

# Animal models and the embodiment of emotions

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## ABSTRACT

*This review draws some parallels between the results of experiments, none very recent, of rewarding and aversive brain stimulation in brain stem sectioned cats and the blunting of negative emotions which occurs in the human locked-in syndrome. Within the framework of theories of embodied emotions, it is suggested that a participation of bodily inputs to cerebral mechanisms of emotion is required for negative but not positive emotions.*

*Keywords:* Positive and negative emotions; Affective brain stimulation; Mid-pontine petrigeminal cat; Locked-in syndrome; Facial feedback

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## 1. EMOTION, THE BODY AND THE FACE

Can a brain isolated from the body experience emotional feelings? This question began to be asked well over a century ago, when the then freshly proposed James-Lange theory of emotion (Lange & James, 1922) came under scientific scrutiny. The question is still being asked and at least partly answered today within the framework of current hypotheses about embodied emotion (Niedenthal, 2007) and the brain-body loop (Damasio, 1999; 2010). According to the James-Lange peripheral theory (Lange & James, 1922), emotion is the feeling of the bodily changes which occur directly upon the perception of an exciting stimulus. The experience engendered by potentially emotive stimuli in a body-less brain would be, in James's words, "purely cognitive in form, pale, colourless, destitute of emotional warmth" (James,

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1884). James (1884) thought that the peripheral theory of emotion would be proved if a totally anesthetic but not paralytic subject would produce a typical behavioural reaction to an emotive stimulus while at the same time introspectively denying any subjective affection. Animals can neither introspect nor directly communicate their subjective experience, but knowledge about their behaviour and the underlying neural mechanisms strongly suggest that at least those with a relatively complex brain can have affective feelings and lives (Panksepp, 2011). How much those presumptive feelings depend on bodily inputs to the brain can in principle be tested experimentally by isolating as much as possible the brain from the body. Sherrington (1900) made the first attempt to challenge the James-Lange theory (Lange & James, 1922) in an experiment on dogs in which the spinal cord was sectioned below the emergence of the phrenic nerves, to allow for spontaneous respiration, and both vagus nerves were cut in the neck. Despite the surgical suppression of all sensory inputs from the body below the head, these animals could still display clear outbursts of anger, fear, disgust and delight by means of the limited behaviours still controllable by the brain, i.e. vocalizations and motor reactions in the cephalic region. Sherrington (1900) thought that his results went some way toward disproving the James-Lange theory of emotion, and he was right insofar as he had shown that vascular and visceral inputs from the thoracic, abdominal and pelvic districts were totally unnecessary for the observed emotional manifestations. He could not deny, however, that if his dogs had any emotional experience, this could well be induced, in accordance with the James-Lange theory, by those very same vocalizations and cephalic bodily changes which were taken as hallmarks of the occurrence of emotions. Indeed it is now current knowledge that in humans feedback from facial muscles participating in emotional expression may react back on and influence, or perhaps even generate, the associated subjective experience, as discussed below.

Granted that Sherrington's results (1900) were insufficient to disprove the importance of bodily feedbacks for the occurrence of emotional phenomena, it remains to be seen whether or not experimental animals with more radical brain-body separations than those of Sherrington (1900) will undergo a suppression of all emotional events. The classic polar division of emotions into positive and negative can be linked to the neurophysiological mechanisms of reward/approach on one hand and punishment/avoidance on the other (Rolls, 1999). Electrical stimulation of specific brain sites in unanesthetized freely moving animals can produce reward or punishment effects which can be attributed a respective positive or negative emotional valence. Animals can learn to self-stimulate at brain positive sites and to actively avoid stimulation at negative brain sites with the same or greater

intensity with which they react to natural reinforcers or punishments from the real world (Panksepp, 2005). Humans undergoing direct brain stimulation for clinical purposes can report phenomenal consciousness of emotions such as anxiety, sadness, sexual arousal, mirth and other affective feelings and subjective mood states (Heath, 1996; Selimbeyoglu & Parvizi, 2010). There is very little evidence as to the participation of bodily changes to these emotional phenomena induced by direct brain stimulation in both humans and animals. To assess this potential participation, one must explore experimentally whether rewarding or punishing brain stimulation can take place in a brain disconnected from the body. To my knowledge this has been done very rarely. In what follows I propose to discuss some aspects of emotional potentialities in two conditions of severe isolation of the brain from the body in an animal experimental preparation, the midpontine pretrigeminal cat, and the human locked-in syndrome.

## 2. REWARDING AND AVERSIVE BRAIN STIMULATION IN MIDPONTINE PRETRIGEMINAL CATS

In a largely forgotten series of experiments, Kawamura and his collaborators have made one of a few attempts to check in almost totally isolated cat brains the effects of electrical stimulations which prove rewarding or punishing in intact cats (Ikegami, Nishioka & Kawamura, 1977; 1979; Ikegami & Kawamura, 1981). They did so in the midpontine pretrigeminal cat preparation first described by Batini, Moruzzi, Palestini, Rossi and Zanchetti (1959), see Berlucchi (2012), in which the brain stem is completely transected at the pons in front of the exit of the fifth nerve, so that all sensory inputs to the brain are removed except for olfaction and vision. On the motor side the brain can control solely vertical ocular movements through the third and fourth cranial nerves, and accommodate the eye and constrict or dilate the pupil through the ocular parasympathetic system. The electroencephalogram of this preparation shows a waking pattern most of the time, and vertical ocular movements occur spontaneously and in pursuit of appropriate visual stimuli. Habituation of the above movements on repeated stimulation, pupil dilatation in response to emotional stimuli, Pavlovian conditioning of pupil responses, and eye accommodation for near vision are further indications of the existence a waking state possibly compatible with conscious awareness (Moruzzi, 1963).

Ikegami et al. (1977; 1979) showed that midpontine cats could learn by operant conditioning to use vertical eye movements in order to obtain

a stimulation of their own lateral hypothalamic area, a brain region which is associated with self-stimulation and presumably with pleasurable feelings in intact cats. By contrast, when the same cats were given the possibility of refraining from moving the eyes for interrupting stimuli of the midbrain central gray and other subcortical sites, all of which prove aversive when stimulated in intact cats, they did not do so (Ikegami & Kawamura, 1981). It was as if their brain could feel the pleasurable but not the potentially unpleasant stimulus, which instead proved neutral and in some cases even slightly rewarding since it increased the eye movement rate. Based on these results, Ikegami and Kawamura (1981) postulated that in intact cats positive emotional effects can be elicited from brain stimulation per se, without requiring a peripheral feedback from the body, whereas such a feedback is needed in the case of brain stimulations yielding negative emotional effects. They tested this possibility by repeating the experiment in *encephale isolé* cats, in which all cranial nerves remain connected to the brain so that head and face are sentient and under voluntary and automatic motor control. Like midpontine cats, these cats learned to use vertical eye movements to obtain a positive stimulation in the lateral hypothalamic area, but unlike the former cats they also learned to refrain from moving the eyes in order to avoid stimulation of the ventroposteromedial thalamic nucleus and other “aversive” sites in the hypothalamus and brainstem. All these stimulations induced in *encephale isolé* cats a contraction of facial and masticatory muscles, and such contraction, which is absent in pontine cats because of the separation between brain and facial motoneurons, is likely to afford the peripheral bodily feedback necessary for engendering a negative emotional reaction. Ikegami and Kawamura (1981) obtained proof for this possibility by showing that pharmacological blockade of the fifth (trigeminal) and seventh (facial) nerves abolished the conditioned oculomotor response to the aversive brain stimulation, along with, by inference, the attendant negative emotion. Even more important is their demonstration that the sole blockade of the (motor) facial nerve sufficed to produce the same effect, indicating that a crucial factor of the conditioned response, and presumably of the felt emotion, was indeed the sensory feedback from the facial muscular reaction to the brain stimulation. Taken together, the findings suggest that the midpontine cats’ negative emotions are dulled because their paralyzed body, and especially their paralyzed face, can no longer be involved in such emotions. By contrast, positive emotions presumably caused by direct brain stimulation in midpontine cats do not appear to require an involvement of bodily and facial reactions for their instantiation.

### 3. FACIAL MUSCLE ACTIVITY AND EMOTIONS

Darwin (1872) and James (1884) were the first to call attention to a likely reciprocal relation between animal rage and facial muscle activities, whereby the lowering of the ears, the dilatation of the nostrils, and the baring and clenching of the teeth could all be seen as both expressions and intensifiers or even generators of the emotional experience. The notion of a special importance of the face for emotional experience and expression in humans was elaborated in the last decades of the past century (Buck, 1980; Adelman & Zajonc, 1989), and the so called facial feedback hypothesis continues to occupy an important position in most current theories of the biological bases of emotion. Experimental manipulations of facial muscles, ranging from volitional or automatic contraction to relaxation to reversible paralysation, have been shown to be capable of modulating present emotions or of bringing about a previously non-existing emotional state (Niedenthal, 2007; Oberman, Winkielman & Ramachandran, 2007; Dimberg & Söderkvist, 2011). When viewing photographs of angry and happy faces, a normal human involuntary and fast reaction is to mimic the seen expression, which occurs even when the face stimuli are processed at a subconscious level (Dimberg, Thunberg & Elmehed, 2000; Dimberg, Thunberg & Grunedal, 2002). Such reactions can be objectively documented by recording the electromyographic activity of two facial muscles, the *corrugator supercilii* in the brow and the *zygomatic major* in the cheek (Dimberg & Söderkvist, 2011). The former muscle is the main agonist in the expression of anger and the second muscle is the main agonist in the expression of happiness. But even the voluntary contraction of one of this muscles, initially unaccompanied by any emotion, will eventually trigger the corresponding emotional feelings. In addition, the activity of facial muscles, whether automatic or voluntary, and the attendant emotional feelings can aid in or interfere with the recognition of emotional expressions by others, depending on whether the expression to be recognized is matched or not by one's own facial actions and emotions (Niedenthal, 2007). The two types of neural control, voluntary and automatic, of facial muscle actions are partly separated because either of them can be selectively damaged or spared by localized brain lesions (Holstege, 2002; Wild, Rodden, Grodd & Ruch, 2003).

Are there human pathological conditions in which brain damage causes, as in midpontine cats, a blunting of negative emotions through the lack of a facial feedback, while leaving positive emotions unaltered? There are some indications that severe traumatic brain damage in humans can differentially affect mimicry reactions to positive and negative emotional facial expressions. Patients with traumatic brain damage were indeed found to exhibit a general

reduction of mimicry of seen facial expressions, but viewing positive emotions (happy faces) evoked a near normal electromyographic mimicry reaction, whereas viewing negative emotions (angry faces) did not (McDonald, Li, De Sousa, Rushby, Dimoska, James & Tate, 2011). Of greater interest to the present paper is the similarity between some of the described emotional alterations of the midpontine cat preparation and the pattern of emotional states and reactions characteristic of humans with the so called locked-in syndrome.

#### 4. THE LOCKED-IN SYNDROME

This syndrome is usually caused by an acute bilateral basal pontine lesion of vascular or traumatic origin (Patterson & Grabois, 1986; Smith & Delargy, 2005; Schnakers, Majerus, Goldman, Boly, Van Eeckhout, Gay, Pellas, Bartsch, Peigneux, Moonen & Laureys, 2008). Clinically locked-in patients are unable to speak and move except for an extremely scant repertoire of voluntary motor behaviors, usually restricted to vertical eye movements or blinking. Automatic but not voluntary activation of facial muscles may be present in the form of context-adequate emotional reactions or of pathologic crying and laughter. The existence of a fully preserved conscious awareness and near-normal sensory and cognitive functions is detected by means of coded communication utilizing blinking, or, similarly to the midpontine cat, up and down ocular movements, or, in a few cases, specific patterns of brain activity generated on command and visualized by neuroimaging. As first shown by Cappa, Pirovano and Vignolo (1985), on an intellectual level locked-in patients do not appear particularly distressed by their huge behavioural limitations, despite being fully aware of them. They are generally content with their interactions with family and caretakers and have realistic and level-headed goals in their lives which can last for many years. Countering the popular belief that death would be preferable to imprisonment in one's own body, suicidal thoughts and requests of euthanasia are rare and their frequency is correlated with the presence of physical pain. A recent survey in France on self-assessed well-being in chronic locked-in patients revealed that 47 out of 65 cases professed happiness as opposed to only 18 who reported unhappiness (Bruno, Bernheim, Ledoux, Pellas, Demertzi & Laureys, 2011).

Damasio (1999; 2010) has attempted to provide a neurophysiological explanation of the surprisingly serene attitude toward life of locked-in patients. He believes that what is lacking in these patients is the neural component of the "body loop", that is the neural feedback from the bodily changes which in an intact organism initiate or contribute to emotional

experience. Because in the locked-in state the brain cannot act on the body, “any mental process which would normally induce an emotion fails to do so through the body loop mechanism: the brain is deprived of the body as a theatre for emotional realization” (Damasio, 1999; 2010). The findings of Ikegami and Kawamura (1981) indicate that presence of rewarding effects from brain stimulation after pretrigeminal section in cats may fit Damasio’s (1999; 2010) concept of the “as if body loop”, that is the enacting of bodily changes entirely within the brain. In contrast, the apparent lack of aversive effects from brain stimulation in midpontine cats seems amenable to the impossibility of bodily, and more precisely facial, motor reactions to such stimulation. One may thus assume that the emotional balance in locked-in patients is shifted toward positive emotions because negative emotions are blunted by the lack of the bodily and especially facial contributions which normally occur in able-bodied individuals. An interesting impairment in the processing of facial emotions by locked-in patients furnishes an indirect support to this assumption.

#### 5. LOCKED-IN PATIENTS ARE IMPAIRED IN RECOGNIZING NEGATIVE FACIAL EXPRESSION

Pistoia, Conson, Trojano, Grossi, Ponari, Colonnese, Pistoia, Carducci and Sarà (2010) investigated recognition of facial expressions in seven chronic locked-in patients who communicated by saying yes and no with upward and downward eye movements. Patients were asked to identify and rate the emotional intensity of photographs of faces posing six basic expressions (anger, disgust, fear, happiness, sadness and surprise). A second task involved a corresponding categorization and intensity rating of pictures of complex scenes which by consensus of a large majority of able-bodied observers were evocative of the same six basic emotions. Compared to a group of 20 able-bodied participants matched for age, sex and schooling, locked-in patients were significantly impaired in the categorization of faces expressing anger, disgust, fear and sadness, but not in that of faces expressing happiness and surprise. Nor were they impaired in the categorization of all emotional scenes and in the intensity rating of all stimuli, whether faces or scenes. Independent controls excluded that the locked-in patients’ deficit with the categorization of the negative facial expressions could be attributed to their being intrinsically harder to discriminate than those expressing happiness or surprise. Like most locked-in patients those in the study by Pistoia et al. (2010) had a complete abolition of voluntary facial motility, as assessed clinically and by elec-

tromyography. Instead they could sometimes produce active facial actions by laughing or crying in response to appropriate emotional inputs. Pistoia et al. (2010) attribute the differential reactions of their locked in patients to the absence of voluntary motor facial control and to the alteration of central neural mechanisms for emotion processing resulting from the pontine lesion causing the condition. Yet, they have not investigated the possible occurrence of automatic facial reactions of their patients to the presented facial expressions, and whether or not such reactions, if present, matched the expressions on the face stimuli. The impairment in the recognition of negative facial expressions by patients with bilateral damage of the amygdala (Adolphs, Tranel, Hamann, Young, Calder, Phelps, Anderson, Lee & Damasio, 1999) does not seem to be related to a lack of matched facial mimicry, but rather to an imperfect exploration of the eye region (Adolphs et al., 2005). It is unknown if a similar imperfection may affect the performance of locked-in patients. While all these issues require further work, the evidence of an impaired recognition of negative but not positive facial emotions by locked-in patients tends to agree with the suggestion that their balance between positive and negative emotions has been shifted by the lesion toward the former emotion.

Ikegami and Kawamura (1981) have specifically proposed the midpontine pretrigeminal cat as an animal model of the human locked-in syndrome because both display preserved awareness, a generalized paralysis and a possibility to communicate via vertical eye movements. Yet some important differences between the two conditions must not be neglected, especially with regard to the representation of the body in the brain (Berlucchi & Aglioti, 1997; 2010). Because of the complete section of the pons, the brain of the midpontine cat receives absolutely no neural sensory inputs from the whole body, whereas the usual incompleteness of the pontine lesion allows the somatic senses of locked-in patients to function normally or near normally. This may explain the preserved corporeal awareness and sense of body ownership of these patients (Nizzi, Demertzi, Gosseries, Bruno, Jouen & Laureys, 2011), in spite of their extensive motor paralysis. It is possible that the total absence of any bodily somatosensory and visual feedbacks generated by their own actions can be compensated by the congruence of visual and proprioceptive inputs from visible body parts during passive mobilization (Walsh, Moseley, Taylor & Gandevia, 2011). In addition, the many locked-in patients who breath spontaneously can feel their respiratory movements, which can be influenced by and in turn influence emotional states. As already shown by Sherrington (1900), even in absence of proprioceptive inputs from breathing movements, changes in such movements can affect the brain by altering the blood pressure and the general circulation.



## 6. TO CONCLUDE

Animal models with various degrees of brain-body separations can shed light on the neural mechanisms of the embodiment of emotions. The evidence from rewarding or punishing brain stimulation in midpontine cats suggests that positive emotions can occur entirely within the brain, without contributions of sensory feedbacks from the body, whereas negative emotions obligatorily require for their existence emotion-bound bodily inputs. The prevalence of positive over negative emotions in the human locked-in syndrome appears to share some features with the condition of midpontine cats and may depend on the absence of the bodily feedbacks supporting negative emotions.

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