CORTEX 59 (2014) 197–202

Available online at www.sciencedirect.com

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Journal homepage: www.elsevier.com/locate/cortex

Discussion forum

Submodalities of emotion in the context of cingulate subregions

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Early views of cingulate cortex employed a grand view of emotion that was subserved by the entire cingulate gyrus (MacLean, 1990). This view was abandoned because the content of emotion and its role in responses to emotion-provoking stimuli and decision making are subserved by cingulate subregions. Rolls (2014a) synthesized and clarified many of the underlying schemes that mediate these events and considers how emotional systems employ cognitive rules such as weighing valenced outcomes to direct behavior. His sections on the role of cingulate cortex in these functions are very informative and the present discussion builds on these views. Most important to refining our work is his view that emotions are states evoked by instrumental reinforcers; rewards or punishers. Indeed, actions are arbitrary and not determined by emotions but rather set value states that maintain goals for actions. This perspective has important implications for interpreting brain functions evoked by reinforcers and the roles of cingulate cortex therein.

The last two decades of human functional imaging has produced a fundamental shift in our understanding of valenced functions with the ability to interrogate affective feeling states in ways not previously possible in primates. Imaging studies have activated multiple cortical regions with standardized pictures, scripts, movie clips and sensory stimuli and this diversity of cortical activation raises new issues of how the brain records emotional events and uses such information for decision making. One problem with this new wealth of information is interpreting the role of many areas in emotion. Although emotion-provoking stimuli are perceived as a uniform conscious event, different aspects of emotion are stored and retrieved to resolve particular metabolic, personal and social needs. It need not be the case that every region activated during emotion-generating tasks such as acute noxious stimulation is engaged in affect *per se*. Shackman et al. (2011) argue that because an emotional task driven by facial expressions or words activate posterior cingulate cortex (PCC), it is therefore involved in emotion. While PCC is activated during tasks involving reward and punishment, it is equally active during non-emotional control conditions (Vogt, 2005) and there is a more subtle level of information processing that requires going beyond a singular view of emotion and consider it in the framework of information processing, decision making and unique cingulate structure/function entities. To achieve this goal, we must understand the submodalities of emotion-evoking conditions associated with instrumental reinforcers and how each relates to cingulate subregions.

For decades pain physiologists referred to cingulate cortex as being engaged in the affective-motivational component of pain based on studies showing activity mainly in midcingulate cortex (MCC). The temporal resolution of such methods is limited, however, and electroencephalography demonstrates that posterior MCC and dorsal PCC are activated very early in the nociceptive response (Bentley, Derbyshire, Youell, & Jones, 2003; Frot, Mauguiere, Magnin, & Garcia-Larrea, 2008); within 200–300 msec before conscious cognitive processing can occur. What then is the meaning of pain-evoked activity in pMCC/dPCC as it is not part of conscious experience? Below it is suggested that these subregions have a role in cognitive orienting of the head and body to the noxious stimulus and provides a pre-potent signal for withdrawal responses should one be required. This one problem of the role of pMCC/dPCC in pain

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http://dx.doi.org/10.1016/j.cortex.2014.04.002

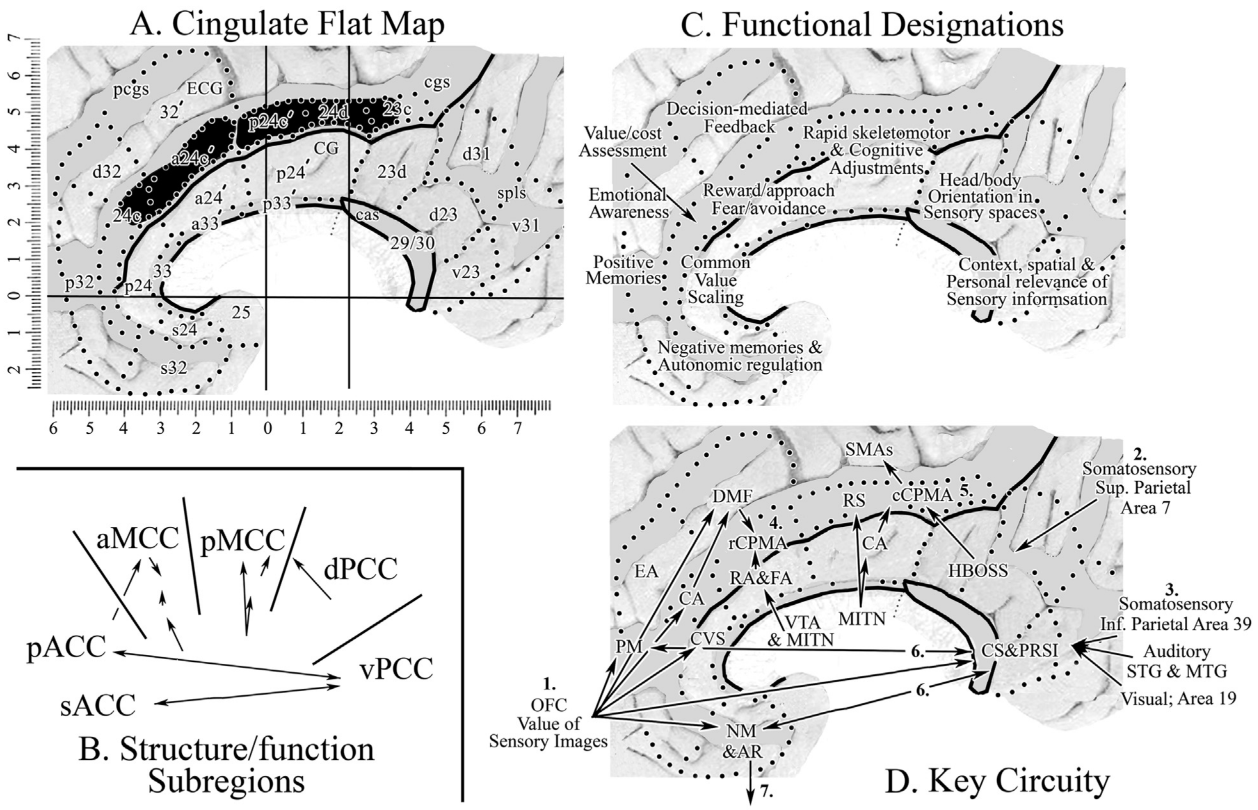

Fig. 1 – Perspectives on cingulate organization. A. Flat map of cingulate areas with reference to Talairach and Tournoux (1988). The rCPMA and cCPMA are shown in black in the cingulate sulcus (cgs; see abbreviation list for others). B. A conceptual view of cingulate subregions derived from the flat map. The arrows are from D. and show key cingulate interactions and the vertical organization of circuitry in MCC. C. Taxonomy of cingulate functions. D. The letters are abbreviations of terms used in C. Key circuits are shown for those connections mediating information flow into cingulate cortex (1., 2., 3.), within cingulate cortex (4., 5., 6.) and autonomic outflow (7.). Skeletomotor output originates from the cingulate premotor areas in the cingulate sulcus.

alerts to the fact that there are intermediate stages of processing of pain information from which the emotional gestalt emerges; the brain is using nociceptive information in different ways to achieve different cognitive/action outcomes. As there are numerous submodalities of sensory cortical processing, it is not surprising that emotion-evoked activity is also organized into submodalities providing for a rich means of processing sensory information to achieve different behavioral outcomes.

1. Cingulate subregional organization

Conceptualizing cingulate organization in terms of 8 subregions provides a powerful tool to analyze the details of structure/connection/function relationships and requires consideration of emotion submodalities. A broad dissociation of limbic structures into anterior and posterior divisions is reflected in cingulate cortex with the former including the orbitofrontal cortex (OFC) and amygdala involved in emotion, reward valuation, and value representations transmitted to ACC and MCC for action-outcome learning (Devinsky, Morrell, & Vogt, 1995; Rolls, 2014b). In contrast, the posterior limbic system is involved mainly in spatial, object and episodic memory and includes PCC, retrosplenial cortex and their afferents from the anterior thalamic nuclei. In view of MCC, one wonders if there is a distinct sensorimotor action system governed by a third limbic system.

Fig. 1 provides different perspectives on cingulate organization. Panel A. is a flat map (Vogt, 2009) with areas and borders designated. The two cingulate premotor areas (rostral-rCPMA and caudal-cCPMA; also panel D.) in the cingulate sulcus are pivotal to final output pathways. Panel B. emphasize the structural orientation of each subregion. Also, the anterior and posterior divisions of retrosplenial cortex are considered extensions of dPCC and ventral PCC (vPCC), respectively, until their specific contributions to cingulate/brain functions are identified in primates.

2. Subregional cingulate functions

Functional imaging observations in humans and single neuron recording in monkeys have opened new avenues for explaining how cingulate cortex processes submodalities of emotion and these are related to its subregions in the following ways (Fig. 1, panel C.):

2.1. Positive and negative memories of objects and experiences activate areas p32 and s32/s24/25, respectively (Phan, Wager, Taylor, & Liberzon, 2002; Vogt, Berger, & Derbyshire, 2003). Rolls (2014a-Fig. 4.47; Grabenhorst & Rolls, 2011) reinforces and extends this view by demonstrating that aMCC represents negative values produced by a punisher or non-reward that correlate with the subjective state of unpleasantness, while pACC represents positive, reward value that correlates with the subjective state of pleasure. It appears that each of these emotion states are dependent on OFC which plays a major role in cingulate functions and this presents a critical change in our past views of aMCC and pACC functions. Additionally, the subgenual ACC has direct projections in autonomic regulatory centers including the lateral hypothalamus, amygdala, periaqueductal grey, and parabrachial nucleus (Vogt & Vogt, 2009). It is likely, therefore, that somatic markers as conceptualized by Damasio (1996) are of particular relevance to this region where autonomic function is sensed and regulated. Notice that MCC and PCC do not have these projections, relegating them to a secondary role in emotion-mediated processing.

2.2 Emotional awareness is reflected in activations in pACC area 32 and adjacent medial prefrontal cortex. Lane, Fink, Chua, and Dolan (1997) examined neural activation associated with attending to one's own emotional experience. By having subjects attend to and valence their experience during assessment of pictures expressing different valences, they examined reflective awareness. Assessment of internal emotional states by this region including part of area 24 is supported by Grabenhorst, Rolls, and Parris (2008) and Rolls (2014a) who showed this region is active when making continuous versus binary decisions about the pleasantness or aversiveness of sensory stimuli.

2.3. Common value scaling is critical for action outcomes. Another important part of our model that has been revised based on Rolls' treatise is the notion that in order to select a specific goal during decision making, neuronal activity must be scaled in the same value range (Rolls, 2014a, Section 9.5.2). Grabenhorst, D'Souza, Parris, Rolls, and Passingham (2010) showed that fundamentally different primary rewards (taste in the mouth and warmth on the hand) evoked responses in OFC and pACC that were scaled to the same range. Thus, different rewards (and punishers) are expressed on a similar scale for decision making in pACC area 24 to which many emotional states have access including nociceptive responses (Kulkarni et al., 2005; Vogt, 2005). This function may be a core to motivated behavior and intermediate between the remainder of ACC and aMCC functions.

2.4. Cost assessment of actions is a critical feature of decision making mediated by pACC area 24c. Hayden, Pearson, and Platt (2011) explored this area in monkeys during foraging in a virtual reality task. Single neurons encoded a decision variable signaling the relative value of leaving a depleting resource for a new one. Neurons fired during each sequential decision to stay in a patch and, for each travel time, these responses reached a threshold for patch-leaving. Longer travel times reduced the gain of neural responses for choosing to stay in a patch and increased firing rate threshold mandating patch-leaving. As area 24c is the rostral end of the rCPMA representing the face and head, it is not surprising that such an area would take the lead in decisions relating to identifying sources of food and water.

2.5. Feedback-mediated decision making for reward/approach and fear/avoidance selection is a key function of aMCC and most of cingulate information processing likely focusses on the function of this subregion. Bush (2009) discussed the role of anterior/dorsal MCC (areas a24c′ and 32′) in feedback-mediated decision making. He emphasized that no single "unimodal" theory accounts for the functions of this subregion. Thus, novelty and error detection, anticipation, and target and response selection are all subserved by it and it is a critical hub mediating final decisions. Huster et al. (2011) showed independent components that were significantly correlated with the single-trial electroencephalography components for go-, stop- and error-trials and the aMCC maxima in fMRI were greatest on stop- and error-related conditions. One of the keys to the significance of MCC is its activation by emotion-generating stimuli (fear and reward) and decisions involving cognitive (non-valenced) processing. Shima and Tanji (1998) reported neurons that encode reward-based decision making including target detection, motor response and reduced rewards with very few neurons responding to constant rewards. This latter finding was later confirmed in humans by Bush et al. (2002). Finally, the intermingling of nociceptive and reward coding neurons reported by Koyama, Kato, Tanaka, and Mikami (2001) emphasizes the important point that this is the final common site for selecting between reward/approach and fear/avoidance behaviors. Thus, the cost of actions and their outcomes is determined in areas 24c′ and 32′.

2.6. Rapid cognitive and skeletomotor adjustments are made in pMCC that do not reflect internal emotional assessments of sensory stimuli. Grabenhorst et al. (2008) evaluated graded or yes-no responses to pleasant warm, noxious cold or combinations thereof and pMCC had greater activations on yes versus. no trials. These activations were related to a yes decision, and not to the particular response. Importantly, this area did not reflect the pleasantness of the stimuli when ratings were being made, so their activations are related to a 'Go' decision, compared with a decision not to Go. Further, the Cingulate Premotor Pain Model (Vogt & Sikes, 2009) proposes that the pMCC is involved in rapid adjustments based on early nociceptive responses that occur within 200–300 msec that are not engaged in pain affect (Bentley et al., 2003; Frot et al., 2008). Also, the features of cCPMA neuron responses indicate earlier premotor activity in pMCC than in aMCC (Shima & Tanji, 1998) reflecting rapid responses on rewarded trials with less intervening cognitive/emotional modulation. Finally, Mohr, Binkofsli, Erdmann, Büchel, and Helmchen (2005) showed three parts of cingulate cortex are differentially activated by either externally or self-administered noxious stimuli with pMCC activation during externally generated noxious stimuli; suggesting a limited intervention of internal emotional assessment.

2.7. Eye, head and body orientation in sensory spaces are coded by neurons in dPCC. The position of the eye in the orbit has been reported by Olson, Musil, and Goldberg (1996). Also, dPCC is activated very early in the nociceptive response (Bentley et al., 2003) occurring within 200–300 msec before conscious cognitive processing occurs. The pre-movement responses of neurons in the cCPMA are much shorter than those of the rCPMA suggesting there is a system for more rapid responses. Richer, Martinez, Robert, Bouvier, and Saint-Hilaire (1993) electrically stimulated PCC in epileptic patients and evoked complex proprioceptive sensations in the form of bilateral feelings of levitation unaccompanied by movement. Activity in dPCC provides a pre-potent signal that prepares for withdrawal responses should one be required.

2.8. The vPCC is engaged in assessing the context- spatial- and personal-relevance of sensory information; i.e., sensory information is not captured by vPCC unless it has personal importance. Bar and Aminoff (2003) scanned subjects while they observed highly contextual objects (e.g., a beach chair versus a beach chair on the beach) and suggested that activated cortices mediate spatial and non-spatial contexts. Once the personal relevance of an object or experience has been coded in vPCC, it becomes available to sACC via direct connections for combining value and actions in MCC (e.g., sitting on the beach chair). It should be noted that personal relevance is also coded in pACC area 24. Enzi, de Greck, Prosch, Tempelmann, and Northoff (2009) showed that responses evoked by reward and the attribution of personal relevance during reward and personal relevance included the pACC. Although we showed basal glucose correlations between vPCC and OFC (Vogt, Vogt, & Laureys, 2006), Rolls' perspectives on value representations in OFC has required a more explicit connection between OFC and vPCC that participates in the personal relevance proposition. Thus, the interactions among vPCC, pACC and OFC are critical to defining ensuing decision making.

3. Connection/function systems

Panel D. in Fig. 1 shows a number of essential afferent connections (1., 2., 3.), intracingulate connections (4., 5., 6.) and autonomic output (7.). According to Rolls (2014a), OFC provides assessments of the reward value of many sensory cues including establishing stimulus-reward associations, subjective pleasantness and reward value and flavor of food and taste. Reward or punishment are reinforced with visual cues and code for relative preference. The OFC projections provide this information shown in panel D and cingulate operations using this information include value cost assessment, determining positive and negative objects and events, scaling of common values, decision-mediated feedback about predicted outcomes and identifying the personal relevance of objects and contexts in vPCC.

Multisensory innervation of PCC is provided by pathways 2 and 3 (Vogt & Laureys, 2009). This information interacts with sACC and pACC to determine the emotional valence and context of sensory information via pathway 6. Reward and nociceptive inputs arrive in aMCC from the ventral tegmental area (VTA) and midline, mediodorsal and intralaminar thalamic nuclei (MITN), respectively, to set task valence and expectations. Finally, the decision-mediated feedback system uses this information in driving the rCPMA. In a parallel way but on a much briefer timescale with limited conscious emotional awareness, the MITN project to pMCC to drive the cCPMA which also interacts with SMA to generate skeletomotor output. The cCPMA also receives inputs from dPCC to guide orientation of the head and body in space.

4. Cingulate structure/connection/function systems in psychopathy

Rolls' "*Emotion and Decision Making Explained*" led us to significantly modify the subregional functions of ACC and the role of OFC therein which contributes to our understanding of emotional submodalities and information processing in psychiatric diseases. Psychopathy is of particular interest because it involves deficits in emotional responses to others, shallow affect, lack of empathy, and poor long-term planning. An fMRI study in criminal psychopaths assessed subjects during encoding, rehearsal and retrieval of neutral and negative emotional words. Responses were aggregated for the emotion conditions separately from neutral conditions and showed that, in negative emotion conditions, criminal psychopaths manifested reduced activity relative to non-psychopaths in three subregions: pACC, aMCC, vPCC (Kiehl et al., 2001). Müller et al. (2003) also reported that activation of pACC and dPCC is reduced in criminal psychopaths versus normals when viewing pictures. A detailed consideration of defective information processing in the psychopathic brain is available (Vogt & Lane, 2009).

A direct link between psychopathy and impaired autonomic output was shown during imagery of fearful scenes with heart rate and skin conductance being attenuated (Patrick, Cuthbert, & Lang, 1994). Birbaumer et al. (2005) showed that during the acquisition of fear, psychopaths failed to generate responses in pACC area 24 that were characteristic of controls. Psychopaths also failed to show conditioned skin conductance and emotional valence ratings. Thus, failure of coupling occurs between autonomic output and events associated with common scaling of rewards and punishers in pACC (Rolls, 2014a).

Another feature of psychopathic behavior is an over focus on immediate goals that result in a lack of well-planned, long-term goals (Cleckley, 1976). They fail to slow responses after making errors in a task involving punishment or reward and are unable to inhibit punishable responses. Kiehl, Liddle, and Hopfinger (2000) reported errors of commission during a go-nogo task with fMRI and showed activation of aMCC. Finally, Ly et al. (2012) showed thinning along the entire MCC that could debilitate this region in functions enumerated above. Thus, decision making, planning, fear activation, and avoidance behaviors together are part of the integrative premotor function of aMCC impaired in the psychopathic brain. The views of Rolls embodied in his treatise provide new insight into these mechanisms as more detailed assessments of psychopathic brain impairments become available.

A lack of empathy is a key feature of psychopaths and this may reflect dysfunction of aMCC as demonstrated with empathy for pain in others. Jackson, Meltzoff, and Decety (2005) showed that aMCC is active while observing another individual in pain. Activity in the aMCC is correlated with the intensity of the participants' rating of the other person's pain (Morrison & Downing, 2007). Decety, Chen, Harenski, and Kiehl (2013) evaluated incarcerated males (classified as high, intermediate or low) and scanned them while viewing stimuli depicting bodily injuries and adopting an imagine-self or imagine-other perspective. During the imagine-self perspective, participants with high psychopathy showed atypical responses in aMCC and supplementary motor area (SMA). In high-scoring psychopaths, negative connectivity was found between the anterior insula, OFC and PCC and this would be expected given the theoretical framework of Rolls (2014a).

Moving caudally, Juárez, Kiehl, and Calhoun (2013) assessed subjects while they performed an auditory target detection "oddball" task and fMRI task correlations with psychopathy scores. Independent components demonstrating significant correlations with psychopathy included a visual/PCC component and modulation trends correlated strongly with impulsivity in this network. A prominent feature of psychopaths is an inability to detect the emotional significance of sensory information like emotion-generating words (Patrick et al., 1994) and entry of personally relevant sensory information into the cingulate gyrus via vPCC is blocked. Moreover, reduced activity during the coding of valenced sensory stimuli from OFC, middle temporal gyrus, and inferior parietal cortex to vPCC is also blocked according to the cingulate circuitry model (Fig. 1D).

Finally, psychopaths have the sensory capability to identify some but not all differences in facial expression (Deeley et al., 2006). Activity in the fusiform gyrus (involved in facial recognition) shows an increase in BOLD signal when observing happy faces versus controls, while the activity in this region was reduced when observing fearful faces. Thus, a precursor signal for negative facial expression precedes the inactivation noted in valence coding of self-relevant information in vPCC. Altered processing in this domain could be associated with altered response inhibition and avoidance behavior. Thus, the behavioral and emotional features of psychopathy are interrelated. The transmission of affective information from sensory cortices to the cingulate gyrus is associated with both the conscious instantiation of feeling and the top-down modulation of visceromotor and skeletomotor expressions of emotion. Lower emotional awareness or emotional intelligence is characterized by impulsive behavior, an inability to delay gratification, and a tendency for action rather than contemplation. From this perspective we can appreciate how deficits in vPCC, pACC and aMCC may explain many of the clinical features of psychopathy and the importance of OFC (Rolls, 2014a) in these impairments requires further investigation.

Conflicts of interest

The author has no financial, personal or other conflicts of interest.

Financial support

Financial support was provided by Cingulum Neurosciences Institute.

Abbreviations

ACC	anterior cingulate cortex
aMCC	anterior midcingulate cortex
cas	callosal sulcus
CG	cingulate gyrus
cgs	cingulate sulcus
dPCC	dorsal posterior cingulate cortex
ECG	external cingulate gyrus
MITN	midline, mediodorsal and intralaminar thalamic nuclei
MTG	middle temporal gyrus
OFC	orbitofrontal cortex
pcgs	paracingulate sulcus
pMCC	posterior midcingulate cortex
SMA	supplementary motor area
vPCC	ventral posterior cingulate cortex
VTA	ventral tegmental area

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Received 17 March 2014
Reviewed 21 March 2014
Revised 28 March 2014
Accepted 2 April 2014