

How do you feel?

John S. Morris

Does your heart pound because you feel afraid, or do you feel afraid *because* your heart is racing? This question is the crux of a century-old controversy, stemming from a proposal by William James. A recent neuroimaging study addresses this issue and suggests that the functional connectivity of the insula could provide the key to resolving the debate.

In an article published in *Mind* in 1884 [1], William James addressed the question, 'What is an emotion?' In his answer, he distinguished between sensory processing of emotionally arousing stimuli (S), emotional responses (R), and subjective emotional feelings (F). James famously proposed that rather than running away (R) from a threatening object (S) because we feel afraid (F), we instead feel afraid (F) *because* we are running away (R): the 'bodily changes (R) follow directly the perception of the exciting fact (S)' (see Fig. 1a). This early model of emotional processing has proved to be enormously influential, laying the foundation for more recent theorizing, such as the 'somatic-marker hypothesis' [2,3].

James's 'peripheralist' approach has been strongly opposed, however, by 'centralist' cognitive theorists (e.g. [4]), who argue that peripheral bodily feedback is too vague and ill-defined to give rise to specific emotional feelings. 'Centralists' propose that emotional feelings arise from a cognitive 'appraisal' of emotional stimuli, and that bodily feedback (if it has a role at all) merely provides non-specific enhancement of cognitively produced feelings. For much of the last century, the debate between peripheralists and centralists centered on findings from social psychology experiments [5]: the underlying neural mechanisms remained largely uninvestigated and unknown. A recent study by Critchley *et al.* [6], however, steps into this highly contested arena, and provides functional neuroimaging data that address the issues first raised by William James. Could the century-old controversy be about to be resolved?

Critchley *et al.* studied patients with pure autonomic failure (PAF), an acquired

disorder of the peripheral autonomic nervous system. Patients with PAF do not increase their heart rate or blood pressure, or show sympathetic skin conductance changes, in response to emotional stimuli (or physical stressors). Because PAF patients show no evidence of central neurological degeneration, the role of peripheral autonomic feedback on emotional processing can be selectively investigated, and William James's theory of emotion can be directly tested in terms of brain function.

Critchley *et al.* chose fear conditioning as the behavioural paradigm for their study, because the neural circuitry involved (centered on the amygdala in the medial temporal lobe) is well defined in both animals [7] and humans [8–10]. Critchley *et al.* also used a backward masking technique, thus allowing another crucial component of William James's theory to be tested: whether emotional responses 'follow directly' the sensory processing of the emotional stimulus, or whether conscious cognitive appraisal of the stimulus is required. Previous neuroimaging experiments using backward masking have demonstrated that the human amygdala responds to fear conditioned stimuli that are outside subjects' conscious awareness [9–11].

In Critchley *et al.*'s experiments, eight PAF patients and nine healthy controls were studied using event-related BOLD fMRI. Two angry faces were used as stimuli: one face (CS+) was paired with a loud noise on 30% of trials, the other face (CS-) was never paired with the noise. The target angry faces were presented either unmasked or masked by neutral faces. Response times in making a two-alternative forced choice 'like/dislike' judgment of each face were used to index conditioning. Four PAF and six control subjects showed progressive decreases in response times to CS+ faces (relative to CS-), and neuroimaging data from these subjects were analyzed and compared.

Analysis of behavioural data indicated that subjects were unaware of masked CS+ face presentations. Statistical parametric mapping analysis of the

neuroimaging data showed increased responses in right amygdala to both masked and unmasked CS+ faces. Right amygdala responses were not modulated, therefore, by conscious awareness of the stimuli. By contrast, a region of insular cortex showed increased CS+ responses only during unmasked ('aware') presentations. Comparison of PAF patients and controls showed no difference in neural responses to masked CS+ faces. However, PAF patients showed *decreased* responses to unmasked CS+ faces (compared with controls) in left orbitofrontal cortex, amygdala bilaterally and right insula. A formal test of the three-way interaction (arousal \times awareness \times conditioning) revealed a single region in right insula where responses to CS+ faces were enhanced by both conscious awareness and autonomic arousal.

Critchley *et al.*'s findings support previous studies that indicate a critical role for the amygdala in mediating automatic, unconscious responses to emotional stimuli [9–11]. Moreover, the fact that amygdala responses to masked CS+ faces were not modulated by arousal supports William James's model of causal relationships in emotional processing (Fig. 1a). A persistent criticism of James's original model of emotion is that it failed to specify how an individual stimulus is able to elicit a specific emotional response in the absence of conscious, cognitive mediation. Critchley *et al.*'s data support the view that amygdala and direct thalamo-amygdala sensory pathways [10] are plausible candidates to fill this gap in the model (Fig. 1b).

The most interesting and novel results reported by Critchley *et al.* relate to responses elicited by unmasked fear-conditioned stimuli. These data provide further evidence for a functional dissociation of conscious and unconscious emotional learning: whereas only right amygdala responded to masked CS+ faces, both right and left amygdalae responded to unmasked CS+ faces. Moreover, amygdala responses to masked stimuli did not show any dependence on autonomic arousal, whereas amygdala responses to

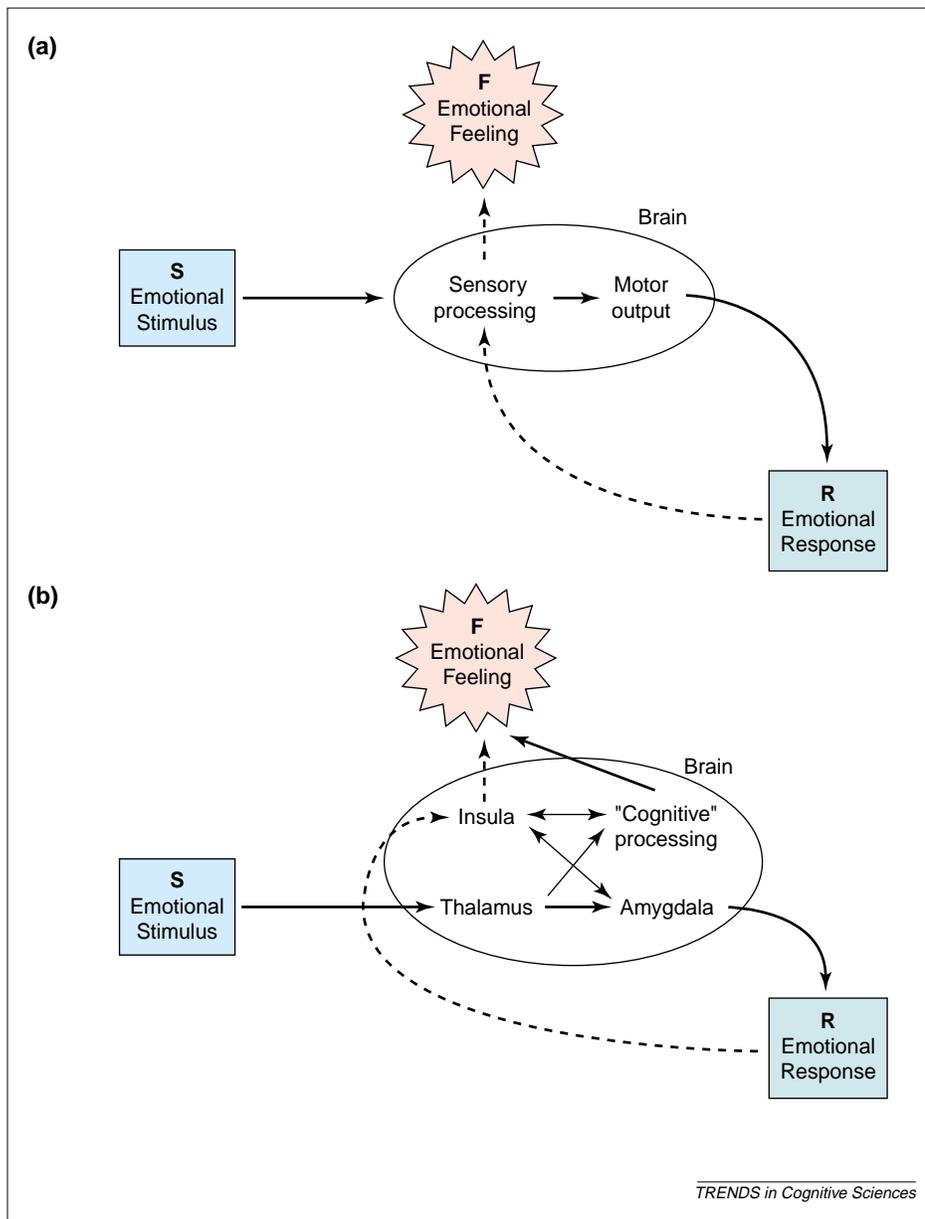


Fig. 1 (a) William James's (1884) model of emotional processing. Emotional stimuli (S) elicit automatic emotional responses (R) (solid line arrows). Perception of emotional responses produces conscious emotional feelings (F) (broken line arrows). (b) Functional neuroanatomical modification of James's model. Emotional stimuli elicit automatic emotional responses via thalamo-amygdala pathways (solid line arrows), independently of conscious, 'cognitive' processing. Peripheral autonomic responses are fed back to insula (broken line arrows), where there is an interaction with central 'cognitive' processing. On this model, conscious emotional feelings are therefore dependent on a 'peripheral-central' interaction in insula cortex.

unmasked stimuli were modulated by arousal. Perhaps the most intriguing results, however, relate to the pattern of activation observed in insula. Responses to CS+ faces in the same region of insula cortex showed interactions with both conscious awareness and peripheral autonomic arousal. These results suggest a crucial integrative function for insula in explicit emotional processing.

Insula is well placed to fulfill such an integrative role by virtue of its convergent visceral, gustatory, somatosensory, visual

and auditory inputs, and its extensive reciprocal connections with amygdala, hypothalamus, cingulate gyrus and orbitofrontal cortex. The insula has been implicated in the recognition and experience of disgust [12,13], sadness [14] and fear [15]. Increased insula responses have also been reported during fear conditioning [8], the experience of phobic symptoms [16], hunger and satiety states [17], perception of noxious stimuli [18] and explicit facial emotion categorization [19]. The diverse nature of these activations

suggests that insula has a generalized role that is not specific to any particular emotion or behavioural context. Critchley *et al.* propose that this role is to 'support feedback representations of peripheral autonomic arousal that provides input to conscious awareness of emotional states'.

Critchley *et al.*'s results indicate distinct functional roles for insula and amygdala. These contrasting roles can be neatly conceptualized in terms of William James's model of emotion (Fig. 1). The results suggest that amygdala is involved in the early translation of sensory processing into automatic emotional responses (S→R), and that insula is engaged in the transfer of these automatic emotional responses into subjective emotional feelings (R→F) (Fig. 1b). Because of the extensive anatomical connectivity between insula and amygdala, complete segregation of function between these structures is unlikely. The insula, for example, might contribute to the arousal-dependent modulation of amygdala responses to unmasked CS+ faces. Nevertheless, even in the context of a functionally integrated neural system, Critchley *et al.*'s [6] data provide strong evidence of specialized roles for amygdala and insula cortex in emotional processing.

Despite having absent peripheral autonomic responses, PAF patients still report emotional feelings, although the intensity of these feelings is greatly reduced compared with control subjects [20]. This observation presents a potential problem for William James's original proposal that emotional feelings are *totally* dependent on the perception of automatically elicited bodily changes. However, PAF patients continue to have feedback from vestibular, facial, and other musculoskeletal responses elicited by emotional stimuli, and sensory processing of this non-autonomic feedback could be sufficient to explain the persistence of emotional feelings. Critchley *et al.*'s neuroimaging data suggest another possible explanation, however. Activity related to fear conditioning in insula and amygdala was modulated by autonomic arousal *only* during unmasked (i.e. consciously perceived) presentations. Perhaps a modification of James's model is required, therefore, in which peripheral autonomic (and non-autonomic) feedback (R) *interacts* with central, conscious, 'cognitive' processing of emotional stimuli (S) in order to produce

emotional 'feelings' (F) (Fig. 1b). Critchley *et al.*'s study indicates that insula cortex could be a crucial integrative structure at the heart of such a modified Jamesian model. Understanding the intrinsic processing and extrinsic functional connectivity of insula might provide the key, therefore, to reconciling peripheralist and centralist approaches to the neural organization of human emotion.

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Where was that? – human auditory spatial processing

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The auditory system is charged with two primary goals: to determine what an acoustic stimulus is (bird call, human speech, etc.) and to determine where that stimulus came from in external space. Although our understanding of the cortical processing of visual information in humans and non-human primates has been steadily growing over the past few decades, research investigating the analogous problems in auditory perception has lagged much farther behind. This is probably because fewer laboratories are studying auditory perception in non-human primates than visual perception, as well as the fact that producing realistic auditory stimuli in modern human imaging facilities is technically extremely difficult. In the visual system, anatomical, physiological and lesion evidence suggest that there are two main information processing streams within the neocortex: a dorsal 'where' processing stream and a ventral 'what' processing stream [1,2]. Although this division of computational resources is by no means an exclusive dichotomy, the idea has helped shape our interpretations of the particular processing specifics of different visual

cortical areas. A similar type of parallel organization that segregates auditory information into 'what' and 'where' components has also been proposed [3]. The current evidence on auditory cortical processing is considerably less than that from the visual system, but so far most studies in primates are in general support of this idea.

A recent set of experiments reported by Warren *et al.* has specifically tested the notion that 'where' information is processed in the caudal auditory cortical areas in humans [4]. Previous anatomical and electrophysiological experiments in macaque monkeys have indicated that the auditory cortex comprises multiple distinct cortical areas that are interconnected in a rostral–lateral direction and a caudal–lateral direction [5–7]. The difficulty in studying auditory spatial perceptions in human imaging studies lies in the fact that the use of headphones to deliver acoustic stimuli does not generate the percept of sounds coming from the external world; rather, they are localized to a point somewhere inside the head. In natural conditions the torso, head, and particularly the pinnae,

filter incoming signals to generate small differences in the amplitudes of different frequencies depending on where the sound is in space. These filtering properties generate transfer functions of the incoming stimuli, termed the head-related transfer functions (HRTFs), that are crucial cues in normal sound location percepts [8,9].

The studies by Warren *et al.* overcame this difficulty by filtering dichotic acoustic stimuli with generic HRTFs to provide the listener with the percept of the sound coming from outside the head. In the first set of experiments, stimuli consisted of either stationary sounds in front of the head, sounds rotating around the head at a constant velocity, or sounds rotating around the head with a changing velocity. Both PET and fMRI experiments were conducted, in different laboratories. The results across these two experimental techniques were consistent: subtracting the motion condition from the stationary condition revealed bilateral activation of the cortical areas caudal to the primary auditory cortex (Heschl's gyrus) in the planum temporale (PT) and parieto-temporal operculum (PTO). There was no