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Rivalry of homeostatic and sensory-evoked emotions: Dehydration attenuates olfactory disgust and its neural correlates

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ABSTRACT

Neural correlates have been described for emotions evoked by states of homeostatic imbalance (e.g. thirst, hunger, and breathlessness) and for emotions induced by external sensory stimulation (such as fear and disgust). However, the neurobiological mechanisms of their interaction, when they are experienced simultaneously, are still unknown. We investigated the interaction on the neurobiological and the perceptional level using subjective ratings, serum parameters, and functional magnetic resonance imaging (fMRI) in a situation of emotional rivalry, when both a homeostatic and a sensory-evoked emotion were experienced at the same time. Twenty highly dehydrated male subjects rated a disgusting odor as significantly less repulsive when they were thirsty. On the neurobiological level, we found that this reduction in subjective disgust during thirst was accompanied by a significantly reduced neural activity in the insular cortex, a brain area known to be considerably involved in processing of disgust. Furthermore, during the experience of disgust in the satiated condition, we observed a significant functional connectivity between brain areas responding to the disgusting odor, which was absent during the stimulation in the thirsty condition. These results suggest interference of conflicting emotions: an acute homeostatic imbalance can attenuate the experience of another emotion evoked by the sensory perception of a potentially harmful external agent. This finding offers novel insights with regard to the behavioral relevance of biologically different types of emotions, indicating that some types of emotions are more imperative for behavior than others. As a general principle, this modulatory effect during the conflict of homeostatic and sensory-evoked emotions may function to safeguard survival.

Introduction

Emotions play a crucial role in human survival. They are essential for satisfying basic needs, and are required for regulation of personal life and successful integration into social structures (Moss and Damasio, 2001; Damasio and Carvalho, 2013). Human emotions can be characterized by the nature of their eliciting stimulus (e.g. physical or social), the type of peripheral receptors (interoceptive or exteroceptive), the processing neural pathways (e.g. reward or fear system), the physiological goals (e.g. to restore or maintain homeostasis, romantic love), or their elicited behavioral response (e.g. fight, flight, approach/avoidance behavior).

The experience of emotions is closely linked to the homeostatic state of the body. Both an acute homeostatic imbalance, detected by the interoceptive system, and a potential threat to the homeostatic equilibrium, signaled by events in the external environment, can elicit certain emotional responses in humans. Physiological changes in homeostasis such as alterations in blood volume, blood glucose or carbon dioxide level elicit physiological reactions as well as mental experiences, e.g. thirst, hunger or need for air, which are referred to as homeostatic emotions (Craig, 2003; Panksepp, 2007). These changes in the internal environment are processed by the interoceptive system and signaled to the sensory regions of the central nervous system dedicated to body functions (Damasio and Carvalho, 2013). The subjective experience of homeostatic emotions is reflected by a spectrum ranging from a mild appetite to an intense urge or a desperate craving. It leads to approach or avoidance behavior in order to restore the homeostatic balance (e.g. by intake of water, fresh air, or food) (Denton et al., 2009).

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Other emotions aim to protect from potential physiological imbalance (e.g. disgust), to avoid physical or social damage (e.g. fear, shame), and to support offspring and other individuals (e.g. maternal love, compassion). They are elicited by external inputs (e.g. visual, tactile, acoustic, olfactory) and their mental representations (Damasio and Carvalho, 2013). Emotions such as fear, disgust, or anger are triggered by the stimulation of sensory organs with simple stimuli or more complex figures and sequences (Damasio and Carvalho, 2013). Alternatively, they are elicited by mental imagery or recall of external stimuli (Fallgatter et al., 1997; Damasio and Carvalho, 2013). Those emotions are commonly referred to as basic emotions (Ekman, 1992; Panksepp, 1992). In this study we apply the term "homeostatic" to emotions elicited by homeostatic imbalances, which are detected and mediated by the interoceptive system. For a consistent distinction with regard to the underlying functional neuroanatomy, we use the term "sensory-evoked" for those emotions elicited by external stimuli.

A number of studies have explored neural correlates of homeostatic (Tataranni et al., 1999; Liotti et al., 2001; Parsons et al., 2001; Denton et al., 2009; Farrell et al., 2011) or sensory-evoked (LeDoux, 2003, 2012; Dalgleish, 2004; Craig, 2009; Vytal and Hamann, 2010; Chapman and Anderson, 2012; Krusemark et al., 2013) emotions independently. However, there has been no scientific focus on the co-occurrence of homeostatic and sensory-evoked emotions. Only a few studies have examined their behavioral interaction (Hoefling et al., 2009; Stevenson et al., 2010). An investigation of hunger and its influence on disgust revealed that hungry subjects express less disgust in response to pictures of unpalatable foods compared to satiated controls (Hoefling et al., 2009). Neurobiological data concerning this interaction is still lacking. In addition to the collection of subjective rating data, in the present study we investigated the interaction between emotions elicited by a homeostatic imbalance and emotions elicited by external stimulation using neurobiological measures.

To that end, we measured cortical activity in response to a disgusting stimulus (i.e. sensory-evoked emotion) in healthy male subjects during intense thirst (i.e. homeostatic emotion) and after drinking to satiation. Since olfactory stimulation has repeatedly been shown to be a highly effective method for eliciting disgust (Heining et al., 2003; Rolls et al., 2003; Wicker et al., 2003; de Araujo et al., 2005), we chose a fermented fish odor as disgusting stimulus. Neuronal activity was measured using blood oxygen level dependent (BOLD) functional magnetic resonance imaging (fMRI) while subjects received olfactory stimulation during both a session of intense thirst and a session conducted after drinking to satiation (Description of paradigm in Fig. 1). We hypothesized that the unpleasantness of disgust is modulated by dehydration. This modulation was expected to be reflected by a neurobiological interaction effect in a brain area significantly involved in disgust processing (i.e. the insular cortex).

Materials and methods

Subjects

Twenty-one healthy male subjects participated in the study. All subjects were right-handed and had normal olfaction. All participants were screened by means of a psychophysical olfactory test (Sniffin' Sticks test, Burghart GmbH, Wedel, Germany (Hummel et al., 1997)) and a nasal examination by an experienced otolaryngologist to confirm normal odor perception and exclude nasal abnormalities. One subject was excluded for rating the fermented fish odor as pleasant, leaving 20 subjects for the statistical analysis (age 25.3 ± 3.0 years ($M \pm SD$); range 20–31 years). All participants gave written consent, and the study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee (ethics committee of the Kanton Bern, Switzerland: KEK Bern, 081/12). We recruited subjects at the University of Bern and among the employees of the Inselspital, University Hospital in Bern. In exchange for their participation, the subjects were given a voucher worth 50 Swiss Francs (approximately 55 United States dollars).

Stimuli and stimulus delivery

Odors were presented birhinally with a computer-controlled four-channel airflow olfactometer (Sommer et al., 2012) inside the magnetic resonance (MR) scanner, by means of a passive stimulation technique, with a closed velum and exclusive mouth breathing (Hummel et al., 1992; Kettenmann et al., 1996; Welge-Lussen et al., 2003). Olfactory runs followed a 4-s 'on'/24-s 'off' event-related design, with two experimental conditions: a disgusting odor (odor of interest) and a pleasant odor (control odor). In the disgusting condition, we presented a fermented fish odor. Orange (a sweet citrus odor) was chosen as the pleasant stimulus, since this odor has been shown to be consistently rated as pleasant (Freiherr et al., 2012). The olfactometer comprised three glass bottles containing one of three fluids: fermented fish oil (herring), citrus oil (mixtures provided by the manufacturer of the Sniffin' Sticks test, Burghart GmbH, Wedel, Germany) and normal water. Depending on the condition, airflow was directed through the corresponding bottle in which the air was odorized (detailed information about the technical setup of the olfactometer and the stimulation procedure are described in Sommer et al., 2012). In each stimulation odors were presented for 4 s only, in order to minimize olfactory habituation. Olfactory stimulations were followed by a 24 s washing out period with fresh air flow to prevent carry-over effects to the next stimulation.

Procedure

The night before the MR measurement (i.e. from 8 p.m. until the experimental session), subjects had to abstain from drinks (water and others) and watery food products. For safety reasons, the morning of water deprivation was spent in the laboratory. There, subjects were offered a standardized breakfast and lunch (dry, salty snacks). The study session in the MR scanner was conducted after a total of 18 h of water deprivation. The two odors were presented to the subjects inside the scanner in two experimental conditions: a thirsty and a satiated condition. In each condition, both odors were presented 12 times in a pseudo-randomized order. The subjects were instructed to breathe normally through their mouth and keep their heads absolutely still throughout the whole experiment. Thirty minutes after the fMRI measurement in

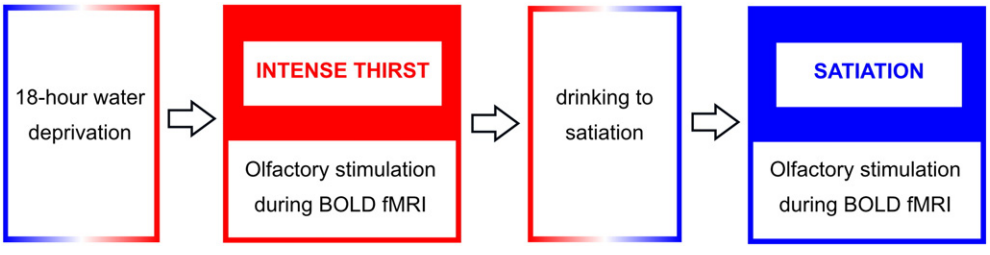

Fig. 1. Experimental paradigm. See Materials and methods for detailed information.