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Defining Positive Emotion

In humans, positive emotional states are positively valenced feeling states that are associated with the propensity toward approach and/or consummatory behavior. There are two main classes of positive emotions: appetitive positive emotional states (e.g., joy) are associated with approach behavior and pleasure is associated with consummatory behavior. The primary function of positive emotions is to elicit and maintain appetitive or consummatory behavior as well to produce positive reinforcement.

Positive Affective States in Humans

Appetitive Positive Affective States

Socializing with friends or romantic partners is the activity that most robustly elicits appetitive positive affective states. However, not all socializing is hedonic. The same studies show that interacting with supervisors or other family members is not consistently hedonic. Therefore, positive affective states are primarily related to positive prosocial interactions.

Experimental studies that elicit positive affective states generally use social positive affective stimuli (i.e., positive feedback, giving a small gift, or watching a video tape eliciting positive affective states). Positive affective states that are elicited in an experimental setting by these stimuli have been shown to increase gregariousness, optimism, and openness to new experiences. These phenomena have been referred to by Barbara Fredrickson and colleagues as ‘broaden and build’.

Consummatory Positive Affective States

Experimental studies of pleasure have primarily focused on the hedonic effects of food or thermal regulation. These studies show that the function of pleasure is to maintain behaviors that return the body to homeostasis. For example, a warm stimulus would be experienced as pleasurable by a cold individual, with the magnitude of the pleasure being proportional to the ability of the stimulus to return the body to homeostatic conditions. This emotionally driven change in sensation associated with a return to homeostasis is referred to by Michel Cabanac and colleagues as sensory alliesthesia.

Health Benefits of Positive Affective States

Positive affective states, as studied longitudinally in humans, confer resilience to depression and anxiety, and lead to an increase in overall health and a decrease in mortality from all causes. The psychological and physical health benefits of positive affective states are likely due to increases in resilience (continued global functioning despite the presence of stressors). For example, following a major life stressor, individuals exhibiting greater positive affect are less likely to develop psychological disorders such as anxiety and depression. Longitudinal studies also show that positive affective states precede the health benefit effect of positive affect. Therefore, positive affect is not simply a secondary consequence of overall good health. Conversely, individuals who have low levels of positive emotion are at greater risk of developing anxiety disorders, depression, and global health problems. Interventions that increase positive affective states have been shown to reduce levels of depression and anxiety.
Neurobiology of Positive Affective States in the Human Brain

The primary neuroanatomical underpinnings of positive emotion are associated with the ascending mesolimbic dopamine system, as described by brain imaging studies (i.e., functional magnetic resonance imaging or positron emission tomography), as well as the direct elicitation of positive affective states through drug administration or electrical brain stimulation. Brain imaging studies using recall of positive affective memories, listening to positive music, male orgasm, and positive anticipation of monetary reward have been shown to activate aspects of the ascending mesolimbic dopamine system (which includes the ventral tegmental area, nucleus accumbens, medial prefrontal and orbital frontal cortices). The euphoric effects of intravenous amphetamine have been shown to be directly related to dopamine activity in the nucleus accumbens. Direct electrical brain stimulation of the accumbens has been shown to elicit Duchenne laughter and self-report of positive affect. Patients given the opportunity to self-administer electrical stimulation to the nucleus accumbens or to an area at or near the ventral tegmental area repeatedly self-administered this stimulation and reported that the stimulation elicited a positive affective state.

The molecular underpinnings of positive affective states are still largely unknown. The endogenous molecules associated with the euphoric effects of drugs of abuse have received the most study. These consist of the endogenous opiates acting on \( \mu \)-receptors (endorphins, met-enkephalin, and \( \beta \)-endorphin) and dopamine. \( \mu \)-Opiate and dopamine levels in the mesolimbic positive affect circuit have been found to be positively correlated with the euphoric effect of exercise and amphetamine, respectively.

Intravenous administration of \( \mu \)-opiate and dopamine agonists produced positive affective states in humans. \( \mu \)-Opiate receptor antagonists have been shown to blunt the positive affective states elicited by exercise and alcohol. Dopamine receptor antagonists decreased positive affective states associated with psychostimulants. However, aversive stimuli also increased \( \mu \)-opiopiate and dopamine levels in the nucleus accumbens. Therefore, the \( \mu \)-opioid and dopamine systems are not completely specific to positive emotions.

Measuring Positive Affective States in Animals

In order to establish that an animal behavior reflects a positive affective state, at least two criteria must be met: (1) the behavior must serve as a positive reinforcer and (2) in humans a homologous behavior must be associated with the self-report of a positive affective feeling state.

Is Reinforcement Sufficient for Positive Affective States?

Positive reinforcement is specific to positive affective states, whereas negative reinforcement is not. Negative reinforcement serves to reduce negative affective states, which is not the same as increasing positive emotion. Compulsive behaviors (e.g., checking or hand washing) and frustrating nonreward are examples of nonhedonic reinforcement.

Positive reinforcement as measured by conditioned place preference is a sensitive and specific index of positive emotional states in laboratory animals. Conditioned place preference can distinguish between positive and negative reinforcement. Stimuli that elicit positive affective states in humans increase conditioned place preference, whereas negative affective stimuli induce conditioned place aversion.

Operant responding alone is not a sufficient index of a positive emotional state. Rates of operant responding (i.e., bar pressing) can be increased both by positive affective stimuli (positive reinforcement) and the avoidance of aversive stimuli (negative reinforcement).

In humans, there is not a clear positive relationship between the frequency at which a behavior is performed and the level of positive affect associated with that behavior. In the study of positive affect in the everyday lives of Americans, watching television is only weakly hedonic but is engaged in more frequently than more hedonic activities such as prosocial behavior and exercise. In addition, working, cleaning, and commuting are high-frequency behaviors that are nonhedonic.

Taxonomy of Positive Affective States in Humans

The scientific study of positive affective states primarily relies on affective self-report. In these studies, the most consistent and robust elicitors of positive affect are prosocial interactions, eating, and exercise. Each of these behaviors has clear homologies in animals.

There are other behaviors that are hedonic in both humans and laboratory animals that do not occur frequently enough in everyday life to be captured by these self-report studies. Offensive aggression and predatory behavior are hedonic in laboratory animals, and are probably also hedonic in humans.

Some hedonic behaviors in humans have either not yet been adequately modeled in laboratory animals be modeled in animals. Relaxation is a major source of pleasure in humans, but has not yet been adequately modeled in laboratory animals.
Communicated Positive Affective States in Laboratory Animals

Some positive affective states are communicated by facial/vocal displays in both humans and laboratory animals; these displays can be used as unconditional indices of positive emotional states. Prosocial behavior elicits hedonic Duchenne smiling and laughter in humans. In laboratory rats, hedonic 50-kHz ultrasonic vocalizations (USVs) are a homolog of these behaviors. Hedonic food elicits hedonic oral facial behavior (e.g., lip smacking) in humans. In laboratory rats, hedonic taste reactivity responses are a homolog of these behaviors.

Hedonic 50-kHz USVs in Rats

Frequency-modulated 50-kHz USVs have been shown to reflect a positive affective state in rats. Positively reinforcing social interactions (i.e., mating and rough-and-tumble play), anticipation of food, and action of euphorogenic drugs of abuse increased number of emitted 50-kHz USVs, whereas aversive stimuli such as social defeat, frustrating nonrewarding situations, sickness-inducing doses of lithium chloride, and foot shock all decreased the number of 50-kHz USVs. The rewarding value of the stimuli eliciting positive affective states was positively correlated with the rates of 50-kHz USVs elicited by positive social, drug, and electrical brain stimulation reward. µ-Opiate and dopamine agonists, as well as electrical brain stimulation of the mesolimbic dopamine system, also increased rates of 50-kHz USVs in rats. The neuronal and pharmacological underpinnings of rat 50-kHz USVs appear to be consistent with those of human positive emotions.

Alternative nonhedonic interpretations of the emission of 50-kHz USVs are not supported by the available data. (1) 50-kHz USVs have been hypothesized to be an artifact of locomotor activity-induced thoracic compressions. However, additional studies found that only 10% of 50-kHz USVs were coincident with thoracic compressions, and 50-kHz USVs could be dissociated from locomotion. (2) 50-kHz USVs have been hypothesized to reflect a nonaffective contact call. More detailed studies found that flat 50-kHz calls appear to be a nonaffective contact call, occurring at the highest rates during nonpositive affective social interactions. However, frequency-modulated 50-kHz calls appeared to be selective for positive affective social interactions. (3) 50-kHz calls have been hypothesized to reflect a nonpositive affective wanting state. 50-kHz USVs are increased in the anticipation of delivered reward, which in humans has been shown to elicit a positive affective state. However, during extinction bursts or frustrating nonreward, such appetitive behavior decreased rates of 50-kHz calls and increased rates of aversive 22-kHz calls. Therefore, only positively valenced appetitive behavior appears to elicit frequency-modulated 50-kHz USVs. (4) 50-kHz ultrasonic calls have been hypothesized to reflect a state of high arousal that is not specific to positive affective states. Highly arousing aversive stimuli such as predatory odor, foot shock, and bright light decrease rates of 50-kHz calls, whereas rewarding stimuli increase rates of 50-kHz calls.

Hedonic Taste Reactivity

Hedonic taste reactivity responses in rats, consisting of midline and lateral tongue protrusions and paw licking in response to oral infusions of tastants, have been shown to be homologous to positive affective states in humans. Hedonic sweet solutions (e.g., sucrose or saccharin), or salty (NaCl) solutions in salt-deprived animals, increase hedonic taste reactivity scores. Aversive solutions (e.g., quinine) and conditioned taste aversion produced by LiCl reduce rates of hedonic taste reactivity scores. Both sucrose and saccharin produce conditioned place preference, and LiCl produces conditioned place aversion in rats. µ-Opiates and cannabinoids increase positive affect in humans and increase hedonic taste reactivity responses when injected into the nucleus accumbens.

Noncommunicated Positive Affective States in Laboratory Animals

Not all positive affective states have a social communication component. The communication of positive affective states serves to both promote prosocial behavior and provide positive reinforcement in the receiver. During offensive aggression, the communication of positive affective states is inappropriate given that prosocial behavior and positive reinforcement in the attacked animal is not warranted. Exercise and predatory behavior do not necessarily involve conspecifics. Therefore, communication of a positive affective state during exercise and predation is also not warranted.

Offensive Aggression

Offensive male–male aggression serves as a positive reinforcer for the dominant animal in the conditioned place preference test, and therefore is considered to reflect a positive affective state. The rewarding and positive affective value of aggression is probably limited to only certain kinds of aggressive behaviors. Defensive male resident-intruder or maternal aggressive behavior may be motivated by negative reinforcement (i.e., avoid loss of sexual partner, offspring, and/or territory), and therefore not necessarily associated with a positive affective state. In contrast to the dominant animal, submissive animals have...
been shown to exhibit diminished positive affective states and increased levels of depression and anxiety.

**Predatory Behavior**

Predatory behavior has also been shown to reflect a positive affective state in laboratory animals. In rats, animals that readily engage in mouse-killing behavior show conditioned place preference for environments paired with mice. In cats, electrode sites that support electrical brain stimulation-induced mouse killing also uniformly support self-stimulation.

**Exercise**

Rats will show place preference for environments paired with voluntary wheel-running behavior. In a similar manner as human positive affect, voluntary wheel running induces resilience to depression and increases the lifespan of the animal. It is unclear if forced exercise is hedonic in laboratory animals.

**Drugs of Abuse**

Rats will show place preference for drugs that robustly increase positive affect in humans. In contrast, aversive substances such as LiCl induce robust-conditioned place aversion. Therefore, the hedonic value of drugs of abuse can also be measured in laboratory animals.

**Conclusions**

The 50-kHz USVs and hedonic taste reactivity have been shown to reflect a positive affective state in rats. Noncommunicated positive affective states can be measured by conditioned place preference. Because it is now possible to study positive emotional states in rats, the neuroanatomical basis and molecular mechanisms of these forms of positive affect can now be elucidated. These studies should lead to a deeper understanding of positive affect in humans and should lead to the development of novel therapeutics for the treatment of depression.

See also: Evolution of Emotions; Play Behavior; Subjective Experience and the Expression of Emotion in Man.

**Further Reading**