Incentive Relativity

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Introduction: From Folk Psychology to Experimental Research

Helen saw a picture of an attractive man in an online dating page and is happy that he accepted to meet her in a coffee house. As he arrives, Helen feels disappointed because the picture posted online does not reflect the current looks of the person. Is Helen's disappointment caused by his current looks or by the expectation she developed after seeing his picture? Tom used to like sweets, but after being treated for surgery-related pain, he developed an opioid addiction. Now, whenever he is having ice cream all he can think of is going home and taking a few pills. Has Tom lost his sweet tooth or does anticipating an opioid high make him lose his appetite for that ice cream he used to like so much? These two examples illustrate the fact that in addition to its absolute value, an incentive's value may depend on how it compares to other incentives that were expected to occur (as it happened to Helen) or are expected to occur in the near future (as in Tom's situation). *Incentive relativity* refers to a distortion in the absolute value of an incentive when the incentive occurs in the presence of expectancies of different value.

Incentive relativity is connected to a variety of psychological processes, including expectancy, motivation, emotion, and memory. To illustrate its relevance, imagine living surrounded by people who can only evaluate incentives by their absolute value. In such a society, the same outcome would have the same emotional impact regardless of prior experience. Two people losing a thousand dollars in a Las Vegas casino would have a similar emotional response whether one of them is a successful lawyer in a Manhattan firm and the other an unemployed worker. Incentive relativity may allow the lawyer to remember the casino experience as exciting, while the jobless worker would feel emotionally devastated. Similarly, a wave of public protest against government decisions can be described in terms of "relative deprivation," that is, the experience of being deprived of something a person feels entitled to receive. Incentive relativity can also interfere with our ability to empathize with friends when we see their problem from our perspective, rather than theirs, or lead us to underestimate or overestimate our resources and abilities because we have inaccurate expectations of what we can achieve. The pervasive influence of incentive relativity in daily life makes it relevant to understand the conditions, mechanisms, and neural machinery that make such comparisons possible.

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Brief Historical and Terminological Background

The role of incentives in animal learning has been a major topic of interest since the early twentieth century (Flaherty 1996). Initially, the interest was in comparing the effectiveness of rewards that differed either qualitatively or quantitatively in their capacity to change behavior. Incentives were conceptualized as the goal that aroused, directed, and brought to a conclusion the behavior of an animal. A major breakthrough came when Tolman (1932) demonstrated that animals form expectations of future events, rather than responding via stimulus-response associations, as proposed by Thorndike (1911). Some years earlier, O. L. Tinklepaugh, a graduate student in Tolman's lab, reported that monkeys accepted a piece of lettuce under a cup after seeing the experimenter depositing the lettuce there, but they refused to eat the lettuce after seeing the experimenter placing a piece of banana, their favorite incentive, under the cup and even displayed aggressive responses directed at the experimenter. Similar results were reported in analogous experiments with rats exposed to a downshift from a more preferred food to a less preferred, but acceptable food, or from a larger amount of food to a smaller amount of food. In these experiments, the instrumental performance of downshifted animals rapidly deteriorated in comparison to that of animals always receiving sunflower seeds – the unshifted control. *Incentive relativity* refers to the fact that the value of an available reward is in some cases weighed against the value of expected rewards.

Incentive relativity effects were not compatible with then dominant learning theories (e.g., Thorndike 1911). As a result, this research had a long-lasting influence on the development of learning theory that reaches to our day, about a hundred years later. There are several procedures designed to study incentive relativity and the terminology requires clarification (see Table 1). The term *contrast* refers to an apparent exaggeration of reward differences brought about in animals experiencing two rewards in a particular situation (Flaherty 1996). Contrast implies a comparison of incentives in which one is always present and the other may be present, remembered, or anticipated. In successive contrast effects, the organism is exposed to a transition in incentive value from higher to lower (*successive negative contrast*, SNC) or from lower to higher (*successive positive contrast*, SPC). *Incentive* has been used traditionally to refer to a reward expectancy, but here it is used simply as a synonym of reward and appetitive reinforcer. *Expectancy*, in turn, refers to a prediction of the impending presentation of an incentive with specific properties. Typical incentives include sucrose, saccharin, food pellets, natural foods, drugs, and brain stimulation. The term *successive* refers to the fact that there is usually a single transition in reward that occurs across sessions. Successive contrasts have been studied in instrumental (iSNC, iSPC) and consummatory (cSNC, cSPC) situations. *Instrumental responses* are assessed before the animal comes into direct contact with the incentive and are thus anticipatory. Typical measures involve errors, latency, speed, and response frequency. *Consummatory responses* involve interaction with the incentive, usually in terms of consumption. Typical measures include licking frequency, cumulative time in contact with the reward, and fluid intake. In a cSNC experiment, the effects of reward downshifts are assessed in terms of consummatory behavior, typically after a downshift in sucrose concentration (e.g., a downshift from 32% to 4% sucrose). Such a downshift leads to a transient suppression of consummatory behavior relative to that of an unshifted 4% sucrose control. This model is playing a key role in our understanding of incentive relativity processes and is covered below in detail.

In addition to successive contrast, reward relativity has also been studied in simultaneous and anticipatory contrast procedures (Flaherty 1996). In *simultaneous contrast* situations, trials with small or large rewards, each signaled by a discriminative stimulus, are mixed randomly within a session and the performance in either of these trials is compared to unshifted small and unshifted large controls, respectively. The key outcome in simultaneous contrast experiments is that animals receiving both reward magnitudes exhibit lower

Incentive Relativity, Table 1 Incentive relativity procedures mentioned in this entry as typically studied in rats

Task and description
Consummatory successive negative contrast (cSNC)
Downshift condition: Exposure to a large reward followed after a few sessions by exposure to a small reward
Control: Always exposed to the small reward
Dependent variable: Reward consumption (fluid intake, lick frequency)
Effect: Downshifted animals consume less of the small reward than unshifted controls
Instrumental successive negative contrast (iSNC)
Downshift condition: Exposure to a large reward followed after a few sessions by exposure to a small reward
Control: Always exposed to the small reward
Dependent variable: Anticipatory behavior (running, lever pressing)
Effect: Downshifted animals respond less for the small reward than unshifted controls
Anticipatory negative contrast (ANC)
Experimental condition: Exposure to a small reward followed every day after a short interval by exposure to a large reward (small➔large)
Control: Exposure to the small reward followed every day after a short interval by exposure to a small reward (small➔small)
Dependent variable: Consummatory behavior (fluid intake, lick frequency)
Effect: Animals respond less to the small reward when it is followed by the large reward than when it is followed by the small reward
Consummatory successive positive contrast (cSPC)
Unshift condition: Exposure to a small reward followed after a few sessions by exposure to a large reward
Control: Always exposed to the large reward
Dependent variable: Reward consumption (fluid intake, lick frequency)
Effect: Upshifted animals consume more of the large reward than unshifted controls
Instrumental successive positive contrast (iSPC)
Upshift condition: Exposure to a small reward followed after a few sessions by exposure to a large reward
Control: Always exposed to the large reward
Dependent variable: Anticipatory behavior (running, lever pressing)
Effect: Downshifted animals respond more for the large reward than unshifted controls
Simultaneous negative or positive contrast
Experimental condition: Responding for a small reward in one stimulus condition and for a large reward in a different stimulus condition
Controls: Exposure to the small reward or to the large reward in both stimulus conditions in different control groups
Dependent variable: Anticipatory behavior (running, lever pressing)
Effects: Experimental animals respond less for the small reward than small-reward controls (negative), but more for the large reward than large-reward controls (positive)
Behavioral contrast
Conditions: Receiving a large reward magnitude or high reward frequency under one stimulus and a small magnitude or low frequency under another stimulus, within a session (multiple schedules of reinforcement)
Dependent variable: Response rate
Effect: Low responding for a small reward when the previous or following component involves a large reward relative to responding for a low reward when the previous or following component also involves a small reward (negative). High responding for a large reward when the previous or following component involves a small reward relative to responding for a large reward when the previous or following component also involves a large reward (positive)

performance for the small reward than animals that only receive the small reward (i.e., an instrumental simultaneous negative contrast effect). Negative simultaneous contrast is also obtained in consummatory procedures. For example, animals exposed to repeated access to two sucrose solutions (32% and 4%) within the same session consumed more of the 32% and less of the 4% than unshifted controls exposed just to 32% sucrose or just to 4% sucrose, respectively.

In a similar procedure, often termed *behavioral contrast*, two or three reward schedules differing in reward magnitude or frequency alternate within a session, each with its own discriminative stimulus. Performing an operant response (lever press, nose poke) in each component is usually the key response measure. In this case, the rate of responding maintained by a constant schedule during one stimulus is increased by reductions in

the reinforcement rate during an alternative component of the schedule (Flaherty 1996).

Incentive relativity may also influence behavior in an anticipatory manner (see below). Rats exposed to two palatable solutions in sequence may suppress intake of the first solution (e.g., 0.15% saccharin, 4% sucrose) if the second solution is preferred (e.g., 32% sucrose).

In the rest of this entry, we will focus on two incentive relativity paradigms extensively analyzed from a psychobiological perspective: successive and anticipatory contrast, especially as they are studied in consummatory situations involving reward downshifts. References to other procedures may be brought to bear on specific issues. This concentration reflects contemporary interests in these forms of contrast, in their similarities and differences, and in their usefulness as models for the study of psychological pain, conflict, and addictive behavior.

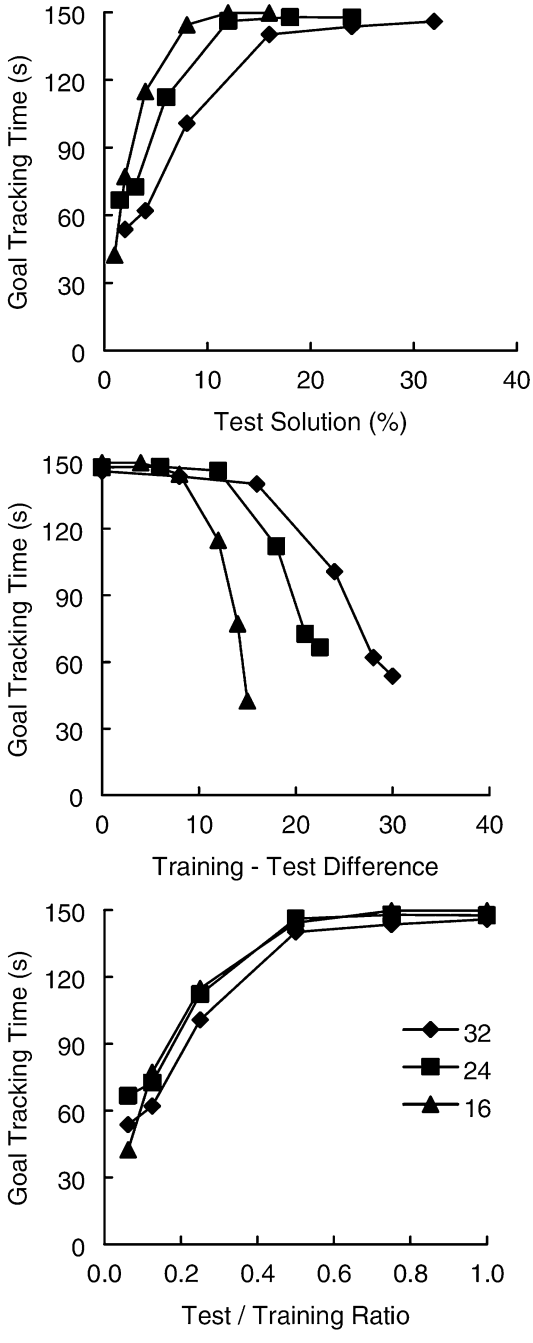
Consummatory Successive Negative Contrast (cSNC)

Basic behavioral phenomena associated to cSNC have been extensively reviewed in readily available articles (Flaherty 1996; Ortega et al. 2017; Papini et al. 2015; Torres and Papini 2016). Here we will center on four factors: detection, motivation, emotion, and memory.

Detection

Rats trained in a runway to collect various numbers of food pellets and then downshifted to one pellet exhibit an iSNC effect directly proportional to the size of the disparity between pre- and postshift magnitudes. What is the rule regulating the detection of such reward disparity? To uncover the detection rule, Papini and Pellegrini (2006) gave three groups of rats access to either 16%, 24%, or 32% sucrose in four trials per day. Every other day, the second or third trial in the session involved an occasional downshift. For each group, six concentrations were used in downshift trials chosen so as to generate the same postshift/preshift ratios (8-to-1). When the cumulative time in contact with the sipper tube for each group was plotted against the absolute postshift concentration or against the difference between the preshift minus postshift concentrations, the functions for these three groups diverged significantly. However, when consummatory behavior was plotted against the ratio of postshift/preshift concentrations, the three functions overlapped and all differences disappeared (see Fig. 1). Therefore, consummatory behavior during a downshift episode was determined by a *ratio invariance rule* akin to Weber's law for sensory comparisons. A second experiment using the conventional cSNC preparation confirmed these results, except when the postshift solutions were either too high (above 16% sucrose) or too low (below 2% sucrose). This ratio invariance rule also applies iSNC (Pellegrini and Papini 2007). Rats reinforced for running with either 32 or 16 pellets exhibited overlapping postshift performance after a downshift to four or two pellets, respectively. Interestingly, ratio invariance was strong far from the goal, but it was less clearly observed close to the goal compartment of the runway. Using a rat autoshaping preparation with sucrose solutions as the reward, Pellegrini and Papini (2007) replicated the absence of iSNC when sucrose solutions are used as the reinforcer (see Flaherty 1996), but still observed ratio invariance after reward downshifts.

Little is known about the neural basis of ratio invariance in the SNC situation, but the hypothesis that opioid receptors are involved has received some support (Ortega et al. 2017). In one experiment, independent groups were exposed to the following downshifts: 32-to-6% and 16-to-3% sucrose (ratio: 0.19), and 32-to-12% and 16-to-6% sucrose (ratio: 0.38). Treatment with naloxone, a nonselective opioid receptor antagonist, before the first downshift session shifted the behavioral response from a ratio-based to a difference-based rule: the suppression was maximal for animals exposed to the 32-to-6% sucrose downshift, which experienced a 26% drop in sucrose concentration, and minimal for animals exposed to the 16-to-6% sucrose downshift, which were subject to a 10% reduction in sucrose concentration. Antagonist drugs, like naloxone, do not generate action potentials; rather, they



Incentive Relativity, Fig. 1 Groups exposed to 32%, 24%, or 16% sucrose (called "training solutions") were occasionally downshifted to a series of sucrose concentrations between 1.5% and 24% sucrose (called "test solutions"). When the results were plotted as a function of the test solution *top*) or the training minus test difference (*middle*), there were significant differences between groups receiving reward downshifts from different training

prevent endogenous opioids to act on the receptor. Therefore, this naloxone effect on cSNC implies that endogenous opioids must be released during an experience of reward devaluation. Although the brain site of this effect is not known, one prime candidate is the amygdala (see below).

Motivation

Behavior in a situation involving reward shifts also depends on internal factors. A major internal factor in situations involving access to food is the extent of food deprivation (Flaherty 1996). In the cSNC situation, for example, nondeprived animals usually drink less 32% sucrose than 4% sucrose, a fact that complicates the analysis of postshift performance. Nondeprived animals also respond differently to reward downshift relative to deprived animals, showing an extended cSNC effect. This extended cSNC effect may be related to a reduced need for calories in nondeprived rats, provided that a downshift from 32% sucrose to 0.15% saccharin, which lacks caloric content, also leads to an extended cSNC effect. Similarly, inducing a need for sugar with exogenous insulin eliminates the cSNC effect based on sucrose intake.

The value of a reward also seems to depend on the internal state of the animal at the time the reward is consumed. Cuenya et al. (2015) fed animals with food pellets either before or after a session involving access to sucrose solutions during ten preshift sessions in a cSNC situation. Presession feeding should have devalued the sucrose solution, whereas postsession feeding should have had at best a modest effect on sucrose consumption. All animals experienced presession feeding before each postshift session, when the

Incentive Relativity, Fig. 1 (continued) solution to the same test solution (e.g., 16-to-8% vs. 32-to-8% sucrose). However, when the same results were plotted as a function of the test/training ratio, the functions overlapped and differences were not observed. Such overlap suggests that the degree of consummatory suppression during a downshift depends on the proportion between the two solutions, rather than their absolute values or their difference. Results from Papini and Pellegrini (*Learning and Motivation*, 2006, Fig. 2, reproduced with permission from Elsevier)

concentration of the sucrose solution was devalued from 32% to 4%. Whereas animals that had experienced postsession feeding during preshift sessions exhibited a cSNC effect, those that had experienced presession feeding failed to show evidence of a cSNC effect. The implication is that presession feeding had devalued the 32% sucrose such that a downshift to 4% sucrose was not experienced as particularly significant. Overall, these data suggest that the value of the 32% sucrose reward depends not only on its absolute properties but also on the internal state of the animal at the time of its consumption.

Emotion

Since the early demonstrations of incentive relativity, interpretations have favored either emotional or cognitive mechanisms to account for the response to reward downshift. There is no question that reward downshift provokes an increase in search behaviors that seem appropriate to either find the missing resource or switch to another source of reward (Flaherty 1996). For example, when trained in a small conditioning box, rats subjected to a 32-to-4% sucrose downshift exhibit increased activity and rearing behavior and when trained in a radial arm maze, exploratory behavior in nonbaited arms increases during postshift trials. While emotional and cognitive changes are not necessarily incompatible, there is evidence that search behavior is not necessary for a cSNC effect to occur. Lopez Seal et al. (2013) trained rats to voluntarily enter a tube to collect sucrose solutions. Once inside, animals were unable to turn around but could either lick or not at the sipper tube dispensing the solution. Under conditions that prevented full-blown search behavior, rats still exhibited a cSNC effect. The implication is that incentive relativity is accompanied by a negative emotional response that inhibits or redirects approach to the site previously associated with a highly valuable reward.

In fact, unexpected reward omissions and devaluations are known to induce changes associated with negative emotion, including distress vocalizations, odor emissions, stress hormones, and aggressive behaviors, among others (see Papini and Dudley 1997). An additional aspect that evokes a clear connection with emotion is the extensive overlapping between incentive relativity and physical pain, leading to the notion that reward loss and devaluation can be conceptualized as psychological pain (Papini et al. 2015). In accordance with this view, opioid and cannabinoid agonists reduce the cSNC effect, whereas opioid antagonists enhance it (Ortega et al. 2017). Another source of evidence involves the bidirectional interacting relationships between reward relativity and sensitivity to peripheral pain. Animals exposed to a 32-to-4% sucrose devaluation exhibit reduced sensitivity to physical pain in a variety of situations. By contrast, exposure to peripheral pain and restraint stress enhance the size of the cSNC effect (Papini et al. 2015).

The attenuating effect on cSNC of anxiolytics provides a third source of evidence that reward relativity is accompanied by negative emotion. Flaherty (1996) reviews extensive evidence that benzodiazepine anxiolytics (e.g., chlordiazepoxide, midazolam) and ethanol reduce the cSNC effect during the second downshift session but have no measurable effect during the first downshift session. If the typical 5-min session is substantially lengthened or several cycles of reward devaluation are administered, then the cSNC effect is reduced by anxiolytics during the initial downshift session. Thus, some experience with reward devaluation is needed before anxiolytics can act, a fact that prompted Flaherty (1996) to propose a multistage model of cSNC. According to this model, negative emotion arises when the animal enters into an approach-avoidance conflict stage, with the anxiolytics then reducing avoidance and ameliorating the cSNC effect.

Compelling evidence that reward relativity induces negative emotion comes from a phenomenon traditionally known as escape from frustration. In this situation, rats are confined to a location where they have access to a large reward for several sessions. On one session, they encounter no reward (extinction) and then, after a few seconds, a door that had been closed is opened. These animals exit the extinction location faster than controls that had never received a reward in that box. This effect is eliminated by opioid blockage with naloxone (Papini et al. 2015).

Extensive research with inbred Roman high- (RHA-I) and low- (RLA-I) avoidance strains also provides evidence consistent with a relationship between reward downshift and negative emotion (Torres and Sabariego 2014). RLA-I rats, which exhibit high anxiety levels in a variety of situations, also show a longer cSNC, a greater iSNC, and a faster extinction after reward omission. Interestingly, RLA-I increased ethanol consumption and preference immediately after experiencing appetitive extinction, a result interpreted in terms of emotional self-medication. Outbred Wistar rats also showed increased consumption and preference for ethanol and the anxiolytic chlordiazepoxide immediately after experiencing a 32-to-4% sucrose devaluation (Torres and Papini 2016).

Finally, evidence suggesting a link between reward relativity and negative emotion comes from the effects of neural manipulations on cSNC. For example, transient lidocaine inactivation of the centromedial amygdala impairs the cSNC effect, increased activity in the open field, and had no effect on ANC (Kawasaki et al. 2015). Several studies further show that corticomedial amygdala lesions, diazepam infusions into the central amygdala, lesions of the insular cortex, lesions of the ventrolateral orbital cortex, and lesions of the anterior cingulate cortex modulate the cSNC effect (Ortega et al. 2017; Papini et al. 2015).

Memory

Adjustment to the cSNC situation implicates several memory processes (Papini 2003). First, the animal learns to expect access to 32% sucrose during the initial ten sessions. This *expectancy memory* is required to account for the rejection of the 4% sucrose on session 11, once the animal has detected the negative discrepancy between obtained and expected rewards. Second, if the initial downshift event is sufficiently aversive, an emotional memory may be encoded. Because this memory includes aspects of the animal's own emotional reaction to the downshift, it is called *egocentric memory*. Third, every time the animal tastes the downshifted solution a process of memory update would adjust the expectancy learned during preshift sessions (32%) to the new value (4%). Because this memory encodes information of the new reward, it could be called *allocentric memory* – a memory of the environmental change. Allocentric memory would reduce and eventually eliminate the negative discrepancy. Fourth, during downshift sessions, there is the inevitable pairing between negative emotion and 4% sucrose, which, although less than expected, it is still rewarding, especially for a food-deprived animal. Such pairings would result in a *counterconditioned memory* of negative emotion, a process that would attenuate rejection and promote approach to the downshifted solution (Amsel 1992). Therefore, allocentric memory and counterconditioning should both contribute to the recovery of consummatory behavior to the level of unshifted controls.

Research has attempted to provide evidence for these memory processes in experiments with a variety of designs, for example, by varying the retention interval between the last preshift session and the first postshift session. Flaherty (1996, pp. 40–42) summarized several studies with retention intervals ranging between 1 and 32 days, suggesting that between 10 and 17 days, the cSNC effect is attenuated by the interval. He suggested that long retention intervals weaken the memory of the preshift solution, thus attenuating contrast.

Theoretically egocentric and allocentric memories are formed somewhat simultaneously during the initial downshift session. Whereas the former encourages behavioral suppression, the latter prompts the animal to consume the downshifted reward. Therefore, the cSNC effect should be prolonged either by enhancing egocentric memory or by interfering with allocentric memory, whereas the cSNC effect should be reduced either by interfering with egocentric memory or by enhancing allocentric memory. Following this rationale, memory enhancers such as corticosterone (a stress hormone) and D-cycloserine (an NMDA-receptor partial agonist) administered immediately after the first downshift session prolong the cSNC effect in subsequent sessions (see Papini et al. 2015). It is hypothesized that corticosterone and D-cycloserine enhanced the

reactivation of the egocentric memory of the reward devaluation. Posttraining administration of benzodiazepine anxiolytic chlordiazepoxide also extends cSNC. Because chlordiazepoxide has a memory-interfering effect, these results were interpreted in terms of disruption of allocentric memory.

Counterconditioned memory can be studied by assessing transsituational transfer effects. Amsel (1992) argued that partial reinforcement training counterconditions a frustration response that increases persistence during extinction. Furthermore, the reactivation of frustration in other situations would induce persistence even in the absence of partial reinforcement training. Consistent with this view, partial reinforcement training during preshift trials (random mixture of 32% sucrose and water sessions) attenuates the cSNC effect after a 32-to-4% sucrose downshift. In addition, anxiety-prone rats (RLA-I) trained in the cSNC situation later exhibit a reduced iSNC effect and, vice versa, first trained in iSNC later reduced the cSNC effect. Interestingly, such transfer effects were not observed in the RHA-I strain (Cuenya et al. 2015). Thus, it appears that recovery from one situation involving incentive relativity and negative emotion may attenuate the impact of an analogous manipulation under different conditions.

Anticipatory Negative Contrast (ANC)

ANC was first observed in the course of a study investigating whether conditioning could affect the glucoregulatory system. Animals were exposed to pairings of saccharin as the conditioned stimulus (CS) and sucrose as the unconditioned stimulus (US). As a consequence of such pairings, the intake of saccharin was reduced when it served as a predictor of sucrose, suggesting that incentives can influence behavior in an anticipatory manner (Flaherty 1996). The occurrence of ANC is paradoxical with respect to a simple application of the law of effect and from a reinforcement perspective: following a behavior with a preferred substance should increase, not decrease, the initial behavior. In fact, if one alters slightly the procedure to produce ANC, the opposite result (referred to as positive induction) may occur. For example, if rats are trained to press a lever to obtain a low-valued food reward, the rate of responding for this reward increases if a high-valued food reward is available within the session. For example, animals decrease their consumption of a 1% sucrose when the solution is followed by access to a 32% sucrose, but the same animals increase their rate of operant lever pressing for a 1% sucrose if a 32% sucrose or food pellet is upcoming (King et al. 2002).

When ANC is obtained, the most common interpretation assumes that it represents Pavlovian conditioning in which the initial substance functions as a CS and the second one as a US. After several pairings, the CS would enter into an association with the US, enabling the animals to learn predictive relationships and reducing the hedonic value of the first solution (Flaherty 1996). However, alternative explanations based on the insensitivity of ANC to devaluation of the preferred substance have also been proposed. For example, Onishi and Xavier (2011) argued that ANC depends on two memory processes: (1) the memory of the relative value of the first solution (which is daily updated on the basis of gustatory and/or post-ingestive comparison of the first and second solutions) and (2) the memory of past pairings.

Detection

Many studies focusing on the factors influencing the detection of disparities between rewards suggest that the ANC effect depends on the absolute and relative incentive value of the first and second rewards, their hedonic/nutritional properties, and the temporal interval between reward presentations. The first evidence of this phenomenon involved the use of a 0.15% saccharin solution available for 3 min and followed after an intersolution interval of 5 min by a 32% sucrose solution for 5 min. Control groups received either 2% sucrose as the second solution or only the 0.15% saccharin. After 12 sessions, groups receiving saccharin only or saccharin followed by 2% sucrose showed a more accelerated lick function as compared with animals receiving 0.15%–32% pairings. This result was interpreted on the basis of

the greater hedonic value of 32% sucrose solution compared to the 0.15% saccharin (see Flaherty 1996). However, the question remained whether this phenomenon was anticipatory (i.e., based on the anticipation of the impending sucrose) or successive (triggered by the comparison between the current 0.15% saccharin and the 32% sucrose presented as the second reward on the previous day). Several experiments discarded the latter interpretation. First, increasing the inter-solution interval from 5 to 30 min significantly reduced the suppressive effect of 32% sucrose on saccharin intake. Additional support for a within-day anterograde process was reported by Flaherty and Rowan (1985), who conducted a within-subjects study in which both the contrast (0.15%–32%) and the control (0.15%–0.15%) conditions were presented to the same subject in alternation across days. The rationale behind this experimental design was as follows. If contrast is based on the 32% sucrose presented on the previous day, then lick rates for the initial 0.15% saccharin solution should be lower on days when the animals received the 0.15%–0.15%, provided that these days always follow a 32% sucrose trial. By contrast, if a within-day anticipation is involved in ANC, then the lick rate for the 0.15% solution should be lower when the 0.15% saccharin predicts 32% sucrose. The results indicated that rats licked less for the 0.15% saccharin on 0.15%–32% days than on 0.15%–0.15% days. The differences between trials appeared regardless of the inter-solution interval (15 s vs. 1 min) and even after reversing the cue-solution pairings.

Once it was demonstrated that ANC depends on anterograde mechanisms, subsequent experiments showed that variations in either the first or the second reward influence the size of the effect (see Flaherty 1996). For example, when the initial substance has low hedonic value relative to the second one (e.g., water or an empty tube followed by 32% sucrose), positive induction is observed. Increasing the hedonic value of the first solution resulted in ANC, rather than positive induction. The greater the hedonic value of the first solution, the sooner and the larger the ANC. However, when other reward combinations are used the results are far from conclusive.

In addition to their gustatory/hedonic properties, differences in nutricaloric load between rewards may also influence the ANC effect in a complex manner. Moss et al. (2002) systematically studied the relative contributions of hedonic/gustatory properties and nutricaloric loads to the ANC, by replacing the first 0.15% saccharin solution with soy milk. Soy milk has a greater hedonic value than sucrose (16%), but similar nutritive properties. According to the hedonic disparity hypothesis, ANC should have been found when using sucrose-soy milk pairings, but not soy milk-sucrose pairings. Contrary to what was expected, the sucrose-soy milk sequence failed to produce ANC, whereas the soy milk-sucrose sequence did yield a reliable suppression of soy milk intake, showing a direct function of the sucrose concentration. Taken together, these results reveal the complexity of the factors taking part in the detection of reward disparity in the ANC paradigm.

Motivation

Apart from the hedonic properties, the rewards, their caloric value, and the temporal presentation pattern, ANC is also modulated by motivational factors (see Flaherty 1996). Some studies have explored how food deprivation influences animal's behavior in anticipatory situations. In food-deprived animals, ANC was obtained when 2% or 4% sucrose preceded by 15 s, but not by 5 min, access to 32% sucrose. In nondeprived animals, the reduced intake of either 2% or 4% sucrose appeared whenever these rewards were presented 5 min before 32% sucrose. Interestingly, the influence of the deprivation condition was not observed when saccharin-sucrose pairings were used, suggesting that the caloric value becomes important with long inter-solution intervals under conditions of food deprivation.

The level of deprivation has also been investigated by Weatherly et al. (2005), who found that deprivation promoted positive induction, rather than ANC. Induction was observed when subjects were food deprived and exposed twice a day to 1% sucrose (3 min) followed (after 0, 15, or 60 s) by a 3 min access to 32% sucrose. However, nondeprived animals did not show either a reliable

positive induction or an ANC effect. The authors concluded that although induction was never observed when subjects were not food deprived, eliminating food deprivation was not sufficient to produce contrast.

A different approach to address the issue of how motivation impacts ANC involves using rewards with high incentive value, such as abuse drugs. The model was initially based on the frequent observation that rats avoid the intake of a gustatory CS such as saccharin after it has been paired with and aversive US (e.g., the toxin lithium chloride). Drugs of abuse (e.g., cocaine, morphine, heroine) also suppress saccharin intake following repeated pairings. Based on its similarity with conditioned taste aversion procedures, this effect was initially interpreted as indicative that abuse drugs have both reinforcing and aversive properties. However, the suppressive effects of drugs of abuse differ in many ways from those of aversive stimuli, leading to an interpretation of this phenomenon based on reward comparison: Rats would decrease saccharin because its value is outweighed by that of a highly reinforcing psychoactive drug (Grigson 1997).

As opposed to ANC tests, in which free access to both rewards is the standard procedure, drug-induced suppression of CS intake usually involves forced administration of the US. Despite such differences, the suppressive effects of abuse drugs and sucrose on CS intake share a number of similarities: (a) both depend on the nature of the gustatory CS; (b) both are attenuated by food deprivation; (c) both are greater in selected rats highly reactive to abuse drugs (Lewis rats); (d) both are increased in rats exposed to chronic morphine; and (e) both are disrupted by lesions of the gustatory cortex and gustatory thalamus (Grigson 2008). Overall, the data suggest that both behavioral phenomena are related to mechanisms of anticipated reward comparison and devaluation. Supporting this contention, recent results showed that a reduction in CS intake induced by a single saccharin-morphine pairing is accompanied by a marked blunting of the nucleus accumbens dopamine response to the saccharin reward cue (Grigson and Hajnal 2007).

Emotion

While hedonic devaluation provides a parsimonious explanation of ANC, alternative mechanisms have also been proposed. One possibility is that the presentation of a low reward after being paired with a high reward triggers negative emotion (Flaherty 1996). While there is evidence for such a mechanism in other forms of contrast (as in SNC, see above), three sources speak against this possibility in the case of ANC (Flaherty 1996; Papini et al. 2015). First, anxiolytics (such as chlordiazepoxide, cyproheptadine, buspirone, and testosterone) fail to affect ANC. Similarly, the administration of drugs known to enhance aversive memories of reward downshift events (such as corticosterone), do not influence ANC. The pharmacological manipulation of opioid receptors (known to be involved in psychological pain) also shows negative results when applied to the ANC effect (Katsuura and Taha 2014).

Second, lesion studies involving brain regions known to regulate negative emotions fail to alter ANC. Unlike cSNC, neither electrolytic lesions of the central nucleus of the amygdala (see Flaherty 1996), nor the transient inactivation of the centromedial region of the amygdala induced by lidocaine microinfusions affected ANC (Kawasaki et al. 2015).

Third, studies based on comparisons between strains of rats that differ in emotional reactivity are not conclusive with respect to ANC. Maudsley reactive (MR) and Maudsley nonreactive (MNRA) rats showed little difference in ANC when licking frequency was used as dependent variable. However, whereas MNRA rats exhibited longer latencies to lick 0.15% saccharin when this solution was followed by 32% sucrose, a positive induction effect was found in the MR strain (Flaherty 1996). Regarding the extensively phenotyped RHA-I and RLA-I rats in anxiety tasks, no differences in ANC were found (Torres and Sabariego 2014).

Taken together, these data suggest that ANC situations may not involve negative emotion. However, this conclusion should be taken with caution. For example, Gómez et al. (2000) explored whether individual differences in saccharin intake suppression induced by morphine

correlated with circulating corticosterone levels. Greater suppression of CS intake was associated with higher corticosterone levels. In the same vein, McFalls et al. (2016) found that those animals exhibiting greater levels of saccharin intake suppression showed increased mRNA expression for elements of the stress/CRF signaling pathway within the hippocampus, medial prefrontal cortex, and ventral tegmental area.

Memory

Since its discovery, the ANC effect was thought to be due to Pavlovian associations and anterograde memory processes, both involving the anticipation of the highly preferred sucrose reward when the less preferred saccharin solution is presented. A few studies have addressed the neurobiological basis of the memory processes that support ANC. Electrolytic lesions of the gustatory thalamus impaired ANC but had no influence on simultaneous contrast (Reilly et al. 2004). These results suggest a role of the gustatory thalamus in the comparison between the value of an available reward and the memory of a preferred reward that is anticipated in the near future.

The gustatory insular cortex has also been involved in reward anticipation. Kesner and Gilbert (2007) found that quinolinic acid lesions of the agranular insular cortex disrupted ANC in rats receiving 2%–32% sucrose pairings in their home cages. The fact that animals did not show any deficit in the discrimination between both solutions (as shown by preference testing) suggests that the gustatory insular cortex may be involved in memory and reward anticipation. Finally, ANC has been proposed not to depend on anticipation of the second reward since it is insensitive to the devaluation of the second reward (Onishi and Xavier 2011). According to this view, the relative incentive value of the first solution would be estimated on the basis of the memory of past pairings, as well as on daily updating based on both gustatory and/or post-ingestive comparisons between solutions.

Conclusions

The scenarios proposed at the start of this entry on incentive relativity illustrated daily life situations that are simulated in the lab with animal models. Thus, Helen's disappointment when her date did not resemble what she had seen in a picture is an example of SNC. High expectations based on prior experience led to negative emotion, just as expecting 32% sucrose induces frustration when a rat encounters 4% sucrose instead. Tom's problem was akin to ANC. His taste for sweets was reduced when they were paired with opioids, much like anticipating 32% sucrose reduces intake of the lesser-valued 0.15% saccharin. The study of incentive relativity offers an inroad to understand these distortions of reward value.

The study of incentive relativity is providing some insights into several issues of basic and translational importance. Something these effects have in common is their connection to a wide range of psychological processes, despite being produced by seemingly simple situations. Three areas are highlighted here.

First, SNC effects, both instrumental and consummatory, have been studied more extensively from comparative and developmental perspectives. The SNC effect is not a general phenomenon among vertebrates. It has been reported in several species of mammals (e.g., rats, mice, monkeys, dogs, and opossums), but it has failed to occur in studies with pigeons, reptiles, amphibians, and fish (Papini 2003). Similarly, the iSNC effect emerges around 24 days of age in rats, in correlation with the maturation of the hippocampal formation (Amsel 1992). There are no similar comparative data on the ANC effect.

Second, the SNC has become a model to study the consequences of negative emotions. The main idea is that the reduction of an incentive is analogous to an experience involving loss. Experiments show that such experiences may distort sensitivity to peripheral pain, are influenced by manipulations of pain-related systems in the brain (e.g., opioid and cannabinoid receptors), are modulated by tranquilizers, and are affected by lesions in brain sites known to be connected to emotional responses (Papini et al. 2015). These studies have

implications for an understanding of how an experience of loss may affect both the emotional and health spheres of human functioning.

Finally, both SNC and ANC provide useful paradigms to model the connection between incentive relativity and addictive behavior. SNC promotes the voluntary oral consumption of anxiolytics capable of reducing negative emotions – an emotional self-medication effect (Ortega et al. 2017; Torres and Papini 2016). Since anxiolytics such as ethanol and benzodiazepines have addictive potential, this effect offers a possible view of the initial stages of addictive behavior. ANC offers insights into how drugs devalue natural rewards and also how natural rewards may help protect individuals against drug misuse and abuse (Grigson 2008).

Cross-References

- ▶ Associative Learning
- ▶ Conflict
- ▶ Disgust
- ▶ Fear Response
- ▶ Instrumental Learning
- ▶ Omission
- ▶ Operant Conditioning
- ▶ Pain Assessments
- ▶ Partial Reinforcement Effect

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