective goals into cognitive goals takes place, to spread elsewhere (e.g., posterior medial cortex).

ACC can also be activated, expressing *schemes’ assimilation tendency*, in complex cognitive tasks with very low affective relevance and no amygdala participation. Perhaps ACC differs from PCC in that the former is more engaged in high affect or in cognitive conflict/*misleading* situations; whereas the latter is active in less affective and less complex cognitive (*facilitating*) situations. We believe that motivational choices can occur in cognitively simple situations with little participation of cingulate gyrus; however, in more complex cognitive situations, cingulate cortex will be needed. Hence, emotions are not pure affects but combine truth values (cognition) with vital values. Motivation may have intervened in the emergence of emotions via (a) and (b) – see the beginning of this issue-section. Once overlearned, emotions are strengthened as a result of (c).

The third issue concerns mental attention as a neutral brain resource, neither cognitive nor affective. Pessoa formulates the concept of a “performance-resource function” in general terms to characterize any kind of task activity (Pessoa 2013, p. 249). Nonetheless, relations of affect with *mental attention* (mental effort, working memory), and the relation of each to low (simple) cognition versus complex cognition, are unclear in the book. To effectively employ the construct of a performance-resource function, the “resources” must be properly and explicitly defined, which Pessoa does not do. Like most neuroscientists and experimental psychologists, he speaks of resources in plural, but likely means *mental/endogenous attention* – usually construed as working memory (Pascual-Leone & Johnson 2005). Clear definitions are needed of *automatic-perceptual attention* versus *mental/endogenous attention* (Arsalidou et al. 2010; 2013) and other brain resources – such as a neoGestaltist *internal-field* “simplicity” factor (possibly lateral inhibition in the brain) and an *overdetermination principle* – which together would permit *dynamic syntheses* in problem-solving acts. Clarity in these organismic constructs makes easier *process/task analyses* in neuropsychology (Pascual-Leone 2005; Pascual-Leone et al. 2009; Pascual-Leone & Johnson 2005; 2011). From this perspective, mental/endogenous attention appears expressed in the brain as a neutral resource (i.e., neither affective nor cognitive, albeit applicable to both).

The fourth issue addresses *overdetermination* of outcomes of brain processing, as a result of codetermination by many active, often connected, processes (cognitive and affective). Brain’s connectivity spreads activation within cofunctional and often coactivated neuronal lines – along circuits/pathways that *necessarily* express certain semantic-pragmatic probabilistic invariances that give psychological meaning to the circuits. We say *necessarily*,

because (given the anatomy and constraints on processing imposed by experience) pathways are activated and evolve in congruence with organismic and situational constraints. Thus, cofunctional and often coactivated neuronal circuits become unitized (coordinated) under these internal and external constraints, to characterize sorts of action (and change) in new situations. These coordinated functional invariances expressed in circuits are called *schemes* by Piaget and others (Arbib et al. 1998; Pascual-Leone & Johnson 2005; 2011). *Schemes* are unitized circuits or networks, embodying probabilistic *constraints/resistances* of (past, present, future) reality to the subject's actions or representations. They can be seen as self-propelling *systems that coordinate three distinct sorts of component*, all in dynamic/dialectical interaction: (a) a *releasing component* that contains *conditions* predicating features/templates that signal probable applicability of the scheme in question; (b) an *effecting component* that stipulates or carries cognitive, affective, or emotive *effects* of this scheme; effects whose application probabilistically brings results, often in a simultaneous or sequentially organized manner; and (c) a *functional component* that formulates the *gist* or overall functional description of the scheme: its practical importance and potential contribution to activities. In a very real sense, neural circuits are functional infrastructure of the scheme units formulated by constructivist psychological research.

As an illustration of how to apply the scheme construct to interpret brain circuits or networks, consider the connected (cognitive and affective) circuits that embody face recognition in humans (e.g., Arsalidou et al. 2011; Tsao & Livingstone 2008). Face perception and recognition use various brain areas, of which I mention seven of them, from (a) to (f): (a) occipital “face” area in the inferior occipital gyrus (a misnomer, because it analyzes intricate perceptual patterns, not only faces), which extracts figurative constituents (eyes, mouth, nose, etc.); (b) the fusiform “face” area, in the fusiform gyrus, that synthesizes meaningful figurative constituents into organized relational wholes (a face, flower, house, hands, etc.) as distinct perceptual totalities; (c) a site in the superior temporal sulcus (STS); and (d) the posterior middle temporal visual cortex (V5/MT – involved in visual motion awareness) – we note that in the latter two sites, temporally structured patterns of exploration are organized, leading to cognitive appraisal of distal objects such as a face and its meaningful mobile constituents, including gaze direction. (e) A more deeply cognitive interpretation of the complex object (e.g., the dynamic face) may require other areas such as left inferior frontal cortex (BA 47) and the occipito-temporal junction. (f) When emotion-affective relevance such as familiarity is involved, face recognition uses the amygdala. Both right and left hemispheres may participate in this processing, but the right hemisphere may be more involved in ordinary (*automatic*) face recognition.

When we apply the construct of *complex scheme* (a coordinated system of multiple subordinate schemes) to processing of meaning in the face, we notice that the occipital areas may provide *conditions* (releasing component) to the complex face scheme. The fusiform gyri may provide initial perceptual-configural *effects* (effecting component) to this face scheme. These effects would in turn serve as conditions of a further elaboration: a more complex cognitive face scheme produced by STS and V5/MT, which (these areas can coordinate sequentially occurring changes) would relate face movement-and-perspective sequences to yield cognitive-expressive and emotional, not just perceptual, meanings – with contribution from amygdala and BA 47, 37 etc. The *gist* (functional component) of the complex face scheme would of course be the context-relevant salient features of this *face scheme as a functional totality*.

Consider now the *schemes' overdetermination of performance* (Pascual-Leone 1984; 2012; Pascual-Leone & Johnson 2011), a principle that expresses the *self-propelling* disposition of schemes (brain circuits) with their spreading of activation in “multiple waves.” According to this principle, the full meaning of an object (e.g., face) is attained as multiple schemes with different

modes and modalities of processing (located in different sites) become coactivated and rally together to *overdetermine* total meaning (the cognitive-emotional import) of the complex object in question. From this perspective, automatized and controlled processes – embodied in different cofunctional and coactivated scheme circuits – become combined and work together, as Pessoa points out, because they are part of a more *complex* (superordinate) *scheme* they have together constituted with life experience and neuroplasticity.

Pessoa offers new ideas on the neuroscience of cognition and emotion. We have added some new distinctions to neuropsychology relevant for neuroscience, which might help to improve Pessoa's theoretical framework.

When emotion and cognition do (not) work together: Delusions as emotional and executive dysfunctions

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Abstract: In this commentary, I argue that the cognitive-emotional framework put forward by Pessoa (2013) can be successfully applied to psychopathology and, in particular, to the reasoning of *delusional subjects*. More specifically, I show that the notion of *executive competition* (Ch. 7) offers a significant contribution to the idea that delusions may involve both *executive* and *emotional* dysfunctions.

The proposal Pessoa puts forward in *The Cognitive-Emotional Brain* (2013) sets out to counter the standard paradigm of labeling brain regions as either *affective* or *cognitive*, offering instead a framework that does justice to the complex interactions among different neural systems. Notably, Pessoa presents a host of empirical evidence in support of the connection between the *amygdala* – traditionally associated with fear-detection or processing of negative information – and the *prefrontal cortex* (PFC), which is thought to play a central role in cognition. In particular, amygdala and PFC seem to cooperate in a number of tasks connected to *information gathering* and *salience detection*, such as discriminating between threatening and neutral facial expressions (see also Lim et al. 2009). Here, I argue that the cognitive-emotional framework Pessoa proposes can be successfully applied to psychopathology and, in particular, to the reasoning of *delusional subjects* (DS). First, I briefly show that delusions can be characterized in terms of *executive dysfunctions* that affect the ability to detect relevance in a context. Second, I utilize Pessoa's notion of *executive competition* (Ch. 7) to offer an original explanation of the executive deficits observed in DS.

In her recent book, Bortolotti (2009) convincingly argued that the pathological character of delusions cannot derive solely from their being *irrational*. Indeed, several everyday beliefs – for example, superstitious or religious – can be regarded as completely irrational without thereby qualifying as delusional (see Bortolotti 2009, p. 259). If characterizing delusions as irrational beliefs is clearly insufficient, then Bortolotti's conclusion calls for a more detailed explanation of why DS are worthy of clinical attention. One possible solution would be to qualify delusions in terms of *executive dysfunctions*, arising from some disturbance in the ability to detect relevance (or salience) in a context. From a phenomenological perspective, the idea that delusions may involve issues with relevance detection is supported by an analysis of case reports: indeed, DS often describe a peculiar keenness, as well as the feeling of “seeing” hidden connections between things. In

particular, the prepsychotic stage corresponds to a phase of “heightened awareness and emotionality” in which specific perceptions or ideas acquire “exaggerated importance” (Kapur 2003, p. 15). For example, in a first-person account of his illness, Aaron Reina (2009) reports that he gradually became convinced that one could determine “a person’s feelings, thoughts, and even their personality by the color combinations of their clothing” (p. 3).

From a cognitive perspective, the capacity to detect relevance in a context is often connected to *executive functions* such as shifting (i.e., switching between tasks or different aspects of the same task), updating (i.e., incorporating relevant information while removing irrelevant ones) and inhibition – for example filtering out inappropriate responses (see Miyake et al. 2000 for a thorough discussion). Notably, delusional patients seem to face serious challenges in every aspect of the executive domain. With respect to *shifting*, DS are often resistant to belief revision and find it particularly difficult to switch between different mental scenarios or interpretations, thereby displaying a peculiar *fixity* in their reasoning. For example, subjects affected by the Capgras syndrome would insist in claiming that their spouse has been replaced by an impostor, refusing to take other options into account (e.g., maybe my spouse looks different because she is tired). The ability to *update* instead requires some sort of “temporal tagging” in order to pry apart newer, more relevant information from old and no longer relevant data (Miyake et al. 2000, p. 57). Interestingly, one of the most common disruptions in delusional narratives concerns exactly *temporal ordering*: patients often experience “difficulties in indexing events in time,” and their stories are typically characterized by “a derailing of thought, constant tangents ... or the compression of a temporally extended story in a single gesture” (Gallagher 2007, p. 218). With respect to *inhibition*, some recent studies found that delusional patients fare significantly worse than controls in the Stroop Test, frequently employed to measure a subject’s degree of impulsivity (see Ibanez Casas et al. 2013; Rocca et al. 2006). Indeed, the test requires the ability to suppress an automatic response – that is, to read the word regardless of the color – in order to focus on a stimulus that is more relevant for the task at hand – that is, to read the color regardless of the word.

Although the correlation between executive functioning and delusions is at times considered controversial in neuropsychiatric research (see Guillem et al. 2008), more-specific studies have been recently conducted in this direction. For example, Ibanez Casas and colleagues have attempted to explore the degree of executive functioning impairment in patients affected by schizophrenia and delusional disorder. When flexibility, impulsivity, and updating were measured through standardized tests – for example, Stroop Test or Tower of London – DS tended to fare worse than controls (2013, p. 4). In a different study focused on attention and executive functioning, subjects affected by delusional disorder obtained lower scores also with respect to other psychiatric patients such as paranoid schizophrenics (see Grover et al. 2011). However – interestingly enough – DS have also been found to score *better* than controls in some selected areas: for example, they committed fewer errors in the Wisconsin Card Sorting Test (WCST), thereby suggesting some kind of “hyper-vigilance to selectively abstracted stimuli” (Ibanez Casas et al. 2013, p. 7).

The cognitive-emotional framework proposed by Pessoa offers a significant contribution to the characterization of delusions outlined above. On one hand, it describes *relevance detection* as an *affectively laden* process, in which emotions work as cues directing our attention to some elements of the context while disregarding others: in this sense, “vision is never *pure*, but only *affective*” (p. 257). On the other hand, it introduces the notion of *executive competition*, according to which the functions of shifting, inhibition, and updating often interact in a limited resources scenario, so that “resources devoted to one operation will not be available for other operations” (p. 161). Notably, Pessoa maintains that

executive functions and emotional processing share a *common pool of resources*: this means that emotional content may influence executive control in various ways (although the reverse is also possible – see pp. 121 and 251). In particular, when an emotional stimulus is strong enough, task performance will often be impaired because additional resources are diverted from the executive functions in order to process the affective content (see also Mather & Sutherland 2011; Pessoa et al. 2012).

Applying this framework to delusional patients represents an interesting challenge. Indeed, the executive dysfunctions observed in DS may indicate that their attention is disproportionately directed toward specific – and emotionally significant – elements of the context. For example, persecutory delusions might originate from a strong feeling of anxiety that prompts patients to attend more closely to threatening stimuli in the environment. In these cases, a highly threatening emotional content causes resources to be diverted from the main task, and performance declines as a result (see Pessoa 2009, p. 161). Several studies on highly anxious – although nonclinical – populations already support this point (see Fox et al. 2002; Norberg et al. 2010). Thus, Pessoa’s proposal sheds an interesting light on the pathological reasoning observed in DS, which can then be explained in terms of *resources* that are “taken up” in order to process complex – and often threatening – emotional items. For example, a patient affected by Capgras would direct attention to the stimuli related to his “feeling of estrangement” towards the spouse, thereby finding it hard to revise the belief that she or he has been replaced by an impostor in favor of a more “mundane” interpretation.

Connecting delusions, emotional processing, and executive functions requires a greater level of precision in determining what goes wrong in this aberrant process of relevance detection, however. What exactly makes the patient’s reasoning abnormal or pathological? Here, the notion of *negative distractor* introduced by Pessoa may come in handy. Indeed, he argues that emotional contents can modulate attention in a way that either *enhances* or *impairs* task performance, depending on the level of strength – or arousal – of the stimulus. Roughly put, when the affective significance of a stimulus is low, performance would generally increase because the resources can be efficiently “mobilized in the service of handling the task at hand” (p. 167). On the contrary, items with sufficiently high affective significance – regardless of their relevance to the task – tend to compromise performance. In this sense, the emotionally laden items work as negative distractors that drain common pool resources from the main task (see p. 172). If this interpretation is correct, the *executive competition model* proposed by Pessoa would provide an interesting explanation for the specific deficits observed in DS (see Grover et al. 2011; Ibanez Casas et al. 2013). Indeed, the delusional content itself may work as a powerful *distractor* absorbing the patient’s attention and directing resources away from the functions that are needed to complete the task at hand. To make this point more explicit: delusional patients may continually perceive threatening – or otherwise negative – stimuli in the environment, which force them to invest a disproportionate amount of resources that become unavailable to other cognitive functions. From a neurological viewpoint, this process need not translate to decreased activation of the relevant brain areas (e.g., amygdala, PFC), but rather reflects the fact that some common pool resources are “taken up” in dealing with delusional beliefs. This is consistent with Pessoa’s findings, according to which negative distractors can at times produce *increased* activation of the relevant networks (see pp. 128–29). Therefore, the DS’s poor outcome in executive tests may be caused by an *overworking* executive system, where highly significant items continuously drain resources from the current task. In this sense, the proverbial *fixity* associated to delusions would result from the subject’s incapacity to process – or even “see” – other elements of the context as emotionally and functionally relevant.

The application of Pessoa’s proposal to psychopathology also allows us to resolve an apparent inconsistency arising from one

of the studies discussed above (Ibanez Casas et al. 2013). Indeed, the fact that DS fared better than controls in some selected areas (e.g., WCST) indicates that their executive abilities should not be understood as impaired, but rather as *dysfunctional*. In other words, DS disproportionately direct their resources toward specific stimuli in the environment because they perceive them as pervasive, affectively significant, and in need of additional processing. Thus, DS can be regarded as being in a permanent – or at least frequent – condition of *overload*, that phenomenologically reflects the feeling of “hypersalience” observed in several patients (see Kapur 2003; Speechley et al. 2010). As Pessoa would put it, DS continuously face demands that exceed their available capacity of processing, causing performance to suffer when the task specifically requires attention (see pp. 89 and 98).

To sum up, the account of delusions outlined here has two main advantages. First, it offers an explanation of their pathological character that goes *beyond* the mere ascription of irrationality (see Bortolotti 2009). Second, it strengthens the connection between delusions and executive dysfunctions, which is still considered controversial in the neuropsychiatric literature (see Guillem et al. 2008). Notably, the *executive competition* model proposed by Pessoa offers an important contribution to the idea that delusions may involve both *emotional* and *executive* dysfunctions. On one hand, particularly strong emotions shape the patient’s attention and direct it towards specific elements of the context (Ch. 2). Here, the guiding emotion may vary depending on the delusional content, although we can safely assume that *fear* would play a key role (e.g., threatening stimuli in persecutory delusions). On the other hand, affectively laden items work as *negative distractors* that monopolize executive functions that then become unavailable for other tasks (Ch. 7). In order to test this hypothesis empirically, I propose to extend Pessoa’s studies on the relationship between emotions, attention, and executive control to delusional populations (see Pessoa 2005; 2008; 2009). In particular, it would be interesting to see whether the regions connected to cognitive-emotional interactions (e.g., amygdala, PFC) experience an increase or decrease in activation while DS are dealing with emotionally laden interferences in executive tasks.

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Active inference and cognitive-emotional interactions in the brain

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Abstract: All organisms must integrate cognition, emotion, and motivation to guide action toward valuable (goal) states, as described by active inference. Within this framework, cognition, emotion, and motivation interact through the (Bayesian) fusion of exteroceptive, proprioceptive, and interoceptive signals, the precision-weighting of prediction errors, and the “affective tuning” of neuronal representations. Crucially, misregulation of these processes may have profound psychopathological consequences.

The notion that humans have separate and often conflicting faculties for “cognition” and “emotion” has long fascinated scholars and laymen, as exemplified by Pascal’s motto, “The heart has its reasons, which reason does not know,” and by the emotionless (but rational) *Star Trek* character Mr. Spock.

In cognitive science, the distinction between cognition and emotion is echoed in the idea that segregated brain areas implement cognitive and emotional functions and that there are two independent processing “routes,” one cognitive/controlled and one emotional/automatic, which usually compete (but also occasionally cooperate) to control behavior (Kahneman 2003a). However useful this “dual-systems” view might be, one would not expect dichotomies inherited from folk psychology – such as *cognition versus emotion* (or even *perception vs. representation vs. action*) – map one-to-one to functionally segregated brain areas. Compelling evidence, reviewed in Pessoa’s *The Cognitive-Emotional Brain* (2013), challenges the segregation of cognitive and emotional processing in the human brain. The emerging view is that not only cognition interacts with emotion at many levels; but in many respects they are functionally *integrated* and continuously impact each other’s processing.

Studying cognitive-emotional interactions by focusing on advanced cognitive abilities (e.g., how the processing of affectively charged stimuli influences executive control) is important to better understand human cognition. However, this is not the only approach. Cognition and emotion have always been tightly linked; they were linked even before the emergence of sophisticated human abilities. The ancestral reasons for this linkage can be traced back to the demands of situated action control, not of complex cognitive problems; it might be an important requirement of organisms that, as Pavlov (1927) has once put it, need to maintain a balance between the internal milieu of the body and the external world.

The basic design of the human brain was largely evident in simpler animals that had to solve the basic problems of survival in situated environments rather than higher cognitive problems. All that mattered for those animals was deploying adaptive behavior to fulfill their needs and motivations – in other words, acting to disclose “desired” or goal states (Cisek 1999; Friston 2013; Pezzulo & Castelfranchi 2009). In turn, pursuing goals requires animals to select what is *valuable* for them to do (adaptive behavior) or *meaningful* to process, remember, and predict (perception and cognition). In this perspective, solving the most elementary problems of adaptive behavior requires a close synergy between some (perhaps rudimentary) forms of perception, cognition, emotion, and motivation. Indeed, lower species possess emotional and motivational abilities, here broadly conceptualized as processes that mobilize bodily resources and invigorate actions, control interoceptive signals and autonomic states, bear on the value (and saliency) of stimuli, goals, and information gain, modulate selection processes, and deal with ecologically meaningful events such as rewards and punishments or their expectations (Panksepp 2011; Rolls 2005).

Importantly, in order to be useful for adaptive behavior, the contribution of emotion and motivation has to be *integrated* in a timely manner within the organism’s action-perception cycle. What is currently *valuable* is highly contextual and governed by numerous factors that entail perception and cognition, including metabolic costs, affordances, and the available repertoire of choices (e.g., for a gazelle, finding food versus escaping from a lion). Considering all of these factors represents a serious challenge for architectures that segregate perception, action, and utility (Cisek & Pastor-Bernier 2014; Lepora & Pezzulo, in press; Verschure et al. 2014).

The evolutionary perspective pursued here implies that the very fabric of cognition – from its ancestral origins to the most modern and sophisticated skills – is inextricably linked to utility, adaptivity, and meaningfulness; and in turn these should imbue cognitive processing at large, as testified by the ubiquitous presence of value- and outcome-related signals in the brain (Vickery

et al. 2011). Furthermore, this perspective suggests that cognitive-emotional interactions can be better understood within a *systems-level framework* that explains how cognition and emotion resolve basic adaptive problems and how elaborations of these basic processes underpin cognitive abilities.

Active inference offers one such framework (Friston 2010). Active inference considers that organisms act to fulfil prior beliefs or expectations that encode the (evolutionary) values of their states (e.g., having access to food). In this framework, the brain is a statistical organ that learns the structure of the (external and internal) world and the causes of perception (and interoception) in the form of hierarchical models. Such models support both perception (predictive coding) and action (active inference) in a seamless fashion by minimizing free energy or, more simply, prediction error.

Perception corresponds to (Bayesian) inference that tests cognitive hypotheses—encoded at higher hierarchical levels—against sensory evidence. The higher levels generate predictions in a top-down manner, and the discrepancy (prediction error) between descending predictions and sensations compete to update perceptual hypotheses (i.e., select the hypothesis that minimizes prediction error). Crucially, prediction errors can also be minimized through action. Here, *active inference* enters the scene and adds two novel ingredients to the picture (Friston et al. 2009). First, top-down predictions can act as higher level goals for the organism (e.g., being satiated); and, second, goals steer a cascading flow of exteroceptive and proprioceptive predictions that are fulfilled by peripheral (motor and autonomic) reflexes—until the goal state is achieved.

Up to now we have focused on the minimization of exteroceptive and proprioceptive prediction errors. However, the same principles apply to the regulation of interoceptive and bodily information that links to the autonomic system to sympathetic and parasympathetic systems. This *interoceptive inference* has been linked to emotion and self-awareness (Friston et al. 2014; Seth 2013; Seth et al. 2012). In this view, the internal world is controlled by autonomic reflexes that fulfill descending interoceptive predictions—where descending predictions provide homeostatic setpoints. These interoceptive predictions are one aspect of multimodal predictions from high-level beliefs about our embodied self (literally our “gut feelings”). In this formulation, interoceptive information does not cause self awareness, or vice versa: There is a circular causality in which hierarchical representations enslave autonomic reflexes, whereas interoceptive prediction errors inform hierarchical representations. Emotion can therefore be regarded as a necessary attribute of any representation that engenders interoceptive predictions.

To characterize the adaptive function of emotions and feelings (Damasio & Carvalho 2013)—and their integration within the action-perception cycle—we consider how adaptive behavioral control rests on the functional *integration* of exteroceptive, proprioceptive, and interoceptive signals. These have complementary roles: Interoceptive prediction errors inform the current motivational need (or drive) of an animal, in terms of a discrepancy between optimal homeostatic levels (e.g., hunger in terms of low glucose), whereas exteroceptive and proprioceptive prediction errors specify allostatic goals in terms of the sensory states the animal has to solicit by acting (e.g., the sensations of eating). Suppressing the exteroceptive prediction errors (that report the fact that I am not currently eating) can be resolved by acting (eating), which in turn suppresses interoceptive prediction errors engendered by an empty stomach.

That simple scenario exemplifies how hierarchical inference supports motivated behavior, while laying the foundations of emotional-cognitive integration. In turn, this integration spans other domains of perception, cognition, and affect. For example, interoceptive and exteroceptive streams can be integrated to support a “cognitive-emotional” inference. In this *embodied predictive coding* perspective (Pezzulo 2013), the most plausible causes of events are inferred based on both exteroceptive (what I see)

and interoceptive (how do I feel) cues. An affectively charged event, such as the presence of a predator can be recognized and categorized from both its perceptual characteristics and the fear it instills in us—with a form of perception that is not “pure” but affectively biased (Barrett & Bar 2009). This in turn induces a circular causality; where fear is both a cause and a consequence of (predator) perception. The temporal span of this process offers various opportunities to impinge on other processes such as memory and planning.

Note that in embodied predictive coding, some “cognitive” processes are off-loaded to the body, as bodily states (e.g., high arousal state or heart rate) become part and parcel of the inference and can influence it (Garfinkel et al. 2014). The potential adaptive value of this body-based mechanism is apparent in dangerous situations, where high arousal can prioritize cognitive processing. Note also that patients with congenital insensitivity to pain have problems in recognizing potentially harmful scenarios.

Interoceptive signals can report motivational urges, too, so that the mismatch between an internal need (e.g., hunger) and sensory stimuli (e.g., no food) can modulate the importance of visual signals (Montague & King-Casas 2007) and focus attention (Mysore & Knudsen 2011). In active inference, these dynamics depend on a *precision-weighting* mechanism that underpins all hierarchical inference. This mechanism prioritizes top-down ascending prediction errors depending on their precision (inverse variance), and—as a consequence—it regulates various *competitive* processes (Desimone & Duncan 1995), both within levels (e.g., between perceptual hypotheses) and across levels (e.g., giving prominence to prior beliefs over sensory evidence). In addition, precision dynamics regulate the balance between goal achievement and belief revision, because expectations having high precisions are immune to revision by prediction errors and thus act as immutable goals that steer action.

Precision-weighting has been linked to neuromodulation and the control of *attention* (in the perceptual domain) and *affordance* (in action selection) (Feldman & Friston 2010). Precision-weighting is a key source of cognitive-emotional modulations, too. Supposing that valuable goals or needs are reported by exteroceptive or interoceptive signals with high precision, they focus perceptual processing on events that have behavioral significance. Furthermore, they induce a cascade of top-down predictions and subsequent action (Friston et al. 2012). More broadly, *precision-weighting* is a flexible mechanism through which an organism's goals and needs prioritize processing dimensions for cognition and emotion: which events should be attended to and predicted (attention and planning) and what are their outcomes and affective consequences (emotion); which expectations have value and should be fulfilled (goal achievement); which prediction errors should be monitored and corrected (cognitive control); and what should be learned from them (memory). By the same mechanism, conflicts between “cognition” and “emotion” can be created in psychological experiments; for example, by using affectively charged but task-irrelevant stimuli as “distractors.”

We have described how precision dynamics prioritize active inference depending on affective or motivational value. In a similar way, at the longer timescale of learning, neuronal coding resources can be prioritized to capture the most behaviorally significant events in the long-range statistics of interoceptive and exteroceptive signals. This phenomenon might produce an “affective tuning” of neural representations at multiple levels. For example, (Machens et al. 2005) report that auditory neurons in the grasshopper are particularly sensitive to a behaviorally relevant stimuli—mating signals—rather than representing the unbiased distribution of natural sounds. At deeper hierarchical levels, neuronal populations might encode expectations of states that have value for the organism (goal states) with higher resolution. This has cascading consequences on perception and action because—in active inference—precise expectations at higher hierarchical levels enslave behavior. Furthermore—pursuing an embodied view of cognition—the same hierarchies supporting action-

perception loops might be reused for more advanced cognitive abilities such as planning, mindreading, and executive function (Barsalou 2008; Jeannerod 2006; Pezzulo 2012; 2014; Pezzulo et al. 2011; 2013; 2014). This suggests that the same “affective tuning” of neuronal hierarchies naturally biases higher cognitive abilities, too.

In sum, various active inference mechanisms reviewed here – embodied predictive coding, precision dynamics, and the affective tuning of neural representations – offer a rich substrate for cognitive-emotional interactions. At the same time, they are prone to vulnerabilities and misregulations, which might produce psychopathological states such as anxiety disorders and psychotic symptoms (Adams et al. 2013; Friston et al. 2014). Some forms of psychopathology might depend on (precision-mediated) misregulations at the cognitive-emotional interface. For example, eating disorders could arise from the failure to handle conflicting information at the level of interoceptive signals (e.g., hunger) versus body schema and (false) belief (e.g., seeing oneself as fat). In active inference, this deficit is not purely representational but determines how subjects act (and think); for example, anorexics plan their actions as if they had an enlarged body (Keizer et al. 2013). Conceptualizing psychopathological states in terms of active inference may shed light on this intriguing domain, where cognitive-emotional interactions are clearly evident in both a clinical and neuropsychological sense.

The cognitive-emotional brain: Opportunities and challenges for understanding neuropsychiatric disorders

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Abstract: Many of the most common neuropsychiatric disorders are marked by prominent disturbances of cognition and emotion. Characterizing the complex neural circuitry underlying the interplay of cognition and emotion is critically important, not just for clarifying the nature of the mind, but also for discovering the root causes of a broad spectrum of debilitating neuropsychiatric disorders, including anxiety, schizophrenia, and chronic pain.

Until the twentieth century, the study of cognition and emotion was largely a philosophical matter. But recent years have witnessed the emergence of powerful new tools for interrogating the brain and new areas of multidisciplinary research focused on identifying the neurobiological mechanisms underlying cognition, emotion, and their role in mental health and disease. In *The Cognitive-Emotional Brain*, Luiz Pessoa (2013) provides an authoritative perspective on this recent work and its implications for our understanding of the basic building blocks of the mind. Here, we highlight four of the book’s most important implications for understanding neuropsychiatric disorders, including anxiety, schizophrenia, substance abuse, chronic pain, and autism. These

disorders cause enormous suffering for millions of patients and their families, outstripping the global burden of cancer or cardiovascular disease (Collins et al. 2011; Goldberg & McGee 2011; Kessler et al. 2012; Whiteford et al. 2013). Notably, these disorders involve prominent alterations in both cognition and emotion (Millan et al. 2012), pointing to the need for a deeper understanding of the cognitive-emotional brain.

First, *The Cognitive-Emotional Brain* reminds us that mental faculties emerge from the coordinated interactions of large-scale brain networks. Put simply, fear, reward, attention, and other psychological processes cannot be mapped to isolated brain regions because no one region is both necessary and sufficient. Conversely, similar symptoms can emerge from damage to different regions in the same functional network (Karnath & Smith 2014). Pain, which is among the most prevalent clinical disorders (Institute of Medicine 2011), nicely illustrates this point. Pain is a multidimensional experience, involving systematic changes in both cognition and emotion: painful stimuli elicit anxiety, capture attention, and motivate action. Neurobiologically, pain is associated with a complex pattern of regional activation, often termed the “pain matrix” (Iannetti et al. 2013). Stimulation of individual components of the pain matrix does not consistently elicit pain, suggesting that pain and its disorders are emergent properties of regional interactions. This is not a new or contentious idea; pioneers like Mesulam, Goldman-Rakic, and LeDoux highlighted the importance of distributed neural circuits more than two decades ago, and there is widespread agreement among basic and translational researchers (Bullmore & Sporns 2012; Fornito et al. 2015; Goldman-Rakic 1988; LeDoux 1995; 2012; Mesulam 1998; Turk-Browne, 2013; Uhlhaas & Singer 2012). *The Cognitive-Emotional Brain* is a bracing call for accelerating the transition from localization strategies (i.e., mapping brain structures to function; sometimes termed “neophrenology”) to a network-centered approach. From a clinical neuroscience perspective, this suggests that understanding neuropsychiatric disorders will require embracing the kinds of analytic tools (e.g., functional connectivity fingerprinting, graph theoretic and machine learning approaches) that are necessary for elucidating how psychological constructs and mental disorders are realized in brain circuits (Turk-Browne 2013; Woo et al. 2014).

Pessoa’s second key conclusion is that the identity of brain functional networks, including the circuitry that underlies clinically relevant phenotypes, cannot be inferred from neuroanatomy alone. Pessoa makes it clear that the networks identified by functional magnetic resonance imaging (fMRI) and other neurophysiological techniques do not necessarily recapitulate the pattern of direct connections revealed by invasive anatomical tracing techniques. Indeed, there is ample evidence of robust functional connectivity between brain regions that lack direct structural connections (Adachi et al. 2012; Birn et al. 2014; Honey et al. 2009; Vincent et al. 2007) and increasing evidence that regulatory signals can propagate across complex, indirect pathways (Ekstrom et al. 2008). From a clinical perspective, this indicates that fMRI-derived measures of functional connectivity are particularly useful because they can be used to assay dysfunctional networks that encompass polysynaptically connected nodes (Birn et al. 2014), just as viral tracers can be used to delineate polysynaptic anatomical pathways in the nervous system (Dum et al. 2009). More broadly, *The Cognitive-Emotional Brain* implies that many of the signs and symptoms of mental disorders – anhedonia, hypervigilance for threat, working memory impairments, drug seeking, and so on – will reflect complex brain circuits (Okon-Singer et al. 2015; Seminowicz et al. 2004; Shackman et al. 2013; Stout et al. 2013).

The third key conclusion is that emotion and cognition are not different in kind but are instead deeply interwoven in the fabric of the brain. Subjectively, we often experience cognition and emotion as fundamentally different. Emotion is saturated with feelings of pleasure or pain and manifests in readily discerned changes in the body, whereas cognition often appears devoid of substantial hedonic, motivational, or somatic features. These apparent differences in phenomenological experience and peripheral physiology

have led many scholars to treat emotion and cognition as categorically distinct, even oppositional, mental forces that presumably reflect the operation of segregated brain circuits (de Sousa 2014; Schmitter 2014). A similar dichotomy pervades psychiatric nosology. But careful scrutiny reveals contrary evidence; cognition can arouse the face and body; conversely, emotion can profoundly alter attention, working memory, and cognitive control (Grupe & Nitschke 2013; Okon-Singer et al. 2015; Shackman et al. 2011). *The Cognitive-Emotional Brain* provides a useful survey of recent brain imaging research demonstrating the integration of emotional and cognitive processes in the brain (Shackman et al. 2011). Largely on the basis of brain imaging data, Pessoa joins with other theorists in rejecting claims that emotion and cognition are categorically different (Barrett & Satpute 2013; Damasio 2005; Duncan & Barrett 2007; Lindquist & Barrett 2012). Elucidating the contribution of the cognitive-emotional brain to psychopathology mandates the joint efforts of cognitive, affective, computational, and clinical neuroscientists. This kind of multidisciplinary research would refine our understanding of the mechanisms that give rise to “mixed” cognitive-emotional symptoms, such as hypervigilance or aberrant reinforcement learning (Cavanagh & Shackman 2014), and provide novel targets for intervention.

Pessoa’s fourth and most original conclusion is a powerful synthesis of the first three. Pessoa argues that widely held beliefs about the constituents of “the emotional brain” and “the cognitive brain” are fundamentally flawed. Regions such as the amygdala are not “emotional,” and regions such as the dorsolateral prefrontal cortex (dlPFC) are not “cognitive” (Birn et al. 2014; Buhle et al. 2014; Fox et al. 2005; Shackman et al. 2009). Both regions play a central role in the regulation of adaptive behavior. This should not be surprising – the human brain did not evolve to optimize performance on artificial laboratory probes of “pure” cognition or emotion. Pessoa also makes it clear that brain regions can dynamically assume different roles. Just as an individual can perform psychologically distinct roles in different social networks (e.g., executive, mother, sister, daughter), brain regions are poised to perform a range of functions (a property termed functional “superimposition”) in different neural “contexts” corresponding to their level of participation in particular functional networks. To paraphrase Pearson and colleagues (Pearson et al. 2014), key brain regions, such as the orbitofrontal cortex, are functionally heterogeneous, with individual neurons dynamically multiplexed into different functional roles. As such, they will “evade a single, modular, functional role assignment” (p. 954). Our brain reflects evolutionary pressures that demanded distributed neural systems capable of using information about pleasure and pain, derived from stimuli saturated with hedonic and motivational significance, to adaptively regulate attention, learning, somatic mobilization, and action in the service of maximizing reproductive fitness. From this perspective, it is easy to imagine how dysfunction of circumscribed territories of the brain can have a deep impact on distal regions and circuits, as recent work by our group and others demonstrates (Fox & Kalin 2014; Fox et al. 2010; Gratton et al. 2012). This may help to explain the co-occurrence of cognitive and emotional symptoms, as well as frequent comorbidities, among psychiatric and neurological disorders. Clarifying the nature of the cognitive-emotional brain is likely to have substantial benefits for our understanding of disorders marked by symptoms that blend elements of cognition and emotion (e.g., hypervigilance to potential threat or overgeneralization of threat, in the case of the anxiety disorders [Grupe & Nitschke 2013]).

Although many challenges remain, *The Cognitive-Emotional Brain* provides a road map to the most fruitful avenues for future research. One of the most important unresolved questions concerns the functional significance of regions activated by both cognitive and emotional challenges. For example, Pessoa highlights a recent meta-analysis from our group demonstrating that the elicitation of negative affect, pain, and cognitive control are all associated with activation in an overlapping region of the MCC (Shackman et al. 2011). A key unresolved question is whether the MCC and other regions implicated in both cognitive

and emotional processes, such as the anterior insula, perform a single general function (e.g., adaptive control [Cavanagh & Shackman, in press; Shackman et al. 2011]) or salience detection (Iannetti et al. 2013) or multiple specific functions.

On a broader note, much of the evidence surveyed by Pessoa comes from the human brain imaging literature. Accordingly, his conclusions are ultimately tempered by questions about the origins and significance of the fMRI signal and the measures of functional connectivity that underlie network-centered approaches to understanding the cognitive-emotional brain (Akam & Kullmann 2014; Cabral et al. 2014; Logothetis 2008). An important challenge for future studies will be to combine mechanistic techniques in animal models (e.g., optogenetics) with the same whole-brain imaging strategies routinely applied in humans (Birn et al. 2014; Borsook et al. 2006; Casey et al. 2013; Narayanan et al. 2013; Oler et al. 2012; Roseboom et al. 2014). Combining noninvasive mechanistic techniques (e.g., transcranial magnetic stimulation or transcranial direct current stimulation) or pharmacological manipulations with fMRI provides another opportunity for understanding how circumscribed perturbations can produce distributed dysfunction (Chen et al. 2013; Guller et al. 2012; Paulus et al. 2005; Reinhart & Woodman 2014).

For many disorders marked by cognitive and emotional disturbances, extant treatments are inconsistently effective or associated with significant adverse effects (e.g., Bystritsky 2006). *The Cognitive-Emotional Brain* provides an insightful survey of state of the science and a useful stimulus for the next generation of basic and clinical research, reminding us that we have a remarkable opportunity to use new tools for understanding brain function to discover the origins of neuropsychiatric disease.

Strengthening emotion-cognition integration

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Abstract: Pessoa’s (2013) integrative model of emotion and cognition can be strengthened in two ways: first, by clarification and refinement of key concepts and terminology, and second by the incorporation of an additional key neural system into the model, the locus coeruleus/norepinephrine system.

We agree with Pessoa’s (2013) integrative view of emotion and cognition in *The Cognitive-Emotional Brain*, and we agree with his network view of the brain’s cognitive-affective architecture. We suggest, however, that these viewpoints can be strengthened in two ways. First, their key concepts and terminology need clarification and refinement, in order to foster exchange between the parallel but mutually insulated research streams of affective science and the science of decision making. Second, Pessoa’s “dual competition model” of cognition-emotion would benefit from the incorporation of an additional key neural system for the affective biasing of attention, decision making, and control processes – the locus coeruleus/norepinephrine system. In this commentary, we address these two points in turn.

Concepts and terminology. Pessoa states that he will not define the terms “emotion” and “cognition,” but instead will use them “descriptively” to refer to paradigms, task conditions, or “processes” that are closer to the traditional, intended meanings of emotion and cognition” (p. 3). Although he observes that these meanings

do not reflect real distinctions in kind but simply different lines of research, he often unwittingly perpetuates the emotion-cognition dichotomy by following the traditional usage. For example, in chapter 6 he describes “emotion” as referring to positive and negative affective states, and “motivation” as referring to motor actions of approach and avoidance, thereby following the standard division of the disciplinary territory into research on emotion and research on decision making. This division is perpetuated by discussing “motivation” and “value representation” with reference to decision making and by discussing “emotion” with reference to affective science, as well as by discussing these two bodies of literature in separate chapters. Yet, as Pessoa points out, these two lines of research actually investigate a single family of phenomena. Moreover, as he acknowledges, both lines of research manipulate both the positive and negative *value* (to use terminology from decision making) or *valence* (to use terminology from emotion literature) of a stimulus, which in turn influences both selective-attention processes that occur upstream of emotional state and action, and more downstream measures that include accuracy, choice, and eye movement. For example, as Pessoa describes in detail, both emotion and decision-making research employ aversive and appetitive conditioning to examine the influence of affective salience on attention, action, and control processes. The distinction between motivation and emotion also breaks down within affective science itself, as many emotion theorists include action tendencies as constitutive of emotion (e.g., Frijda 1986). Throughout the book there is also conflation between “motivation” and “emotion,” on the one hand, and the actual value or valence of a stimulus, on the other hand, where “emotion” sometimes refers to manipulations of negative value and “motivation” to positive value, in defiance of the previous distinctions between the terms.

For these reasons, we suggest that a consistent terminology would help to foster a common language between the parallel but mutually insulated areas of research in affective science and the science of decision making. Better still would be to treat these two areas as making up one single field of research. Hence, recent research coming from both traditions has benefited from distinguishing between “salience” (overall importance of a stimulus, negative or positive) and “value” in order to parse neural systems sensitive to salience, value, or both (Chikazoe et al. 2014; Kahnt et al. 2014).

This point is important for Pessoa’s comprehensive review of amygdala function. He states, “though the precise contribution of the amygdala in these networks is still unknown, it does not map specifically onto emotion, but, instead, corresponds to broader and more abstract dimensions of information processing, including salience, ambiguity, unpredictability, and other aspects of *biological value*” (p. 78). We propose that positive and negative value (typically discussed in the emotion literature in terms of valence), ambiguity, and unpredictability are all aspects of overall salience. We have previously described “affective salience” as a quality that endows a stimulus with prioritized access to attention and action because it has been associated with pleasure/pain or approach/avoidance (e.g., novelty and surprise signal prediction error, which is arguably intrinsically affectively charged) (Markovic et al. 2014; Todd et al. 2012a). We describe this quality as “affective salience” in order to distinguish it from “objective salience,” which is related to physical features of an object as described in vision research (Todd et al. 2012b). The notion of “affective salience,” which incorporates features of ambiguity, novelty, surprise, and value, maps onto Pessoa’s summary of amygdala function – determining what something is and whether it is important to attend to it and do something about it.

Along similar lines, it is also helpful to clarify the difference between emotional state and the influence of stimulus salience on behavior. “Emotional state” refers to a sustained state of arousal within the perceiver, whereas “stimulus salience” refers to the degree to which a discrete stimulus may bias attention because of its association with arousal, value, etc. This distinction is important but is often conflated in the literature. Pessoa

discusses Mather’s model of arousal-biased competition (Mather & Sutherland 2011), which models the influence of affective state on attention and memory. We in turn have proposed the complementary notion of “affect-biased attention” (Todd et al. 2012a), which is attention biased by the affective salience of the stimulus itself. Affect-biased attention is the predisposition to attend to certain categories of affectively salient stimuli over others; it tunes filters for initial attention and subsequent processing and thereby regulates subsequent emotional responses (Todd et al. 2012a). Hence, it provides an important example of emotion-cognition integration in the brain and behavior.

Enlarging the dual competition model. Pessoa’s dual competition model of cognition-emotion is a timely, sophisticated, and empirically grounded model that unifies disparate findings on the interrelations between affective salience, emotional state, and controlled cognitive processes into a coherent theoretical framework. In outlining this model, Pessoa proposes six key mechanisms for affective modulation of visual activity (pp. 161–66). The locus coeruleus/norepinephrine (LC/NE) system is not a component of this model, although it is discussed briefly in relation to its modulation of frontoparietal attentional networks via basal forebrain cholinergic and GABA projections. Beyond its interactions with other neurochemical systems, we propose that the LC/NE system in itself constitutes a seventh mechanism and is central to understanding the effects of salience on cognition and action.

The locus coeruleus is a brainstem nucleus that produces norepinephrine (NE) and sends projections to most regions of the brain, including the visual cortex, orbitofrontal cortex (OFC)/ventromedial prefrontal cortex (VMPFC), thalamus, and amygdala, as well as important nodes in networks mediating executive attention and motor response (Sara 2009). Our own “biased attention via norepinephrine” (BANE) model outlines the role of this system, in interaction with the amygdala and OFC/VMPFC systems described in Pessoa’s dual competition model, in biasing attention and memory to relevant aspects of the world (Markovic et al. 2014). The LC/NE system plays an important role in the modulation of attention and control processes by affective salience (Sara 2009; Sara & Bouret 2012). The LC is structurally well positioned to facilitate affect-biased attention. It receives inputs from the central nucleus of the amygdala (Berridge & Waterhouse 2003), as well as from ventral prefrontal regions important for stimulus evaluation and decision making (for review, see Aston-Jones & Cohen 2005), facilitating tuning of LC activity to what is motivationally relevant. The LC itself also projects to regions of the thalamus and visual cortex (Jones & Moore 1977), allowing for rapid tuning of sensory responses.

Nonhuman animal studies have found that motivationally relevant stimuli elicit LC response (for review, see Sara 2009; Sara & Bouret 2012), and LC-NE activity has been shown to directly modulate visual cortex activation (Waterhouse et al. 1990). A wide body of evidence suggests that LC neurons facilitate responses to the overall salience of a stimulus (Sara 2009), modulating activity for stimuli that are positive and negative in value, as well as those that are novel and surprising (Berridge & Waterhouse 2003). Arousing stimuli elicit phasic LC activation, resulting in release of NE (Aston-Jones & Bloom 1981; Grant et al. 1988; Herve-Minvielle & Sara 1995; Rasmussen & Jacobs 1986). Released NE may tune target neurons by improving their signal-to-noise ratio, inhibiting responses to neighbouring frequencies while sparing response to the best frequency (Manunta & Edeline 2004). LC activity is also important in associative learning of *what* is salient. LC neurons fire in response to direct reward and punishment and subsequently to any stimuli associated with the salient event (Sara 2009). Moreover, NE modulation of long-term changes in synaptic strength and gene transcription allow the LC/NE system to guide behavior based on stimulus salience within a given context (Berridge & Waterhouse 2003).

NE also plays a crucial role in the emotional enhancement of memory via activity in the amygdala (Cahill et al. 1996; 2003; Roozendaal et al. 2009). In humans, a deletion variant in the *ADRA2b* gene impairs alpha2b NE receptor function, putatively affecting tonic levels of NE availability (Small et al. 2001). The *ADRA2b* deletion variant has been linked to individual differences in tuning to affectively salient aspects of the world, including emotional enhancement of memory (de Quervain et al. 2007). We have found that it also influences selective visual attention to affective salience. In an emotional version of the attentional blink task described by Pessoa (Anderson 2005; Anderson & Phelps 2001), we found that carriers of the deletion variant show an “emotional sparing” or a reduced attentional blink for affectively salient stimuli (Todd et al. 2013). They also showed a stronger link between the perceived salience of stimuli at encoding and accuracy and confidence of subsequent recognition memory (Todd et al. 2014). Moreover, in deletion carriers we have found that enhanced visual processing of affectively salient stimuli is linked to greater activation in nodes of valuation networks (Rasch et al. 2009). These findings support a role for the LC/NE system in affective biasing of visual attention in humans.

The BANE model makes a number of predictions that add to our understanding of processes outlined in Pessoa’s model. These include the prediction that *ADRA2b* will mediate individual differences in the strength and duration of emotional learning. They also address the influence of NE activity on the relation between affective salience and other cognitive processes, as outlined in the dual competition model. One outstanding question concerns the relation between the notion of affective salience itself and that of prediction error: For example, can we say that things are by definition more salient if they elicit higher levels of prediction error? We suggest that a productive area for future research is to develop both the BANE and dual competition models in conversation with current views models of contextual influences on cognition, including predictive coding models (Clark 2013; Grossberg & Seidman 2006; Summerfield & Egner 2009; Summerfield et al. 2006).

Social theory and the cognitive-emotional brain

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Abstract: Pessoa’s (2013) arguments imply that various leading approaches in the social sciences have not adequately conceptualized how emotion and cognition influence human decision making and social behavior. This is particularly unfortunate, as these approaches have been central to the efforts to build bridges between neuroscience and the social sciences. We argue that it would be better to base these efforts on other social theories that appear more compatible with Pessoa’s analysis of the brain.

During the past two decades, brain research has affected the balance between competing approaches within economics, political science, sociology, and anthropology. If empirically further endorsed, then the arguments presented in Pessoa’s *The Cognitive-Emotional Brain* (2013) deserve to have a similar influence on theorizing in these fields, as well as on the efforts to merge neuroscience with the social sciences. To explain why and how, we start by providing an overview of the impact that brain research has had on social theories.

In the 1990s, it became increasingly apparent that the tenets of rational choice theory (Becker 1976) are contradicted by the growing body of neuroscientific insights into how human decision making is influenced by emotions (e.g., Damasio 1994; LeDoux 2000). At the time, rational choice analysis had become the predominant approach in political science and in economics (where it is often called “expected utility theory”) and had also become quite influential in sociology. Its impact on anthropology had been less significant but not negligible. Rational choice analysis presumes that agents (be they individuals, households, or organizations) are able to calculate and choose the one option, from all those available, that gives themselves the highest satisfaction or utility. It thus depicts decision makers as highly informed, self-centered, and calculative. Emotions and feelings are conspicuously absent from the decision-making processes postulated by rational choice analysis. Neuroscientists (Koenigs et al. 2007; Krajchich et al. 2009), however, provided evidence suggesting that human decision making is to a significant extent dependent on emotions. This neuroscientific critique of rational choice theory’s premises coincided with accumulating empirical evidence from the social sciences that its predictions were frequently inaccurate as well (e.g., Henrich et al. 2001). Later these growing doubts were joined by the widespread conviction that the outbreak of the 2008–2009 financial crisis had been caused by “human foibles” not captured by rational choice theory (Leiser et al. 2010).

This confluence of scientific developments and social forces induced social scientists to reconsider the roles that emotions play in social life. Many social scientists have done so by building on dual-systems (or dual-process) models developed in psychology. These models distinguish between two modes of thinking and deciding (Chaiken & Trope 1999; Kahneman 2003b; Stanovich & West 2000). In the first of these two modes, often dubbed System 1, thinking and deciding are fast, automatic, intuitive, effortless, slow-learning, and emotional. By contrast, in System 2, thinking and deciding are slow, deliberate, effortful, rule-governed, emotionally neutral, as well as relatively adaptable. Often, it is assumed that these modes form distinct neural networks in the brain, one of which (System 1) is evolutionary older than the other. According to dual-systems models, human cognition and decision making are routinely processed in System 1. Although less precise, this mode allows people to choose satisfactory courses of action more often than not. It is occasionally overridden and corrected by System 2, which is slower and demands more effort, but is also more accurate. The consequence of people’s preponderant reliance on System 1 is that although human decision making is often adequate for life’s purposes, it still displays systematic biases and fallacies. These errors explain how and why humans fail to display the behavior predicted by rational choice analysis and sometimes embark on courses of action that are against their own interests.

Beyond psychology, dual-systems models have been used in other disciplines to develop such approaches as behavioral economics (Smith 2005; Thaler 1993), behavioral law (Sunstein 2000), and behavioral public policy (Shafir 2012). These approaches employ the biases and fallacies highlighted by dual-systems models to explain a set of seemingly irrational behaviors in finance, consumption, voting, law abidance, and so forth. Their academic popularity should not be underrated. During the past 20 years, chairs, graduate programs, academic societies, annual conferences, and handbooks have sprung up, thus institutionalizing these approaches. In 2002, Kahneman and Smith shared the Nobel Memorial Prize in Economics for their contributions to them. Yet, these are not merely academic debates. The alternative assumptions concerning human cognition and decision making that underlie rational choice analysis and behavioral approaches have rivaling implications for governance (Dow Schüll & Zaloom 2011). If humans are viewed as well informed and rational, then it becomes easier to justify limiting state involvement in people’s lives. If, however, individuals are seen as “predictably irrational” (Arieli 2008) and “unreasonably short-sighted” (Kahneman 2011, p. 286), then benign state

intervention appears prudent. Indeed, in recent years, both the United Kingdom and United States governments have established behavioral insight teams to inform future policy making. Finally, behavioral economics has had a significant influence on the development of neuroeconomics (Camerer et al. 2004). Not all neuroeconomists are behavioral economists, but most of them are. Much effort in neuroeconomics has therefore gone into attempts to uncover the distinct neural networks subserving the emotional/intuitive and cognitive/deliberative modes of decision making (e.g., Albrecht et al. 2010).

As Pessoa acknowledges (p. 250), his book provides a welter of arguments against the dual-systems models that have underpinned the recent behavioral turn in the social sciences. He concludes that labels such as perception, cognition, and emotion may be of use for some descriptive purposes, but such labels do not map onto behavior or the brain. Herein lies the importance of *The Cognitive-Emotional Brain* for the social sciences in general, and for the ongoing efforts to bridge the social sciences and brain research in particular. If Pessoa's arguments are empirically valid, then the attempts to create more realistic models of human decision making by adding a category of apparently irrational emotions to supposedly more rational cognition are deeply flawed and doomed to fail. This is significant in view of the large impact that behavioral approaches have had on the social sciences, neuroeconomics, and policy making during the last two decades.

Pessoa's rejection (2013) of the main premise on which dual-systems models and the new behavioral approaches in economics, law, and political science are built – namely, that emotion and cognition can be treated as separate – is conjoined by other critiques. Volz and Gigerenzer (2014) have noted that the results of neuroeconomic experiments have been contradictory, in that specific brain regions have been associated with intuitive judgments in some studies and with deliberate judgments in others. Keren and Schul (2009) have argued that lack of conceptual precision has rendered dual-systems models, behavioral economics, and neuroeconomics hard to falsify. Last, scholars have criticized the psychological experiments that have purportedly shown the existence of biases and errors in human decision making. For example, Stein (2013) has argued that the choices made in these experiments can easily be interpreted as rational rather than fallacious – for example, by judging them against the standard of Baconian (as opposed to Bayesian) probability. Pessoa's book, in conjunction with these other critiques, puts into doubt whether the attempts to link neuroscience with economics, political science, and other social sciences have started from the right conceptual place.

If so, then this would be a regrettable false start, as brain research and the social sciences can, in principle, support each other. Neuroscience can help ensure that social theories are grounded in empirically valid assumptions regarding cognition, emotions, and decision making. Less often recognized is that brain research itself can also be improved with the help of social theories. The latter can offer conceptually precise, and cross-culturally valid formulations of the social phenomena that neuroscientists have started to investigate, such as ethical behavior, social interaction, beauty, or crime prevention (Turner 2012). In addition, social theories can help neuroscientists become more aware of the political and social biases that they may implicitly display in their research on some of these topics (Whitehead 2012). It is therefore important to continue to build bridges between neuroscience and the social sciences – but henceforth with the help of social theories that are compatible with the latest understandings of the cognitive-emotional brain.

What might these social theories look like? If Pessoa's analysis is empirically valid, then this has two implications for theorizing within economics, political science, sociology, and anthropology. First, theories in these fields should be based on the recognition that emotion, perception, and cognition are highly intertwined. This is the central message of *The Cognitive-Emotional Brain*. Second, Pessoa can be read as supporting the notion that although there may be a rich interlocking of human cognition, emotion, and

decision making, this occurs against a background of functional and anatomical constraints. Even though the embedding of older brain regions (such as the amygdala and hypothalamus) into new neural networks can generate novel functions (pp. 34–36), they still serve an organism's ability to respond to relevant stimuli in its environment, thereby promoting organism survival, maintenance of well-being, and social cohesion. Thus, an elaboration of older functional systems integral to core homeostatic needs has likely emerged over the course of human evolution to support richer patterns of interaction between an organism and its physical and social environment. In this process, each prior form of neural organization would constrain and shape the emergence of new capabilities; a perspective that has been widely explored within neuroscience (e.g., Dehaene & Cohen 2007; Damasio 2010, pp. 251–79). At this point in its development, it would be hard for neuroscience to specify which precise neural constraints might apply to higher-order decision making and social interaction. Nevertheless, it is reasonable to assume that such constraints operate.

Fortunately, there are social theories that meet these two criteria. A prominent example is the cultural theory developed by anthropologists Douglas and Thompson and political scientists Ellis and Wildavsky (Douglas 1982; Thompson et al. 1990). This approach distinguishes among four fundamental ways of organizing, perceiving, justifying, and emotionally experiencing social relations – namely, individualism, egalitarianism, hierarchy, and fatalism. It posits that every social domain (from the family unit to the international level) is characterized by the waxing and waning, and merging and splitting, of these four “ways of life.” As such, cultural theory does not distinguish between perception, cognition, and emotion. Each of its ways of life includes perceptions (of human nature, time, risk, time, space, etc.), cognition (such as information-processing styles), as well as emotional likes and dislikes (Douglas & Ney 1998). Furthermore, the approach recognizes that human behavior and decision making are constrained. Cultural theory argues that any social domain is forever being constructed by the interplay between a limited set of elementary ways of perceiving, knowing, behaving, and experiencing. Hence, it reconciles the wide variety and change of social life with clear constraints on cognition, emotions, decision making, and social interaction.

Douglas's cultural theory is not the only social science approach that meets the criteria outlined above. Others include the relational models theory developed by Fiske (1991) and the heuristics program established by Gigerenzer and colleagues (Hertwig et al. 2013). Such social science frameworks appear to be compatible with, or are at least not contradicted by, the overall arguments laid out in *The Cognitive-Emotional Brain*. As a result, these approaches seem much more suitable pillars on which to build bridges between neuroscience and the social sciences than the “behavioral” social theories that are currently used for this purpose and that are so powerfully undermined by Pessoa's book.

Precision about the automatic emotional brain

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Abstract: The question of automaticity in emotion processing has been debated under different perspectives in recent years. Satisfying answers to this issue will require a better definition of automaticity in terms of relevant behavioral phenomena, ecological conditions of occurrence, and a more precise mechanistic account of the underlying neural circuits.

In his book, *The Cognitive-Emotional Brain*, and in his précis, Pessoa (2013) provides a rich and cogent overview of current emotion research, with a particular emphasis on human neuroimaging work and his own important contributions to the field. A major theme addressed from the start concerns the notion of “automaticity” in emotion processing and the elaboration of a “dual competition model,” whereby emotion and motivation are proposed to interact either synergistically or antagonistically with perception and executive functions. In line with laudable efforts throughout the book to deconstruct the boundaries between affective and cognitive realms of the mind-brain, as encouraged by other scientists in the past (Gray 1990; Ledoux 2000; Leventhal & Scherer 1987), it is notable that Pessoa is embracing a perspective on the functional relationship between “controlled” versus “automatic,” or conscious versus nonconscious, processing of emotional information that appears less dichotomous than earlier views (Pessoa & Ungerleider 2004), and also less crude than ways in which these terms are commonly (unfortunately) used in the literature. Hence, Pessoa puts forward a “continuous framework” for the perception of emotional stimuli and their competition with other information in capacity limited systems.

However, as Pessoa tries to accommodate these general notions with existing data and refers to general psychological concepts and terms (e.g., resource capacity, multiple waves, recurrent loops, etc.), the proposed framework often remains at an abstract level, which makes it difficult to falsify and thus lacks a strong heuristic value. Moreover, Pessoa chose to refrain from providing his own definition for several important notions (e.g., emotion information or automaticity, to start with)—which is wise to avoid a priori biases but then leaves abundant space for ad hoc interpretations and potential inconsistencies. What is needed in the field is a precise mechanistic account of these concepts and the corresponding phenomena, based on specific neuronal processes and circuits.

There is abundant evidence that some form of emotional processing can take place without conscious awareness of stimuli or despite opposing intentional goals, which cannot simply be dismissed by stating that awareness was not probed or attention “exhausted” in an appropriate manner. These effects are subserved not only by the amygdala, but also by high-level cortical areas and other brain structures, including reward pathways (Pessiglione et al. 2008; Pourtois et al. 2013; Raio et al. 2012; Vuilleumier & Righart 2011). What is of interest and remains challenging is not really whether or not emotion-related information is processed without awareness of its presence, but rather what are the differences in processing, nature of representations, neural substrates both in space and in time, etc. For example, fear conditioning occurs without consciousness but shows different temporal features than during conscious processing (Raio et al. 2012). Furthermore, as underscored by several researchers (Bargh 1989; Moors et al. 2005) and acknowledged by Pessoa, automaticity is a broad concept that encompasses several distinct dimensions, including lack of explicit report, intentionality, effort, or control, among others. None of these dimensions is a unique defining feature of “automaticity,” and only some of them may apply to emotion responses (e.g., in amygdala)—as the resource efficiency principle described by Pessoa; but other dimensions may not apply—as lack of control or autonomy, for example (Dominguez-Borras & Vuilleumier 2013; Vuilleumier & Righart 2011). An important goal for future research is to more precisely dissect these dimensions in relation to different kinds of emotion information and different brain circuits. In the light of past research in neuroscience and cognitive science, to which Pessoa has made great contributions, it is hard to argue against or in support of “automaticity” in emotion processing without defining more precisely what is meant by automatic and emotional.

Another issue is that many facets of automaticity and their underlying substrates are not necessarily specific to emotion, but also apply to nonemotional material. Various forms of nonconscious, unintentional, efficient, and fast processing have been observed

in some degree for a large variety of stimuli, for example, ranging from subliminal priming with words or numbers, classic Stroop effects, through to motor preparation and mimicry (Dimberg et al. 2000; Eimer & Schlaghecken 2002; Kouider & Dehaene 2007). These effects imply activations of high-level brain areas several synapses away from primary sensory areas, including motor cortex, hippocampus, language, or even prefrontal executive control areas (Henke et al. 2003; Nakamura et al. 2007; van Gaal et al. 2010). There is no necessity to attribute a “special” privilege to the amygdala in this respect, neither to deprive it.

What might be “special” is a particular threshold to respond to a particular kind of information and the functional impact on particular downstream areas, for example, associated with attention or autonomic arousal (Vuilleumier 2009). Nonconscious or preattentive processing should not be equated with the implication of a subcortical route specialized for emotion information—just as nonconscious word priming does not imply direct subcortical connections to Wernicke’s area. It has long been proposed that such effects may reflect efficient, fast, feed-forward sweeps of inputs into pathways overlapping at least in part with (cortical and subcortical) pathways subserving conscious processing, but presumably unaccompanied by other neural processes engaged in the latter case such as reentrant feedback, sustained activity, rhythmic oscillations, and/or additional inputs through the same or parallel pathways (Vuilleumier 2005). This echoes the notion of “multiple waves” of processing put forward by Pessoa and Adolphs (2010), although the latter account is rather broad and needs to be more specific in order to be testable. The role of a specific subcortical route (e.g., through colliculus, pulvinar, or visual thalamus) is necessary to explain affective blindsight in patients without visual cortex (Hamm et al. 2003; Morris et al. 2001; Pegna et al. 2005), but its role in the healthy brain, exact anatomy, and informational content remain to be elucidated (Schmid et al. 2010).

In any case, it must be underscored that preattentive or nonconscious processing (cortical or subcortical) should not be expected to be similar to “full” conscious processing of the same sensory inputs. It might be limited to coarse or partial information, such as low-frequency cues or eye features in faces (Whalen et al. 2004) (among other possibilities), and thus possible for some stimuli but not others. For example, emotional meaning might be extracted efficiently from faces because of particular features or configural properties present in a single stimulus, thanks to specialized neuronal populations tuned to faces that exist throughout the visual systems. This seems much less likely for visual scenes where emotional meaning derives from specific layouts of more complex, multipart objects. Accordingly, there is evidence for coarse representations of faces (Gabay et al. 2014; Maior et al. 2010; Nguyen et al. 2014) or biologically salient stimuli such as snakes (Van Le et al. 2013) in subcortical visual pathways, although their functional role is unresolved. This accords with the notion that nonconscious processing might be “dumb,” as Pessoa puts it (see also Vuilleumier et al. 2003; Vuilleumier & Righart 2011). An important goal for research is to pinpoint more precisely which information is encoded in which brain region, for which function, and under which conditions.

Furthermore, the existence of nonconscious and unintentional responses does not preclude that they may be modulated by top-down factors, including expectations, context, goal-driven control, and so forth. Subliminal priming is malleable to current task demands and attentional control even when stimuli remain nonconscious (Bahrami et al. 2007; Fischer et al. 2007; Martens et al. 2011; Nakamura et al. 2007). Even exogenous attention, which typically operates in a reflexive (rapid and involuntary) manner, can be modulated by top-down factors related to task goals or readiness to respond to particular events (Ansorge et al. 2009; Folk et al. 1992). Likewise, expectations and affective states influence emotion processing for stimuli outside attention (Bishop et al. 2004; Pichon et al. 2015) and can abolish the

effect of attention load on emotional response (Cornwell et al. 2011). These top-down modulations do not necessarily imply that stimulus processing depends on consciousness and voluntary attention and hence cannot be interpreted against “automaticity” without distinguishing more precisely between different sources of modulation and different components of automaticity.

Although a continuous framework of resource competition neatly account for number of phenomena (Pessoa 2013), it is not sufficient to explain how reduced resources as a result of increased attention load can affect emotion-specific responses in some brain areas (e.g., prefrontal cortex or visual cortex) without affecting others (e.g., amygdala) (Shafer et al. 2012; Vuilleumier et al. 2001), unless one postulates dissociable sensitivities to these effects. Moreover, in some cases, increased attentional load or suppression from awareness may actually increase emotional responses (e.g., in amygdala) to neutral or positive stimuli relative to low-load conditions (Silvert et al. 2007; Williams et al. 2004). Further, a continuous framework does not take into account that key aspects of selective attention and awareness are nonlinear in nature (Dehaene et al. 2014; Sergent & Dehaene 2004) (and presumably emotion too; Sander et al. 2005). Finally, the central concept of resource is relatively vague and lacks precise neural substrates. By focusing on effects rather than causal mechanisms, a resource account runs into the risk of circularity, for example, when appealing to “residual resources” to explain why emotional effects on behavior or amygdala activity are observed under “high load” conditions, without a more direct measure of resource. Whereas in vision, competition for resources can be mapped neurally onto overlapping receptive fields (Desimone 1998), other forms of competition may exist in other brain systems and be resolved by distinct mechanisms. Models of emotion and cognition interactions need to consider that multiple processes operate in parallel and produce distinct (linear or nonlinear) effects on different nodes within distributed networks (Pourtois et al. 2013; Sander et al. 2005).

Lastly, caution must be taken when drawing conclusions based solely on human neuroimaging studies, which have several limitations because of their poor resolution (spatial and temporal) and vascular origin (BOLD contrast in fMRI). This makes it hard to compare processing conditions when they differ in terms of the onset or duration of neuronal responses (Pourtois et al. 2010) or recruit partly distinct neuronal subpopulations within the same brain structure (Zhang et al. 2013). In particular, the amygdala is not homogenous but made of several subnuclei, each containing multiple type of neurons, which might be sensitive to different sources of sensory inputs and top-down modulations (Vuilleumier 2009). Conscious (vs. nonconscious) and attentive (vs. preattentive) processing might also be characterized by distinctive patterns of rhythmic oscillatory activity or connectivity within and/or between subregions, whose impact on BOLD fMRI or other electrophysiological measures is unresolved. Answering these questions will require finer investigations in animal models or novel technologies in humans.

The issues reviewed by Pessoa (2013) should encourage researchers to go beyond simplistic dichotomies (such as automatic vs. controlled processes). However, it is important to be careful in how psychological terms are used, defined, and related to specific neural substrates. Time is now ripe to formulate precise mechanistic hypotheses in order to elucidate the exact functional circuits implicated in emotion phenomena and define them in terms of information processing systems (i.e., by determining which type of information is represented and/or transmitted in specific pathways – rather than just the “amount” of information as in a continuous resource model). This is an exciting prospect for future research.

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Preferences and motivations with and without inferences

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Abstract: Pessoa (2013) makes an impressive case that emotion, motivation, and cognition are neurally intertwined. Our commentary broadens the discussion to the functional, “mind” level. We argue that philosophical and computational considerations justify some modern “separatist” views. We highlight several psychological phenomena that illustrate independence, including affective and motivational reactions to rudimentary inputs, and the guiding role of such reactions in cognition.

In *The Cognitive-Emotional Brain*, Pessoa (2013) makes an impressive case that emotion, motivation, and cognition are intertwined on the neural level and that many behaviors reflect a tight integration of these processes. Admirably, Pessoa does not deny that it is still useful to characterize certain processes and behaviors using traditional terms *emotion*, *motivation*, and *cognition*, but he points out that any strict assignments of brain regions and brain networks to these terms obscures the way the mind and brain typically work.

Being in agreement with much of the book, and coming from the primarily psychological, rather than neuroscientific perspective, our commentary aims to broaden the discussion of the relationship between emotion, motivation, and cognition. We do so by first placing the distinction in a historical and philosophical context, which explains and justifies some modern “separatist” views. We then highlight some psychological phenomena that, in our opinion, fit nicely with the idea of at least occasional independence. Again, we will say relatively little about the brain, but because one of the purposes of neuroscience is to better understand the mind and actual behavior, refocusing some of the discussion onto this more psychological level might be useful.

Philosophical and historical background. Pessoa avoids committing himself to any strict definition of affect, emotion, motivation, and cognition. He dislikes dichotomies and views the differences as a matter of degree rather than kind. And, as an empiricist, he prefers the data to guide definitions (see Ch. 1). But it is useful to at least remind ourselves why many modern functionalist frameworks find it useful to view emotion and cognition as different beasts, though, of course, they have long moved from Plato-like fractionation of the mind into the reasoning, the desiring, and the emotive components, and other simplistic frameworks. So, why would modern functionalist care to distinguish cognition and emotion? Most important, because much of what makes human mind and human behavior in society interesting touches on this difference. Why does the heart seem to have reasons that reason cannot know? Why are we afraid of things that we rationally know are safe and do not like things we rationally should? Why does it seem that some of our decisions seem like mere justifications for emotional preferences? Why can powerful

bodily and feeling reactions be elicited by simple stimulus features, in every sensory domain, such as gentle touches, baby screams, rancid smells, or seeing heights? And why can perception, thinking, decision and action radically change depending on our emotional state? These important questions seem harder to ask and answer when one blurs the emotion-cognition distinction, yet they have inspired decades of fascinating research and insightful theorizing (e.g., Haidt 2001; Loewenstein et al. 2001; Schwarz 1990; Zajonc 1980).

More conceptually, it just seems useful to view cognition as processes concerned primarily with “representing” and “judging” – transformations of representations that aim to be “truth preserving” and which often take a propositional form. In contrast, it seems useful to reserve terms like *affect*, *emotion*, and *motivation* for processes primarily aimed at getting the organism to “care about” and to “do” something, and recruiting necessary physiological and experiential states to handle its concerns (Frijda 1988; Zajonc 1980). Critically, some affective processes can involve precognitive mechanisms of sensation and perception, and even completely noncognitive mechanisms, such as global neuromodulation (Panksepp & Biven 2012). In fact, some of these mechanisms are so basic that they are shared with species with clearly noncognitive status (e.g., neuromodulation of anxiety-like behaviors in species like crayfish, Fossat et al. 2014). Reflecting these insights, there are several modern philosophical works that emphasize low-level, nonpropositional, perceptual, or embodied components of affect and emotion (e.g., Charland 1995; Goldie 2000; Prinz 2006a).

In psychology, the noncognitivist view has always been amply represented, going back to the founding fathers of psychology like Wundt and James, but it found perhaps the most eloquent and passionate expression in the writings of Robert Zajonc (1980; 2000). His proposals of “affective primacy,” as well as his notion that “preferences need no inference,” still inspire contemporary research (see Niedenthal et al. 2010; Winkielman 2010). As such, it is perhaps worth revisiting some of the claims that affect, emotion, and motivation can be induced with minimal significant perceptual and conceptual processing and work in relative dissociation from the explicit belief system.

Affect with minimal cognition. We’ve already mentioned that basic affective states (simple, bivalent reactions) can be induced by rudimentary sensation-like processes. As Zajonc (1980; 2000) has pointed out, inspired by James, affective states can also be influenced by noncognitive manipulations of bodily states, including peripheral and central somatosensory feedback mechanisms (for a recent review, Winkielman et al. 2015). Social psychologists have also provided plenty of examples for implicit, or even unconscious contributions to preferences, attitudes, and prejudices, some of which appear to involve simple learning mechanisms and are impervious to rational interventions (Greenwald & Banaji 1995; Winkielman et al. 2011). Interestingly, there is even a class of phenomena where affect appears to result from the simple dynamics of processing. The best known is the “mere exposure effect” – enhancement of liking as a function of sheer stimulus repetition. But enhancement of liking, as measured with a variety of means, can also be obtained by enhancing perceptual clarity, contrast, or reducing visual noise – all low-level perceptual manipulations. The current view on such phenomena holds that there is a link between greater perceptual fluency and positive affect. Some accounts of this link are inferential in nature, but others merely propose that easy and fast dynamics, nonspecific signals of familiarity, and low conflict are fundamentally, perhaps innately, marked as communicating positive states of affairs (for a recent review, see Winkielman et al. 2012). So, perhaps in the same sense that one does not need to learn or “infer” that sugar tastes good and that injuries are painful, organisms know to “dislike” disfluency and processing conflict. In short, some seemingly “cognitive” phenomena actually illustrate the minimal conditions for affect induction, without much elaborating, structuring, categorizing, or cognitive interpreting needed to explain preferences.

Motivation with minimal cognition. Pessoa proposes that motivational processes are also highly dependent on associated cognition. However, several phenomena highlight the possibility of rudimentary, “subcognitive” influences on motivation. For example, approach-avoidance motivation can be changed by simple manipulations of embodiment, such as direct stimulation of body-related brain areas and actual body position (e.g., Price et al. 2012). They can also be manipulated by direct biological interventions into the underlying brain chemistry, biofeedback, and direct stimulation (for a recent review, see Harmon-Jones et al. 2013). Further, basic motivational signals and states (including reward signals) can spill over to completely unrelated stimuli, highlighting that they are not tightly bound to any particular cognitive representation and operate with a different dynamics (e.g., Inzlicht & Al-Khindi 2012; Knutson et al. 2008; Winkielman et al. 2005). Though Pessoa nicely highlights the neural and computational sophistication of “reward” processing, this analysis slightly detracts from the fact that on a psychological, “person” level such processing often leads to irrational pursuits and alienated desires (Berridge 2003). Though addiction is often taken as a best example of such irrational wanting, psychologically oriented economists have highlighted a wealth of similar phenomena in daily life (Loewenstein 2007).

Cognition without affect is powerless. Notice also that taking a “separatist” perspective highlights key aspects of psychological processes that would otherwise be missed. A low-level example is that most animal learning research relies on the use of unconditioned stimuli and most unconditioned stimuli are emotive. This research illustrates that learning rarely occurs without affective input (though this point is not emphasized often enough in this research literature; Panksepp 2011). A higher-level example is the case of cognitive control – nicely discussed by Pessoa. To remind, cognitive control refers to the mental processes that allow behavior to vary adaptively from moment to moment, with one of its core functions being to inhibit unwanted, yet dominant response tendencies. Often seen as the paragon of higher cognition, recent evidence suggests that cognitive control is often aided by emotion (e.g., Koban & Pourtois 2014; Shackman et al. 2011), with a recent model suggesting that control is initiated when goal conflicts produce phasic twinges of negative affect that not only focus attention but also energize goal-directed behavior (Inzlicht & Legault 2014). Emotional change, according to this view, is at the heart of control, and when emotion is removed by misattributions (Inzlicht & Al-Khindi 2012), reappraisals (Hobson et al. 2014), or using pharmaceutical agents (Bartholow et al. 2012), control becomes impotent. One thus gains a deeper understanding of cognitive control when appreciating some of the emotional ingredients that go into it. Such an understanding would not come into relief by labeling all phenomena as cognitive, as has been in fashion lately. In fact, Pessoa does an admirable job rebalancing the neural picture, though perhaps at the cost of blurring some crucial, heuristically useful distinctions.

Restoring the balance. In conclusion, the target article offers a useful framework showing how cognition and emotion work together in the brain, clarifies imprecise understandings of such terms as “low-road,” or “emotional brain,” and highlights the role of emotion in supposedly cognitive functions. In our commentary, we offered some insights from psychology that support thinking about emotion and cognition as slightly different beasts, and some fascinating phenomena that illustrate their struggle. Curiously, in psychology, we currently have a problem of gratuitous and imperialistic cognitivism. For example, a recent analysis of the theorized process variables in the 2011 volume of the primary journal of social psychology (JPSP Sections I and II) found that cognitive explanatory variables were invoked almost 2.5 times as often as emotional explanatory variables, with emotion process variables accounting for less than 23% of all phenomena (Inzlicht et al. 2013). Given the view that emotion

pervades most, if not all, of social life (Zajonc 2000), the finding that emotion was invoked as a process variable in less than 25% of all papers should raise concerns. According to some views, which assume that any transformation of input is cognition (e.g., Lazarus 1984), there is now a “primacy of cognition,” with the distinctiveness of emotion being practically dismissed, reduced completely to cognition by some writers (e.g. Duncan & Barrett 2007). As such, the target article and the excellent book bring a welcome “balance to the force,” without reestablishing naïve dichotomies. We hope that our commentary can inspire some additional appreciation of how emotion, motivation, and cognition interplay and sometimes separate in the mind and behavior.

Author’s Response

The cognitive-emotional amalgam

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Abstract: In the précis to *The Cognitive-Emotional Brain*, I summarize a framework for understanding the organization of cognition and emotion in the brain. Here, I address six major themes that emerged in the commentaries: (1) emotional perception and automaticity; (2) the status of cognition and emotion: together or separate? (3) evolutionary implications for the understanding of emotion and cognition; (4) the diverse forms of cognitive-emotional integration; (5) dual process theories; and (6) functional diversity of brain regions/networks and cognitive ontologies. The central argument is, again, that cognition and emotion are so highly interactive, and indeed integrated, that these two elements blend into a new amalgam.

R1. Affective perception

The commentaries by **LoBue**, **Todd & Thompson**, **Greening & Mather**, and **Vuilleumier** discuss concepts related to affective perception, including the perennial question of automaticity.

The Cognitive-Emotional Brain (Pessoa 2013) specifies multiple mechanisms for affective modulation of visual processing. **LoBue** also suggests that the field should investigate “multiple pathways” that imbue emotion-laden stimuli with their properties. A particularly compelling

aspect of her work is that she seeks to devise experiments that can unravel diverse sources of bias for emotionally valenced stimuli, including both bottom-up-like and top-down-like contributions.

Despite the “pluralistic” account of affective vision in the book (Ch. 2–4 and 7), it missed an important component. **Todd & Thompson** corrected this omission by describing the contributions of the locus coeruleus to “affect-biased attention,” as recently developed in the “biased attention via norepinephrine” (BANE) model (Markovic et al. 2014). Their point is important for a more general reason, too. The goal of describing *multiple* mechanisms of affective attention was to highlight that the field needs to move past the idea of “single structures” or even “single circuits.” The omission of an important mechanism demonstrates that the list is far from complete; it is likely that several additional mechanisms play important roles in affective vision, too.

Vuilleumier, a major contributor to our understanding of emotional perception, argues that it is time to move past general questions like “Is emotional perception automatic?” to specific, testable mechanistic questions, and that the proposals we offered remain too abstract. Although it is true that more mechanistic accounts are important for the field to advance further (for an example of a formal model, see Grossberg et al. 2014), at this point of model development, my goal was to describe a general (“abstract”) framework that, if persuasive to others, would lend itself to further refinement. Somewhat ambitiously, the situation is analogous to the description of the biased competition model (Desimone & Duncan 1995), which had to await a few years before more mechanistic notions of competition based on receptive fields were developed based on subsequent empirical data (Luck et al. 1997; Reynolds et al. 1999).

Greening & Mather discuss their *arousal-biased competition* model (Mather & Sutherland 2011). The model describes how arousing stimuli enhance perceptual processing of other *neutral* stimuli. It thus clearly covers territory not addressed by the *dual competition* model (Ch. 7). But one of the original goals of my proposal was to describe how competition takes place when items have affective and/or motivational significance, including situations that may involve both negative and positive items (Fig. R1). This is something that is not addressed by the arousal-biased completion model. For example, in a recent study, we investigated the interactions between reward and threat on brain and behavior during a visual discrimination task (Hu et al. 2013). Reward was manipulated by linking

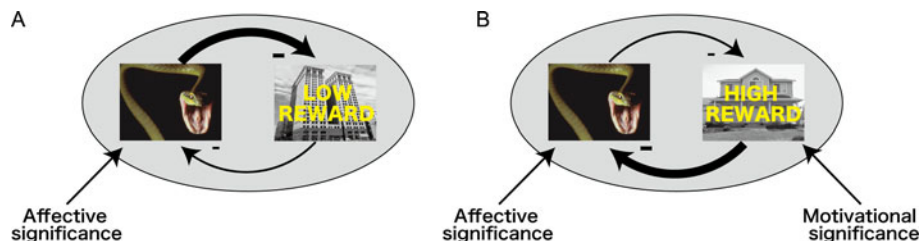


Figure R1. The dual competition model. Visual competition incorporates both affective and motivational factors, such that perception will reflect the interplay of multiple “forces” that sculpt it. In the hypothetical examples here, both a negative-image distractor and a reward-associated target influence perception. (A) Emotional images interfere with perception when the target item is positive but relatively weak. (B) In contrast, when the target item is associated with high reward, it wins the competition and in this way may reduce (or even eliminate) the deleterious impact of the negative image.

the task-relevant stimulus categories (pictures of houses or high-rise buildings) to reward or non-reward, whereas threat was manipulated using task-irrelevant backgrounds (of different colors) that were previously paired or unpaired with aversive electrical stimulation. Behaviorally, an unspecific effect of reward was observed: responses were faster during reward versus non-reward conditions (say, detecting houses when they were reward associated). More important, a reward by threat interaction was detected: The slowing of reaction time by irrelevant threat stimuli (discriminating between house and building stimuli was slowed when a background was a CS+) that was observed during non-reward was *eliminated* during reward conditions. Within the dual competition framework, the reward-associated visual stimulus was thus able to more effectively compete with the background CS+ stimulus (which itself was able to more effectively compete with the no-reward stimulus category).

R2. The status of cognition and emotion: Together or separate?

The Cognitive-Emotional Brain describes how cognition and emotion go together, a notion that was welcomed across several commentaries (see sect. R4 below). However, some commentaries discussed contrasting viewpoints that espouse greater autonomy for cognition and emotion. According to these views, it is best to conceptualize cognition and emotion as somewhat separate processes, or even involving stronger separation in the mind-brain.

Winkelman, Inzlicht, & Harmon-Jones (Winkelman et al.) endorse what they call a *modern separatist approach*. They provide examples of what they refer to as affect and motivation with minimal cognition. More interesting, to my mind, is their discussion of *cognitive control* – “often seen as the paragon of higher cognition,” as they say – and the tight link that it has with emotion. In particular, they discuss the framework of Inzlicht and Legault (2014), who formulated the *affect alarm model* of self-control. In this framework, affect is not a mere moderator of control, nor a by-product of self-control. Instead, it is essential to self-control and signals when control is needed by amplifying the detection of conflict and producing the urgency to conflict resolution. Steps in the direction of uniting cognitive and affective aspects of control were previously taken by Botvinick (2007) in his attempt to link conflict monitoring and decision making. Noting the importance of the anterior cingulate cortex to conflict monitoring, on the one hand, and evaluating action outcomes and learning to avoid aversive events, on the other hand, he described the outline of an initial “integrative account” in which these processes are interrelated. More generally, one of the most elaborate integrative accounts of anterior cingulate cortex function was developed by Shackman and colleagues (2011), who propose that the integration of negative affect, pain, and cognitive control in this region follows from anterior cingulate contributions to *adaptive control*, as discussed by **Shackman, Fox, & Seminowicz (Shackman et al.)**.

Whereas I am sympathetic to **Winkelman et al.**’s suggestion that there is a need to “restore the balance” in accounts of behavior that favor cognition to the exclusion of emotion, and vice versa, I am less certain about the need

to separate (even without dichotomizing) emotion and cognition. But Winkelman et al.’s position is certainly defensible and constitutes an alternative position to the mind-brain than the one described in *The Cognitive-Emotional Brain*. And as the field evolves to describing *how* multiple processes interact during complex behaviors, the question of *whether* they should be described as cognitive or emotional will largely fade.

In contrast, **Pascual-Leone, Pascual-Leone, & Arsalidou (Pascual-Leone et al.)** adopt a traditional separatist stance in conceptualizing emotion and cognition. One of their chief arguments is that emotion is subjectively different from cognition, an issue to which I turn next. I strongly disagree, however, that the distinction between cognition and emotion is one of “two sorts of value,” as they propose – “truth” value for cognition and “vital” value for emotion – a suggestion that is unlikely to move the field forward.

Regarding the subjective difference between cognition and emotion, it is instructive to consider how brain circuits are linked to bodily states. For example, the central amygdala is at times viewed as a “controller of the brainstem” (Cardinal et al. 2002) and uses its widespread projections to the hypothalamus and brainstem nuclei to coordinate behavioral, autonomic, and neuroendocrine responses. Given the effects of these structures on bodily states and the regulation of the internal milieu, a more direct link with emotional “felt states” is established. Furthermore, cortical regions, including medial and orbital frontal sectors, as well as the insula, are strongly interconnected with brain regions in the basal forebrain, midbrain, and hindbrain that can directly affect bodily states, and be affected by them (Pessoa 2013, Ch. 9). If researchers choose to call processes more directly linked to bodily states “emotional,” this would seem reasonable, as long as they also emphasize that such processes are strongly coordinated with others that have a less direct impact on body states. Broadly, this “emotion-cognition” coordination is always present.

Montemayor also espouses a separatist view of emotion and cognition. He misquotes me as saying that emotion is often “dumb,” and suggests that cognition requires inferential and conceptual capacities. But if we consider the frameworks by Botvinick (2007) and by Shackman and colleagues (2011) summarized above, for example, such description is misleading. To put it plainly: How can emotion be dumb if it is part of cognition (say, cognitive control)? Even more troubling, Montemayor suggests that there is a “deep kind of dissociation between emotion and cognition,” venturing as far as stating that it is a “normative kind of dissociation.” But to argue in favor of a normative distinction is to embrace the very dichotomy that even Montemayor acknowledges can be simplistic!

R3. Evolution: Implications for the understanding of emotion and cognition

Dobzhansky famously titled a paper, “Nothing in biology makes sense except in the light of evolution” (Dobzhansky 1973). This is a blessing and a curse, however, because ad hoc evolutionary “explanations” are all too frequent. Here, I will discuss some of the Commentaries that discuss evolution in a way that I found problematic.

Pascual-Leone et al. suggest that an important difference between emotion and cognition is that emotion

(they use the term *affect* to refer to a concept that is dichotomous with cognition) has innate-instinctual, evolutionary roots. In contrast, cognitions are always situation-bound and hence cannot be innate. But this argument runs the risk of suggesting that emotion has deep evolutionary roots for survival, while cognition runs atop and refines the “lower” level depending on context. Instead, the entire brain must be understood in evolutionary terms, not just emotion/motivation. A more appealing and powerful view is described by **Pezzulo, Barca, & Friston (Pezzulo et al.)**, whose evolutionary perspective is one that “implies that the very fabric of cognition – from its ancestral origins to the most modern and sophisticated skills – is inextricably linked to utility, adaptivity, and meaningfulness.”

Another problematic line of reasoning is described by **Montemayor**, who subscribes to antiquated notions of an old emotional system that is autonomous. The brain has, of course, old systems. However, these do not exist within a “layered” architecture, with newer structures added on top of old ones, such that the ones on top control the ones at the bottom (cf. the triune brain). I would argue that evolutionary changes to brain circuits are such that “new” systems are embedded within “old” ones. *This interweaving creates a web of functional and structural coupling in a way that blurs “old” and “new”* (Fig. R2; see also discussion in sect. R3.4). To motivate this perspective, it is relevant to consider a network perspective of the relationship between function and structure in the brain – structure-function mappings (Ch. 8; Pessoa 2014 and associated commentary). More important, the architecture of the brain includes extensive avenues for signal communicating, in general, and cognitive-emotional interactions, in particular. Two particularly interesting examples are those of the hypothalamus and the amygdala (Ch. 9).

R3.1. Hypothalamus

Historically, the hypothalamus has been conceptualized in terms of “descending” systems, such as when described as the “head ganglion” of the autonomic nervous system. However important the hypothalamus may be for descending control, though, a significant recent insight is that the mammalian cerebral cortex and the hypothalamus share massive *bidirectional* connections. Whereas hypothalamic contributions to descending control of bodily functions are well documented, its contributions to *ascending* processing are poorly understood. Notably, the hypothalamus has widespread projections to *all* sectors of prefrontal cortex (Rempel-Clower & Barbas 1998). Given the role of the hypothalamus as a critical component of the central autonomic nervous system, this pattern of connectivity implies that the hypothalamus has the ability to influence processing throughout prefrontal cortex. Notably, this includes lateral prefrontal cortex, which is important for cognitive function.

R3.2. Amygdala

A remarkable property of the primate amygdala is its massive interconnection with cortex. Indeed, as many as 1,000 separate cortical and subcortical pathways may exist (Petrovich et al. 2001). The connectivity is all the more notable given that it involves all cortical lobes, as well as

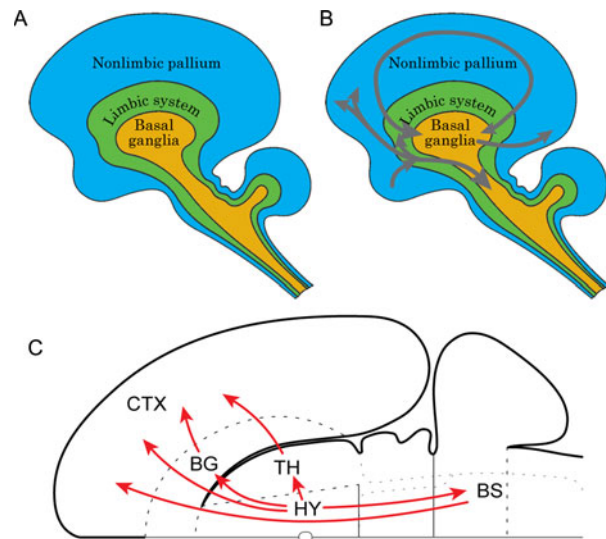


Figure R2. Brain evolution. (A) *Layered* brain evolution where newer structures/circuits are added atop older ones. (B) *Embedded* brain evolution where newer structures/circuits are integrated with older ones, thus expanding the functional repertoire of older regions. Multiple types of integration are possible, including “looped circuits,” widespread influences with both “descending” and “ascending” components, as well as projection systems from older structures that modulate newer ones. Basal ganglia refer to regions at the base of the brain; pallium refers to developmental structures that are precursors to cortex. Panels adapted with permission from Butler (2009) and originally based on MacLean (1990). (C) Hypothalamic ascending connectivity illustrating how old and new brain parts interact, thus integrating diverse types of signals. Summary of four major pathways from the hypothalamus to the cerebral cortex on a flattened representation of the rat brain. The “basal ganglia” refer to the basal forebrain and the amygdala complex. Note that one of the indirect connections first descends to the brainstem. Key: BG: basal ganglia; BS: brainstem; CTX: cortex; HY: hypothalamus; TH: thalamus. Reproduced with permission from Risold et al. (1997).

subcortex. Combined, these properties indicate that the amygdala is an extensively interconnected *connector hub* – where a *hub* is a region with a high degree of connectivity. Furthermore, in a network analysis by Modha and Singh (2010), several amygdala nuclei (e.g., lateral nucleus, accessory basal nucleus) were identified as part of a “core” brain circuit, all of whose regions have extremely high connectivity. Together, these findings reveal that the amygdala has exceptional potential for signal communication.

The pattern of connectivity between the amygdala and prefrontal cortex (Amaral & Price 1984; Ghashghaei et al. 2007) is of particular interest given the latter’s role in cognitive functions. In one study, although the amygdala was estimated to be directly connected to approximately 40% of prefrontal regions, approximately 90% of prefrontal cortex was deemed capable of receiving amygdala signals after a single additional connection *within* prefrontal cortex (Averbeck & Seo 2008). This “one-step” property seriously undermines the notion that “affective” signals are confined to orbital and medial prefrontal territories. Other notable aspects of amygdala connectivity include interactions between the amygdala and the basal forebrain that are important for attentional functions (Ch. 2), and

substantial projections from the amygdala to visual cortex that influence competition in visual cortex (Ch. 7).

R3.3. Beyond immediate structural substrates: Functional connectivity

The interweaving of “old” and “new” circuits is not only created by structural pathways but by *functional* interactions, too.

At a first glance, the notion of an architecture anchored on physical connections is clear-cut. However, the boundary between anatomy and function becomes blurred very quickly once one starts considering factors that characterize the anatomy (Lee et al. 2003): for example, the laminar profile of the connections (often interpreted in terms of “modulatory” vs. “driving” inputs), the presence of excitatory or inhibitory interneurons, the strength of the connection, and so on. Thus, understanding how regions and networks contribute to brain function requires identifying the way regions are “functionally connected,” where *functional connectivity* can be defined as the “temporal correlation between spatially remote neurophysiological events” (Friston et al. 1997), regardless of their anatomical connectivity. The relationship between structural and functional connectivity is a complex one (Ch. 8). For example, in principle, responses in two regions could be perfectly correlated (barring, say, noise) as a result of common inputs. They also could be perfectly correlated, yet having the effect be entirely mediated via an intermediate region.

What determines functional connectivity if structural connectivity does not always determine it? Adachi et al. (2012) compared existing data on structural connectivity in macaques and functional connectivity obtained during MRI scanning of macaques under anesthesia. They analyzed the effect of different types of indirect structural connections on functional connectivity. Remarkably, functional connectivity between pairs of regions *without* a direct corticocortical connection depended more strongly on whether two regions (A and B) had common inputs and outputs ($A \leftarrow C \rightarrow B$; $A \rightarrow C \leftarrow B$) than on whether there was stepwise information flow between them ($A \rightarrow C \rightarrow B$). Adachi and colleagues thus proposed that functional connectivity depends more strongly on *network level* than on pairwise interactions. See also Mantini et al. (2011).

To summarize, the previous sections on the amygdala, hypothalamus, and functional connectivity were aimed at illustrating how a network perspective, together with knowledge about structural and functional connectivity, is compatible with the notion that “new” brain circuits and systems are embedded within “old” ones. If this view is correct, the idea of a layered architecture, with newer structures added on top of, and in control of, old ones must be discarded.

R3.4. Neuroevolutionary perspective

Bos, Brummelman, & Terburg (Bos et al.) correctly point out that a weakness of the book is that it lacks a neuroevolutionary approach in describing brain function. I hope to remedy this in future treatments of brain architecture, structure-function mappings, and cognitive-emotional interactions. But, I disagree with Bos et al. when they propose that, from an evolutionary perspective, “cognition can be seen as the tip of the emotional iceberg.” This is an

unfortunate metaphor because it, once again, perpetuates the “layered” view of brain evolution (MacLean 1990). A traditional view is that cortex is a late addition to the brain plan and that it controls subcortex. Indeed, the idea of cortical inhibition of subcortex has a long history dating to early researchers, such as Hughlings-Jackson (see Parvizi 2009). But what is the *basic plan* of the vertebrate brain? It is now understood that both cortex and subcortex are part of the plan. Figure R3 shows a proposed brain “archetype” by Striedter (2005).

What do we know about the evolution of some “emotional” regions? The amygdala of mammals is composed of more than a dozen subregions. Chareyron and colleagues (2011) found that the lateral, basal, and accessory basal subregions are dramatically more “developed” in monkeys than in rats (based on morphological characteristics, such as cell counts and the volume of subregions). One possibility, as described by the authors, is that the differences between rats and monkeys are linked to their degree of connectivity with other brain structures, in line with the proposal of correlated evolution between components of functional systems (Barton & Harvey 2000). The lateral, basal, and accessory basal nuclei are more developed in primates than in rodents, and *parallel* the greater development of the cortical areas with which these nuclei are interconnected in primates. Chareyron and colleagues (2011) propose that such correlated evolution may be responsible for a higher convergence and integration of information in the primate amygdala, and that the relative development of these amygdala nuclei might be influenced by their interconnections with other brain structures—namely, their afferent and efferent connections (Amaral et al. 1992).

To sum up, an evolutionary perspective to brain function is absolutely needed, as suggested by **Bos et al.** But I disagree with them when they suggest that, in terms of evolution, the network perspective that I adopt runs into problems when faced with amygdala heterogeneity (i.e., multiple subregions). This is far from being the case. For example, the lateral and central amygdala, while strongly interrelated territories, are parts of different brain circuits that have had different evolutionary trajectories. Thus, I describe in Chapter 3 how the amygdala mobilizes both brain (via the lateral amygdala) and the body (via the central amygdala).

R4. Manifold forms of cognitive-emotion integration

Several of the commentators were enthusiastic about a framework in which cognition and emotion are strongly interactive and provided particular examples of the explanatory power of the interaction/integration framework. **Foster & Keane** suggested that the emotion of *surprise* constitutes a good example of when emotion and cognition are interdependent. **Manfrinati** suggests that an integration stance leads to proposals of the brain bases of moral processing that are more closely aligned with those by Moll and colleagues (2005; 2008a) instead of the dichotomist formulation by Greene (Greene et al. 2001). According to Manfrinati, moral judgment is the product of complex interactions between emotional and cognitive mechanisms. **Egidi** discusses how integration plays a role in understanding the impact of happy and sad moods on

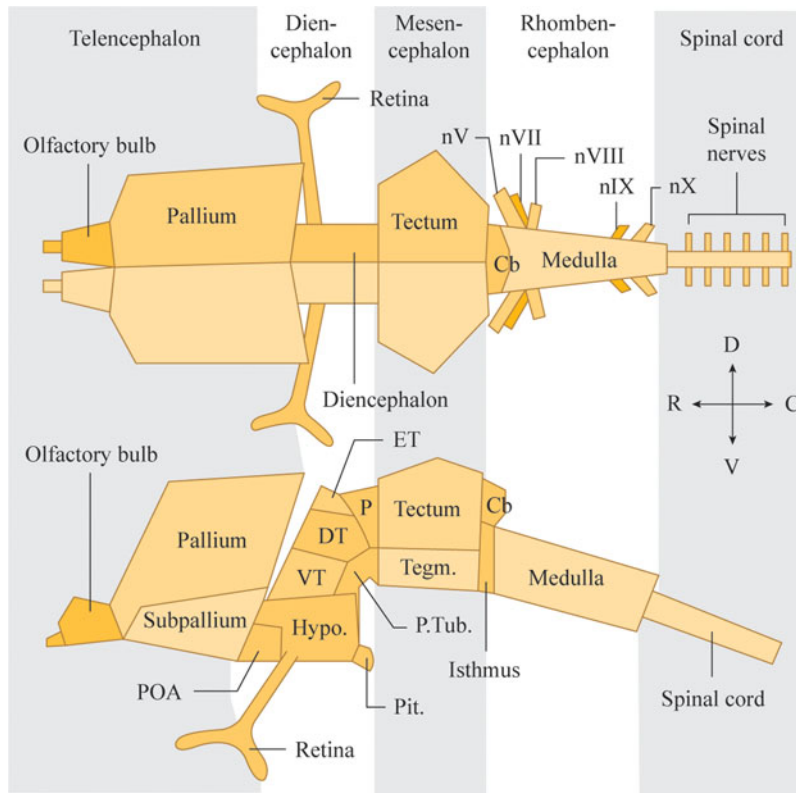


Figure R3. Basic plan of the vertebrate brain. Reproduced with permission (Striedter 2005).

discourse and sentence comprehension. **Verweij & Senior** discuss potential implications of cognitive-emotional integration for the social sciences, broadly defined, and in particular, implications for theorizing within economics, political science, sociology, and anthropology. **Petrolini** argues that the integration framework described in the book can be successfully applied to psychopathology and, in particular, to the reasoning of delusional subjects. **Gardiner** discusses cognition-emotion integration in the context of music. **Kiverstein & Miller** suggest that integration is important for the understanding of the human social brain. **Olds & Marewski** suggest that cognitive-emotional integration needs to be taken seriously by those building formal/computational models of “cognitive architectures,” which as the name implies, largely ignore affective components. **Froese** proposes that the framework of *The Cognitive-Emotional Brain* should inform enactive approaches in the cognitive sciences. Indeed, I found his suggestion of extending the notion of functional connectivity and context dependency to include bodily and environmental dynamics fascinating and very worthwhile of investigation.

R5. Dual process theories

Kiverstein & Miller suggest that the framework of *The Cognitive-Emotional Brain* challenges dual process theories of cognition in general. This is a theme that pervades much of the book. For example, Chapter 4 discusses the notions of automatic and controlled processes and argues instead for a *gradient of processing efficiency*.

Common to all dual process models is the strong assumption of the existence of two *qualitatively* different mental systems, for example, “intuition” and “reasoning” (for a lucid discussion, see Keren & Schul 2009). A common practice is to call the two components “System 1” and “System 2,” where the first is automatic/heuristic/reflexive and the second is controlled/analytic/reflective (Evans 2008). But as others have expressed in the past, the idea of a dual system model is both slippery and conceptually unclear (Keren & Schul 2009). For one thing, nearly all dual process models have as a central component the automatic versus controlled dichotomy, which is not a viable distinction, as discussed in *The Cognitive-Emotional Brain*.

As with the question of automatic versus controlled processing of emotion-laden visual stimuli (Ch. 4), the question of whether there are two systems in dual process models is not an entirely empirical one. This is because no single critical experiment can provide a final, definitive answer. In the end, however irresistible dichotomies are to the human mind (Kelso & Engström 2006; Newell 1973), dichotomizing implies *oversimplifying* (Keren & Schul 2009; Kruglanski et al. 2006). A continuous framework is better, albeit more complex (Kruglanski et al. 2006).

R6. Functional diversity of brain regions and networks, and cognitive ontologies

Kiverstein & Miller suggest that the integration framework of *The Cognitive-Emotional Brain* has implications for understanding so-called “cognitive ontologies.” Indeed,

this is a theme that I have briefly addressed in recent papers (see Pessoa 2014).

If brain regions are engaged in many processes based on the networks they are affiliated with in particular contexts, they should be engaged by a range of tasks. As described in the Précis, we recently (Anderson et al. 2013) characterized the function of brain regions in a *multidimensional* manner via their *functional fingerprint* (Passingham et al. 2002). Activations were classified in terms of *task domains* chosen to represent a range of mental processes, including perception, action, emotion, and cognition. The functional fingerprint for a given region thus represented both the set of domains that systematically engaged the region and the relative degree of engagement (see Fig. 13 of target article). Based on fingerprints, we calculated a *diversity index* to summarize the degree of functional diversity across the brain (see Fig. 14 of target article). The fingerprint concept was extended to brain networks, providing a way to compare them and to advance our understanding of the properties of constituent nodes.

Our findings showed that brain regions – and, importantly, large-scale networks – are very diverse functionally (see also Poldrack 2006; 2011). Beyond the descriptive aspects of the approach, it outlines a framework in which a region's function is viewed as inherently *multidimensional*: a vector defines the fingerprint of a region in the context of a specific domain structure. Although the domain that we explored used a task classification scheme from an existing database, it was not the only one possible. How should one define the domain structure? One hope is that cognitive ontologies can be defined that meaningfully carve the “mental” into stable categories (Bilder et al. 2009; Price & Friston 2005). However, I believe that *no* single ontology will be sufficient. Instead, it is better to conceive of several task domains that are useful and complementary in characterizing brain function and/or behavior. Thus, a region's functional fingerprint needs to be understood in terms of a *family of (possibly related) domains*.

R7. What form of cognitive-emotional brain is better?

Views of the framework advocated in *The Cognitive-Emotional Brain* were mixed. Most commentators praised the integration framework and suggested that they may have implications in many related domains – even to the social sciences more generally. But some questioned the proposed form of interaction/integration between cognition and emotion and, in some cases, argued against it. Perhaps such state of affairs is not surprising in the end. Emotion “feels” different from cognition. These mental states and associated processes also appear, at first blush, to be subserved by fairly independent brain regions and circuits. Yet, when we consider the available neuroscientific data, attempts to characterize regions as either “emotional” or “cognitive” quickly break down. An architecture of rich interconnectivity leads to a structure-function mapping that is both one-to-many and many-to-one. Ultimately, looking at the brain from the perspective of one brain region at a time is bound to produce a highly distorted and, more critically, impoverished description of the brain. What is required is a framework where cognition

and emotion are highly interactive, as I have argued in *The Cognitive-Emotional Brain*.

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[The letters “a” and “r” before author's initials stand for target article and response references, respectively]

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