

# Communication of Appetitive Emotion in Rats:

Exploring the nature of 50KHz Ultrasonic Vocalizations

Psychology of Emotions

## Introduction

From an evolutionary perspective, discrete emotions motivate organisms to act in adaptive ways in specific circumstances. This function of emotions doesn't necessarily require communication. Communication is inherently costly, since it requires specialized anatomical and neural architecture to produce and perceive signals, not to mention that producing signals itself uses energy. Therefore, when emotions *are* communicated, there is likely to be some reason why natural selection favored this capability.

In the case of negative emotions, the functions of communication are fairly straightforward and well elaborated in the literature. For example, take intra-species competition. It is beneficial for strong organisms to be able to communicate anger and the intention to attack to weaker rivals, since doing so may in many cases preclude the necessity of actually engaging in a costly fight. Conversely, weaker organisms are also well served to communicate their fear and intention to submit, if doing so will avoid a fight that they would have lost anyway.

Although emotion and communication thereof are often tightly linked, they are not inextricably so. Emotions primarily serve to motivate behavior in evolutionarily adaptive ways; whereas communication also serves many other functions removed from emotion. It is possible to imagine cases of emotion without communication; for example when emotional expression is suppressed, or an emotion is unconscious and therefore not expressed. Likewise, many everyday instances of communication in human can be argued to be mostly or totally emotional content-free.

### **Adaptive Functions of the Communication of Positive Affect**

As is the case for many issues in emotions research, the communication of positive emotions is less well understood than similar topics surrounding negative emotions. In this paper, I will consider the circumstances under which it might and might not be adaptive to communicate a particular type of positive emotion: appetitive motivation (sometimes called ‘desire’ in humans). Usually, one might expect that desire be a ‘silent’ emotion, since its communication might cause others to seek the same desired reward, thereby necessitating sharing. When rewards are large and sharing is not disadvantageous, or when social rewards are the objective, however, the advantages of communicating motivation might outweigh the costs.

### **Advantages of Communicating Appetitive Emotion**

One type of situation in which communicating an appetitive state might be adaptive would be in initiating cooperation between conspecifics. Cooperation is very useful in many spheres of animal life, with a common thread being that the outcome of cooperation is better for each cooperator than it would have been had the animals pursued the same goal alone. In order to cooperate, however, the problem of the selfish interests of each participant must be addressed. The ideal situation for an animal (Animal A) would be to fake intention to cooperate with Animal B, then cheat—thereby attaining the fruits of cooperation without the costs of actually doing one’s part. Therefore, natural selection will favor some ‘honest’ signal of intention to cooperate to avoid these problems of potential cheaters. One way of ensuring the honesty of affiliative signals would be to tie them to socially appetitive emotional states. In this way, affiliative intentions would be ensured in those who signal affiliative intent.

Communication of appetitive emotion is also adaptive in other social situations. For example, most animals communicate in the context of mating. Although courtship behaviors are quite stereotyped in many animals, they can nonetheless be considered examples of communication of sexual motivation (or lack thereof), since they only occur in the context of mating attempts and have behavioral effects on their perceivers. Another example of appetitive communication may be in play solicitations. Young animals of many species engage in rough and tumble play, presumably serving to hone fighting and social skills for use in later life. Since play behavior can appear quite similar to aggression, it might be necessary for animals to solicit play with specific communicative signals indicating flippant rather than hostile motivation. Finally, some animals are motivated to engage in complex social behaviors, such as grooming in many primates and non-reproductive sex in bonobos. In these encounters, signals of intent to engage in these behaviors are produced along with apparent 'desire' to engage in them, thereby facilitating their actually occurring.

In addition to the aforementioned advantages of communicating appetitive social emotion, it might also sometimes be adaptive for non-social appetitive states to be communicated. For example, take the case of a social animal that discovers a food source. In order to approach and attain this resource, appetitive emotions are necessary, but whether these emotions are communicated would depend on several factors. If the food source were scarce, the animal would be well served to keep quiet and consume it him/herself. On the other hand, if the food source is plentiful, it would cost the animal little to communicate its motivation to conspecifics. This is particularly the case if these conspecifics were relatives, according to the theory of kin selection (Hamilton, 1963), or

if the conspecifics could be expected to return the favor at a later time (reciprocal altruism).

### **Disadvantages of Communicating Appetitive Affect**

In many cases, it could also be maladaptive to communicate non-social appetitive emotion. Appetitive emotion is primarily useful in guiding the behavior of an animal toward fitness-enhancing goals, and this process often does not benefit from communication. For example, if an animal found a small food source, it might be best served to exploit it itself instead of sharing it with others. In addition, any type of communication requires some energy expenditure in both the production and perception of signals, not to mention in developing and maintaining anatomical structures and neural mechanisms necessary to appropriately produce and perceive signals. Another potential disadvantage of communicating appetitive emotions is the potential that conspecifics will use this information about an animal's emotional state to the disadvantage of the communicator. As discussed above, one organism could 'fake' an appetitive emotional signal, or signal an appetitive emotion that it is not really experiencing. For all these reasons, the communication of appetitive emotion is most adaptive when it conveys specific advantages to the communicator that outweigh these costs.

Since the adaptive benefits of communicating appetitive states are conditional, as described above, some species may have evolved the ability to conditionally communicate their appetitive states. An exception to this general premise would be if the neural mechanisms required to differentiate situations in which it is beneficial vs. costly to communicate appetitive emotion were very complicated and/or metabolically costly. In this case, it is possible that the costs of having such a mechanism would be greater

than those of indiscriminately communicating appetitive emotion. This balance of costs and benefits of conditional emotional expression mechanisms will be different based on the particulars of the niches inhabited by different animals. Given these considerations, we might be likely to expect such conditional appetitive communication to occur in social animals, and animals that evolved to eat dispersed, variably sized food sources (like humans, other primates, and rats).

### **So When Can We Expect Appetitive Emotions to be Communicated?**

Given the potential benefits and costs of communicating appetitive emotions described in the above sections, we can expect motivational states to be communicated only under certain circumstances in many social foraging animals. In particular, these would be situations in which there is a powerful benefit to making one's motivation known to others. An obvious example of this would be in motivated social interactions such as sexual encounters, play situations, and social bonding. In addition, one might also expect communication of motivational states in situations where an animal is pursuing or expecting an abundant reward that can be shared with conspecifics without disadvantage to the communicator. These predictions based on the putative adaptive functions of communication of appetitive emotion may yield testable hypotheses about the behavior of specific social species.

### **Communication of Positive Emotions in Laboratory Rats**

Rats are one of the most commonly used experimental animals in a wide variety of scientific research programs. Rats are highly social, natural foragers, easy to maintain in laboratory environments, and easy to work with—making them ideal subjects for experimental examinations of the communication of emotions.

One of the means by which rats communicate is through ultrasonic vocalizations. Two types of vocalizations in particular have been well studied in these animals—22KHz and 50 KHz vocalizations. The former type is expressed primarily in aversive situations, and therefore is most likely associated with negative emotions (Knutson et al, 2002). The latter is primarily expressed in appetitive or possibly consummatory situations, thereby making them likely candidates for being associated with positive emotions. Jaak Panksepp and colleagues have done a great deal of work examining the nature and functions of 50KHz rat vocalizations. Panksepp variously describes these vocalizations as expressions of positive social affect (Burgdorf & Panksepp, 2001), ‘social joy’ and/or an evolutionary precursor of human laughter (Panksepp & Burgdorf, 2003), and as an index of social and non-social reward anticipation or approach (Knutson et al, 2002). Clearly, Panksepp is ambiguous about the exact nature of these vocalizations. Although he does acknowledge that 50KHz calls (hereafter: 50s) have effects on the behavior of other rats, he generally downplays their communicative nature, instead focusing on them as indices of appetitive and consummatory positive emotion.

Rats emit 50s in a variety of situations, most of which are associated with appetitive states of either a social or non-social nature. Juvenile rats robustly emit 50s both in initiating and maintaining rough and tumble play with their cage mates (Knutson et al, 1998). When rats are housed in isolation and therefore are socially deprived, even manual tickling by human experimenters can elicit many 50s, which dissipate over time as the rats presumably tire of playing (Burgdorf & Panksepp, 2001). 50s are also produced during anticipatory stages of sexual encounters, such as upon presentation of sexually receptive opposite-sex rats and during courtship behaviors (Bialy et al, 2000;

McGinnis & Vakulenko, 2003). In addition, rats also emit 50s when they are placed in environments in which they were previously tickled or had sex, suggesting a classical conditioning of the anticipatory emotion (Panksepp & Burgdorf, 2000; Bialy et al, 2000).

All the aforementioned situations involve the maintenance or anticipation of positive social interactions, but 50s are also emitted by rats that are targets of aggression by other rats (Takahashi et al, 1983). Despite the fact that in these situations 22KHz (aversive) calls are more frequent than 50s, it is difficult to reconcile Panksepp's notion of 50s as indicators of general positive affect or joy with being the target of aggression. Although the present paper's conception of 50s as anticipation of social reward is also problematic in the case of 50s emitted during aggressive encounters, it is perhaps somewhat more parsimonious than the other explanations since aggressive encounters are at least social. In addition, Panksepp has pointed out that submissive rats sometimes choose to spend time with dominant rats over being alone in their home cages. It is therefore possible that these victim rats find *any* social interaction to be rewarding to a limited extent, thus accounting for the limited production of 50s by these rats.

Overall, there is strong evidence that 50s are produced in conjunction with socially appetitive emotions. Moreover, these calls are generally produced in situations in which communication of these emotions would be adaptive. This said, Panksepp and others have demonstrated that 50s are also produced in conjunction with motivational states elicited by non-social rewards. For example, 50s are emitted by rats anticipating rewarding electrical stimulation of the Ventral Tegmental Area (VTA) and the Lateral Hypothalamus (Burgdorf et al, 2000). Similarly, both systemic and intra-Nucleus Accumbens (NAc) injections of the dopamine agonist amphetamine elicit 50s (Panksepp



& Burgdorf, 2000; Burgdorf et al, 2001), as does intra VTA infusions of glutamate, which also causes release of DA in the NAc (Fu & Brudzynski, 1994). In addition, exposure to cues predicting morphine administration (but not morphine itself) elicits 50s (Knutson et al, 1999), as do cues predicting food presentation (Burgdorf et al, 2000). It is notable that all these manipulations associated with 50s are linked to increases in dopamine (DA) neurotransmission in the NAc, including rewarding brain stimulation, administration of amphetamine and glutamate, and exposure to reward cues. DA neurotransmission here has long been associated with reward appetitive states (or incentive salience).

If, as I have posited, 50s are fundamentally social communications of appetitive states, why do rats produce them in anticipation of non-social rewards when other rats are not around? One explanation could be that the rats in these studies are attempting to communicate not with other rats, but with a different type of social partner—the experimenter. In all of these non-social reward studies, rats were housed in isolation. Panksepp & Burgdorf (2000) have previously found that socially isolated rats emit many more 50s in anticipation of tickling by familiar experimenters, and find tickling more rewarding than do group housed rats. This provides evidence that lonely rats can sometimes come to treat humans as social partners, so it is possible that the seemingly missing social element of these experimentally induced anticipatory states is in fact provided by the experimenter.

Even if human experimenters are the targets of rats' vocalizations in these experiments, this still does not explain why rats would vocalize at all for non-social rewards. Although DA-mediated appetitive states are induced in these experiments, the

target of the motivation is not social interaction, so communication aimed at soliciting a response from another might not seem necessary. As was previously discussed, it is not adaptive for animals to communicate appetitive emotion unless it is useful to do so, and I am suggesting that 50s are not a necessary component of all motivated states in rats. A possible explanation for this seeming discrepancy could be that the non-social rewards anticipated by the rats are perceived by the rat as an abundant resource that can be shared. In these experiments, cues predicting rewards are always followed by receipt of the rewards, which would be an unlikely scenario in the case of scarce rewards in the natural world. In the lab, reward cues are always followed by rewards, a fact which may be 'interpreted' by the rat as the reward being abundant. Therefore, it might be expected that the rat would communicate to others (in these cases, the experimenter) that an anticipated reward is available, since doing so would not disadvantage the communicator much. In other words, then, rats may be saying something like "come and get it" to the experimenter, as they would normally do to others of their own species.

### **Hypotheses**

Non-social elicitors of appetitive 50KHz calls seem unlikely from a functional perspective, since would seem most adaptive for rats to communicate motivation in certain (social) circumstances. As mentioned above, it is possible that previous reports of 'non-social' elicitors of 50 KHz chirps are actually social, in that individually housed, and therefore socially deprived rats perceive familiar experimenters to be social partners. These rats might then be 'talking' to the experimenter, presumably saying 'here's lots of good stuff (brain stimulation, amphetamine, food, etc.), come'n get it!' This possibility could be explored in a series of relatively simple experiments.

*Experiment 1:* Simply replicate previous experiments finding increased 50s during anticipation of electrical brain stimulation, rewarding drug administrations, and food, as well as direct administration of amphetamine (systemic or intra-NAc) with socially housed rats. Since these non-lonely rats would be less likely to perceive experimenters as social partners, one might expect that the appetitive states elicited with these manipulations conducted in the absence of other rats would not elicit as many 50 KHz calls, since there is ‘no one to talk to.’

*Experiment 2:* Administer AMPH either systemically or intra-NAc from a remote location (via implanted jugular catheters, or automatic brain microinjectors) to infrequently-handled, individually housed rats that are tested in a room totally by themselves. If there is no experimenter or other rat around, one might expect that the appetitive state produced by the drug would be unaccompanied by 50KHz vocalizations.

*Experiment 3:* As mentioned above, rats might be expected to communicate motivational states less often when rewards are scarce, since communication would likely alert other rats to the presence of a reward, thereby decreasing the likelihood that the first rat will get all or most of the reward. This could be tested as follows. Train hungry rats to search for buried sugar pellets in a large sandbox that contains either A) many pellets, or B) few sugar pellets. Each rat will be trained in one type of box only, and will always experience either a bounty or a scarcity. On the testing day, these rats will be placed into the same (pellet-rich or pellet-poor) sandbox, and its vocalizations will be recorded. In addition, a second, task-naïve and equally hungry rat will be placed in the same sandbox with the first. This second rat will have been surgically devocalized so his vocalizations will not be measured. One might expect, then, that rats trained in sandboxes-of-plenty

would emit more 50KHz vocalizations than rats in sandboxes-of-paucity, since they have little to lose from another rat actively pursuing the same rewards. If so, this would provide evidence that these calls are not inherent to all appetitive states, but are conditional upon the adaptive value of communicating motivation in a particular situation.

### **Methods**

*Experiment 1:* The procedures from the previous studies referenced above demonstrating increased 50KHz vocalizations in non-social appetitive states will be followed to the greatest extent possible. The only exception will be that rats will be housed in one of two living conditions: isolated or with 2-3 other rats. Equal numbers of socially and individually housed rats will be run, and comparisons between the 50KHz vocalizations emitted by each group will be performed.

*Experiment 2:* Again, the procedures of Panksepp and colleagues will be followed to the greatest extent possible. Rats will be individually housed, and handled repeatedly by the experimenter to familiarize them with him/her. They will then be anesthetized and implanted with jugular catheters. After a one-week recovery period, rats will be assigned to one of two conditions—isolated or normal testing. Normal testing will consist of one hour of being in the presence of the experimenter, then manual injection of amphetamine through the catheter in the presence of the experimenter. 50KHz vocalizations will be recorded for one hour following drug injection. Isolated testing will occur in a special chamber separated from the sight, smell, and touch of other rats and the experimenter. Rats will be placed in the chamber after being attached to tubes allowing injection of amphetamine to be controlled from another room. A one-hour period of habituation to

the chamber will be allowed, during which time the rat will have no social contacts.

Amphetamine will then be injected, and vocalizations will be recorded. Comparisons between the number of vocalizations by rats in normal and isolation conditions will then be conducted.

*Experiment 3:* Rats will be housed in pairs. One rat from each cage will be trained to forage for food rewards (sugar pellets) in sandboxes containing either many rewards, or few rewards. Ten sessions of training will be given to ensure that rats in both conditions learn about the availability and relative abundance of rewards in their sandboxes. On the last day of training, vocalizations will be recorded in order to provide a baseline measurement for each type of sandbox. The casemate of these rats will undergo surgical removal of their vocal apparatus, which precludes vocalizations, but does not otherwise dramatically affect behavior (Takahashi et al, 1983). After training, both cage mates will be placed in sandboxes containing the same number of rewards as during training. Vocalizations will then be measured over a one-hour period, and comparisons between reward-rich and reward-poor conditions will be made.

### **Results and Discussion**

*Experiment 1:* If 50KHz vocalizations are uniquely social, and not indiscriminately produced in social situations, rats should vocalize more when social partners are present. Unlike socially isolated rats, group housed rats are unlikely to consider human experimenters to be social partners. Therefore, if rats are capable of conditionally expressing appetitive emotion, they group housed rats should vocalize less than isolated rats, due to the perceived difference in availability of a suitable social interactant.

*Experiment 2:* To further explore the putative social nature of 50KHz vocalizations, the vocalization and motivation-enhancing drug amphetamine will be administered in the presence or absence of human social partners. If the appetitive states elicited by amphetamine only occur in the presence of humans, and not in the absence of all social contacts, this will provide evidence that the calls are conditional upon social factors.

*Experiment 3:* The above experiments sought to demonstrate that 50KHz calls are conditionally produced when appetitive emotion is experienced in social situations, and not when 'suitable' social partners are absent. Given evolutionary considerations, it is also possible that appetitive emotions are also conditional upon the nature of the reward being pursued. In this experiment, the relative abundance of available rewards was manipulated to determine whether appetitive states would be communicated more frequently when rewards are more 'sharable.' If rats vocalize less when rewards are less abundant, this would demonstrate that these vocalizations are conditional upon environmental factors, rather than simply being indicative of all appetitive states.

Together, these experiments could provide strong evidence that vocalizations are neither expressions of joy or of all types of appetitive states, but rather of specifically social appetitive states. Such conditional communication of appetitive emotion in social foragers such as rats might be predicted by evolutionary theorizing, as elaborated upon above. Even if 50KHz calls are not indicative of appetitive social emotion as I have suggested, these studies would provide useful insight into the interplay between emotion and communication in rats, and the exact nature and function of 50KHz calls in rats.

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