Published in final edited form as:

Behav Brain Res. 2017 February 15; 319: 174–180. doi:10.1016/j.bbr.2016.11.025.

Aversive properties of negative incentive shifts in Fischer 344 and Lewis rats

Adam Brewer[a,*], **Patrick Johnson**[b], **Jeff Stein**[c], **Michael Schlund**[d], and **Dean C. Williams**[e]

[a]University of Kansas, Lawrence, Kansas, USA

[b]California State University, Chico, California, USA

[c]Virginia Tech Carillion Research Institute, Roanoke, Virginia, USA

[d]University of North Texas, Denton, Texas, USA

[e]Lifespan Institute, University of Kansas, Parsons, Kansas, USA

Abstract

Research on incentive contrast highlights that reward value is not absolute but rather is based upon comparisons we make to rewards we have received and expect to receive. Both human and nonhuman studies on incentive contrast show that shifting from a larger more-valued reward to a smaller less-valued reward is associated with long periods of nonresponding—a negative contrast effect. In this investigation, we used two different genetic rat strains, Fischer 344 and Lewis rats that putatively differ in their sensitivity to aversive stimulation, to assess the aversive properties of large-to-small reward shifts (negative incentive shifts). Additionally, we examined the extent to which increasing cost (fixed-ratio requirements) modulates negative contrast effects. In the presence of a cue that signaled the upcoming reward magnitude, lever pressing was reinforced with one of two different magnitudes of food (large or small). This design created two contrast shifts (small-to-large, large-to-small) and two shifts used as control conditions (small-to-small, large-to-large). Results showed a significant interaction between rat strain and cost requirements only during the negative incentive shift with the emotionally reactive Fischer 344 rats exhibiting significantly longer response latencies with increasing cost, highlighting greater negative contrast. These findings are more consistent with emotionality accounts of negative contrast and results of neurophysiological research that suggests shifting from a large to a small reward is aversive. Findings also highlight how subjective reward value and motivation is a product of gene-environment interactions.

Keywords

Negative contrast; Fischer 344 rats; Lewis rats; cost; emotionality; reward

[*]Corresponding author at: Adam Brewer, Florida Institute of Technology, 150 W. University Blvd., Melbourne, FL 3290, 785-766-6734, abrewer@fit.edu.

1. Introduction

The value of a reward or incentive is not absolute but instead is based upon comparisons that we make to other rewards that we have received or expect. This idea is central to a variety of theories of incentive relativity [1-4]. A reward can lose its value when it is juxtaposed with a relatively more-valued reward which can elicit emotional behaviors and occasion escape—a negative contrast effect. Flaherty [4] and others [5] have suggested that research on negative incentive contrast can shed new insights into numerous applied problems, such as employee responses to salary reductions, irrational decision-making, drug addiction, and emotional behavior associated with an unexpected loss of a loved one. Traditional neurophysiological research has largely focused on brain mechanisms associated with reward processing [6], leaving a substantial gap in our understanding of the biological foundations associated with negative incentive contrast.

While many varieties of negative contrast exist, such as simultaneous [7], successive [8], anticipatory [9], and behavioral contrast [10], a common theme is negative incentive shifts, transitioning from a large to small reward, are a source of aversive stimulation and give rise to negative emotions. In the emotionality account of negative contrast [11, 12], the idea is that animals learn to anticipate an incentive in the presence of stimuli previously paired with a reward (e.g., runway end is paired with food). The effects of these stimuli generalize to the start of the runway. After encountering an incentive reduction in the goal-box, that is a large-to-small reward shift, aversive properties of the reduction in reward amount (a negative incentive shift) elicit unconditioned withdrawal responses (e.g., biting the door) and may occasion a response that terminates the aversive event (e.g., jumping out of the runway) [11]. Importantly, these negative affective responses compete with the anticipation of the reward, often leading to longer response latencies after the negative incentive shift.

Convergent evidence supporting the emotionality account is seen in pharmacological [13-16], physiological [17], neuroanatomical [18-22], and operant studies. For instance, amygdala damage and benzodiazepine administration that reduces fear and negative affective responses is associated with reductions in negative contrast [21]. In the operant literature, simultaneous contrast procedures have been developed as an alternative to runaway methodologies to eliminate handling rats between trials and allow tests of the costs of earning a reward [23]. The procedure involved exposing pigeons to a multiple-schedule procedure where key pecks on a fixed-ratio schedule occurred to a distinct cue color that signaled different magnitudes of upcoming food rewards—either large (7 s access) or small (1 s access) to grain. Within-session, pigeons were exposed to four different incentive shifts: (a) large-to-small (negative contrast), (b) small-to-small (control for negative contrast), (c) small-to-large (positive contrast), and (d) large-large (control for positive contrast). Dependent measures were the percentage of escape/time spent escaping and response latency to the first key peck, when the explicit escape option was removed. Results shows stimuli associated with a negative incentive shift prompt escape responses providing evidence that the negative incentive shift was aversive [24, 25]. Also, in the absence of an explicit escape response, response latencies may be an index of the aversiveness of the negative incentive shift. Another important finding was that larger negative contrast effects were characterized by longer response latencies and more time spent in escape occurred

when the cost to earn either a large or small reward increased, suggesting that larger FR costs may amplify aversiveness [24]. This free-operant operant simultaneous contrast procedure has produced negative incentive contrast effects in different species, with different response topographies, rewards, and clinical populations [26-33].

The emotionality account of negative contrast has also been evaluated using rat strains that are differentially sensitive to aversive stimulation [34-36]. For example, the relatively more emotional/fearful Roman low-avoidance rat strains exhibited greater negative contrast than Roman high-avoidance rats [35]. Two particular strains of interest are the Fischer 344 and Lewis which have been compared in multiple incentive contrast paradigms [37, 38]. While there are admittedly contradictory findings in the literature with regard to the emotional reactivity between these strains, Kosten and Ambrosio's review [39] concluded, “Most data suggest that the Fischer 344 rats are more emotionally reactive than Lewis rats.” Their review also suggests that Fischer 344 rats tend to be more sensitive to aversive stimulation than Lewis rats because of the former's dysfunctional hypothalamic-pituitary-adrenal axis (HPA) related to elevated levels of corticosterone (a stress-induced hormone) and behavioral responses to stressors and aversive stimulation [40-45]. This heightened sensitivity to aversive stimuli makes the Fischer 344 rat strain ideal for examining control by aversive properties of negative incentive shifts. However, in a study of successive negative contrast using a consummatory response, following an abrupt single negative incentive shift from earning sucrose (a relatively more-preferred reward) to a saccharin solution (a less-preferred reward), Lewis rats exhibited larger successive negative contrast effects than Fischer 344 rats [37]. Additionally, in a study of anticipatory negative contrast also using a consummatory response, following sequential pairings of a less-preferred saccharin solution followed by a highly-preferred sucrose solution, Lewis rats exhibited greater anticipatory contrast than Fischer 344 rats [38]. While these results provide evidence against the emotionality account given the direction of the strain difference, the generality of these effects have yet to be compared in a simultaneous contrast paradigm in which subjects are exposed to multiple negative incentive shifts within-session with large FR costs.

The current investigation tested the aversive properties of negative incentive shifts using the Fischer 344 and Lewis rat strains that differ in their emotional reactivity to aversive stimulation. Both strains were exposed to an operant simultaneous contrast paradigm. Rats were exposed to a multiple-schedule procedure whereby pressing levers produced different magnitudes of food rewards—large (i.e., 7 food pellets) or small (i.e., 1 food pellet) amounts of food. Within-session, each rat was exposed to 10 incentive shifts of the each type: (a) large-small (negative contrast), (b) small-small (control for negative contrast), (c) small-large (positive contrast), and (d) large-large (control for positive contrast). Between conditions, the number of FR lever presses to earn a reward (cost) was manipulated (1, 25, 50, 75, 100, and 150). The dependent measure was response latency measured from the onset of multiple schedule-correlated stimuli (e.g., left/right lever position and distinct cue light action) to the first lever press. Negative contrast effects would present as longer response latencies during the large-small reward shift compared to a small-small control shift. In consideration of a host of findings that negative incentive shifts contain aversive properties, organisms with biobehavioral profiles that render them more sensitive to aversive stimulation, such as the emotionally reactive Fischer 344 rat strain, would be expected to

exhibit greater negative contrast effects at larger costs relative to smaller costs compared to the Lewis rats.

2. Methods

All procedures complied with the National Institutes of Health guide for the care and use of Laboratory animals (NIH Publications No. 8023, revised 1978). The animals used in this research were maintained under the standards of the Institutional Animal Care and Use Committee (IACUC) at the University of Kansas.

2.1 Apparatus

Twelve identical operant chambers (Med Associates, St. Albans, VT) were used. Each chamber was 24.1 cm wide, 30.5 cm long, and 21 cm high. One wall of the chamber was equipped with a nonretractable center lever (11 cm above the floor) and two retractable side levers (horizontally aligned 11 cm apart and 6.5 cm above the floor). Above each lever was a white, 2-W light (2.5 cm in diameter and 6 cm above each lever). A feeder (Coulbourn, Allentown, PA) delivered 45-mg grain-based food pellets (Bioserve, Frenchtown, NJ) into a receptacle (3 cm wide and 4 cm long) equipped with a 2-W light in the center (1 cm above the floor and 10 cm below the center lever). Each chamber was enclosed within a light- and sound-attenuation cubicle (Med Associates®) equipped with a ventilation fan and a white noise speaker. A Med Associates® interface system controlled the sessions and collected data.

2.2 Animals

Eighteen male rats (9 F344 and 9 Lewis; Harlan, Indianapolis, IN) were individually housed in plastic cages within a temperature-controlled colony room with a 12:12 hr light/dark cycle. Rats were approximately 18 months old at the start of the experiment, and had prior experience choosing between small-immediate and large-delayed food rewards [46]. However, they were not exposed to tasks involving negative contrast prior to the current study. Rats were weighed daily and maintained at approximately 85% of their free-feeding weights by post-session feeding. Water was continuously available between sessions.

2.3 Procedure

Each session began with a cue light constantly illuminated above the center lever. A center-lever press extinguished the light and initiated the next multiple-schedule component (i.e., either a large or small reward trial) as one of the side levers was inserted into the chamber. This center-lever response was programmed because prior studies suggested that Fischer 344 rats are less active than Lewis rats [47]. To reduce the probability that variability in response latencies might be due to motoric differences (i.e., slower movement associated with longer response latencies rather than due to negative contrast *per se*), the center-lever response ensured that rats were done eating and were active at the moment the multiple schedule-correlated stimuli were presented, were in a position to observe these stimuli, and were positioned approximately equidistant from levers above which the stimuli were presented.

Center-lever responses were followed by the insertion of either the left or right side lever and the illumination of the cue light above the inserted lever. During a large reward schedule-component, the right lever was inserted, the right cue light was continuously lit, and completing the lever press requirement resulted in the delivery of 7 pellets over a period of 5.5 s. Upon initiation of a small reward schedule component, the left lever was inserted, the left cue light flashed (0.25-s intervals), and one food pellet was delivered upon completion of the schedule requirement. After the last pellet was delivered, the center cue light was re-illuminated and the next schedule component could be initiated by pressing the center lever. Across conditions, the lever press requirement ranged from 1 to 150 and rats were exposed to conditions according one of two randomized sequences. Within each strain, the assignment of reward magnitude to side levers was counterbalanced. The main dependent measure was response latency which was timed from the center lever press until the first response on the inserted side lever.

Sessions continued until 41 multiple-schedule components were completed or until 120 min elapsed. Incomplete sessions occurred when subjects failed to complete all the components during a 120-min. session. The sequence of multiple-schedule components arranged within a session was randomly drawn from a pool of 40 different sequences. Each sequence contained either 21 large- and 20 small-schedule components (sessions beginning with a large food reward), or 20 large- and 21 small-schedule components. Each sequence contained 10 of the four possible incentive shifts between multiple-schedule components. Ten times in each session a large food reward component (7 pellets) was programmed following a large component (a large-to-large control shift). Likewise, there were 10 large-small (a negative incentive shift), 10 small-small (control for negative incentive shift), and 10 small-large incentive shifts (a positive incentive shift). The same type of incentive shift never occurred more than three times in a row.

Stability criteria—Conditions lasted for a minimum of 10 sessions and until either (a) the median response latencies for each of the four types of incentive shifts met both a quantitative and qualitative stability criterion, or (b) after a maximum of 50 sessions. Latencies were considered stable when the mean of the final three sessions' median latencies deviated by 5% or less from the preceding three-session mean with no trend observed across the last six sessions. If three consecutive sessions occurred where an individual rat did not complete a single component, then that condition was terminated and that rat was exposed to the next condition. The FR 150 condition was excluded from our analysis because only 3 out the 9 Fischer 344 rats completed this condition, making group comparisons inappropriate.

Statistical Analyses—A *negative contrast* effect was assessed by subtracting small-small control shift response latencies from the large-small negative incentive shift latencies. Conversely, a *positive contrast* effect, was assessed by subtracting large-large latencies from small-large latencies. Both effects were separately examined using two-way repeated measures ANOVA with strain (Fischer 344, Lewis) as a between-subjects factor and cost (1, 25, 50, 75, and 100) as a within-subjects factor. Because Mauchly's tests indicated that the assumption of sphericity had been violated in both ANOVAs (alpha set to $p < .05$: Negative

contrast: $\chi 2$ (9) = 19.28, p = 02; Positive contrast: $\chi 2$ (9) = 52.7, p <001), we employed the appropriate Greenhouse-Geisser correction and a criterion alpha of $p < .05$.

3. Results

Figure 1 depicts response latencies separated according to the four incentive shifts for each strain and cost condition. Figure 2 shows response latency differences associated with negative contrast and positive contrast effects. The left plot in Figure 2 highlights negative contrast effects calculated as the differences between the latencies on large-small and small-small shifts. Results reveal: (a) a significant main effect of strain ($F(1,14) = 8.9$, $p < .01$, $\eta_p^2 = .39$) with Fischer 344 rats exhibiting longer response latencies, (b) main effect of ratio ($F(2,30) = 47.6$, $p < 0.001$, $\eta_p^2 = .77$) with longer latencies associated with increasing costs, and (c) a significant interaction ($F(2,30) = 4.1$, $p < 0.024$, $\eta_p^2 = .23$), with Fischer 344 rats exhibiting longer response latencies with increasing cost. In contrast, the right plot in Figure 2 shows positive contrast effects in the form of latency differences between the small-large and large-large shifts; no significant differences were found. Overall, results point out a larger negative contrast effect in Fisher 344 rats than in Lewis rats.

4. Discussion

The current investigation examined predictions from emotionality accounts of negative contrast that shifts from favorable to less-favorable reward conditions are a source of aversive stimulation using rat strains that differ in emotional reactivity in an operant, simultaneous contrast paradigm. Between sessions, cost (FR requirements) was manipulated to further examine effects on negative contrast. Results showed a significant interaction between rat strain and cost only after the large-small shift with Fischer 344 rats exhibiting significantly longer response latencies with increasing cost than the Lewis rats, highlighting greater negative contrast in the relatively more emotionally reactive Fischer 344 strain.

The Fischer 344 rat strain exhibited significantly longer response latencies at negative incentive shifts than the Lewis at several FR values. Prior research suggests that negative incentive shifts represent a source of aversive stimulation that occasions escape or extended response latencies when no explicit escape option is available [24, 25]. The Fischer 344 strain difference in negative contrast effects supports the emotionality account based on convergent biobehavioral evidence suggesting that Fischer 344 rats' behavior shows greater sensitivity to aversive stimulation compared to Lewis rats [39]. If negative incentive shifts are a source of aversive stimulation, then this would potentially account for the greater negative contrast effects in Fischer 344 rats, as compared to Lewis rats. However, it cannot be definitively concluded that the Fischer 344 rats exhibit a *hyper*sensitive response to aversive negative incentive shifts, whereas the Lewis rats show a *hypo*sensitive response. A comparison of negative contrast effects that includes an outbred strain such as the maternal Sprague Dawley strain would be warranted in future research. Future researchers may wish to add an explicit escape option to provide a stronger test of aversive properties of negative incentive shifts. Nonetheless, the direction of our strain difference supports previous findings regarding strain difference, suggesting the aversive properties of negative incentive shifts

[11, 12; however, see: 22] while highlighting how subjective reward value and motivation is a product of gene-environment interactions.

Another robust finding was that negative contrast increased as a function of the size of the cost between Fischer 344 rats compared to the Lewis strain. The increase in response latencies as a function of the ratio size is consistent with multiple-schedule studies of simultaneous negative contrast [24, 26]. In these studies, the investigators found that pigeons were more likely to escape from relatively large versus smaller ratio requirements, suggesting that large work requirements were aversive [48]. This finding may be due to a negative incentive shift embedded in reinforcement schedules (beyond the negative shift in magnitude arranged by the multiple schedule). That is, on simple FR reinforcement schedules, the abrupt shift from consuming a reward to a period of extinction that occurs at the start of the ratio can be conceptualized as a negative incentive shift. As the ratio size increases, the negative incentive shift becomes exacerbated by a longer delay to reward by virtue of the time to complete a large ratio compared to a small one (i.e., more responses engender longer delays to obtain a reward).The finding that relatively more emotional Fischer 344 rats' behavior was more sensitive to ratio size at larger requirements than Lewis rats provides further evidence for the emotionality account of negative contrast.

A number of limitations in the current investigation restrict generalization of our findings. The current study had a small sample size which limited power. Both strains of rats were 18 months old. It is unknown how simultaneous negative contrast would present in younger Fischer 344 and Lewis rats or how age affects negative contrast more generally. Developmental differences studies of negative contrast are limited and have produced mixed findings [e.g., positive findings in newborn humans: 49; negative findings in infant rats: 50, 51]. To the best of our knowledge, negative incentive contrast effects have yet to be investigated in aged populations. The rats used were also not experimentally naïve. Our rats had prior exposure to the small reward amount [46]; but not to any contrast procedures that could bias responding. Currently, the literature is mixed regarding whether exposure to small rewards can minimize negative contrast effects [e.g., positive findings: 52; negative findings: 53].

Our study did not rule out the possibility that either response or choice impulsivity contributed to our findings. The Lewis rats tend to be characterized as both more choice and responsive “impulsive” than Fischer 344 rats [54]. In terms of choice impulsivity, Lewis rats tend to more often choose an immediate, but smaller reward (the impulsive choice) over larger, but delayed rewards compared to Fischer 344 rats. However, levels of impulsive choice between these strains is unknown when effort is added to the delay via the FR cost. Fixed-ratio costs require both more effort in terms of the number of responses to complete the FR which can also serve to increase the delay to reward [55]. If the Lewis rats devalued the cue signaling the more effortful/delayed small reward (following a large reward) to a greater extent than the Fischer 344 rats, then one might expect the Lewis rats to choose less effortful/immediate rewards like grooming and exploring over a high response effort to obtain the delayed food reward which would manifest as a larger negative contrast effects (because the rats were not responding on the lever). On the other hand, if both large and small food rewards were both devalued more steeply by Lewis than Fischer 344 rats due to

the FR cost, then this might reduce the reward disparity at a negative incentive shift which would result in attenuated negative contrast effects in the Lewis rats. In terms of response impulsivity, or the inability to inhibit a prepotent motor response, it is possible that this tendency to respond quickly may have contributed to smaller negative contrast effects in the Lewis rats compared to Fischer 344 rats. If “impulsivity” (choice or response) was considered a trait variable that was a constant throughout the study, then one might predict that negative contrast effects would be attenuated across all FR costs for the Lewis rats; however, our results showed no difference between strains until larger FR costs. More research is sorely needed to understand the potential role of various types of “impulsivity” in relation to negative contrast effects which represents an exciting new area for future research.

While the biological profile of the Fischer 344 strain suggests that a dysfunctional HPA and stress responses underlie increased sensitivity to aversive negative incentive shifts, this interpretation is necessarily tentative because our current methodology was restricted to examining behavior without any direct manipulations of the HPA. There are also a host of other biological differences between these commonly used strains that may account for our effects. A well-documented set of findings is that the Fischer 344 exhibit higher levels of DA and 5-HT compared to Lewis rats. In addition, Fischer 344 rats show higher immune responses, higher basal glutamate levels, and higher μ-opioid receptor binding than the Lewis [39]. Thus, it is not possible to point to specific neurochemical processes responsible for the effects, nonetheless, the study demonstrates variability in behavioral responses to negative incentive shifts. Future research may attempt to further isolate the effects of HPA function on negative contrast using corticotropin releasing factor receptor 1-deficient knockout mice or administering corticosterone injections to outbred strains.

The direction of our strain difference between Fischer 344 and Lewis in our simultaneous contrast paradigm is not consistent with studies of successive or anticipatory contrast [37, 38] which may be related to procedural differences such as a lack of intake measures and/or the FR cost requirement. We did not explicitly measure consummatory behavior (e.g., intake behavior) because of the free-operant paradigm we used that prevents a direct comparison of our results to studies of successive or anticipatory contrast between these strains. Doing so would have interfered with ongoing behavior and clouded results. However, we did note that both strains of rats reliably ate all the pellets within-session. If we had discovered immediately after the experiment there was any food left uneaten, we would have adjusted our reward parameters because this would have suggested that our rats were satiated. Thus, we cannot reasonably attribute the direction of the strain difference in consummatory behavior. While there is limited research that consummatory response is controlled by different processes than the operant response [36], a fruitful area for research may entail attempting to bridge negative contrast procedures by explicitly measuring both response latencies and consumption at a negative incentive shift within a single study using a reward such as different concentrations of sweetened and condensed milk instead of food pellets.

Another procedural difference that may account for the discrepant findings is that we parametrically investigated much larger FR costs that exceeded the ones used in the consummatory successive and anticipatory studies using the Fischer 344 and Lewis rats [37,

38]. To facilitate comparisons between our studies, it may be fruitful to view the consummatory response as a FR 1 cost as it takes a single lick to receive access to the reward (cf. single lever press earns a reward). Upon visual inspection of our results in the FR 1 condition, the Lewis rats exhibited larger negative contrast than the Fischer 344 rats. While our FR 1 finding was consistent with the consummatory successive and anticipatory contrast studies using the same strains; our results were not statistically significant. We suspect that our results with the FR 1 condition would have obtained significance with a larger sample size. Related to our earlier point of bridging the studies of negative contrast using the consummatory and operant responses, it would also be interesting if future researchers examined whether the consummatory response is affected by larger operant FR costs.

Summary

Genetically inbred Fischer 344 rats' tended to exhibit longer response latencies at negative incentive shifts compared to Lewis rats in an operant simultaneous negative contrast paradigm. Moreover, the strain difference in negative incentive shifts was modulated by cost. This strain difference may be attributed to Fischer 344's genetic predisposition towards increased behavioral sensitivity to aversive events compared to Lewis rats. Overall, findings lend further support to the emotionality account of negative incentive contrast.

Acknowledgments

This report is based on master's thesis of the first author in partial fulfillment of a M.S. in Applied Behavioral Sciences at the University of Kansas. This paper was written with support of National Institutes of Health grants R01HD044731, P01HD055456 (Dean Williams), and P30HD002528 to the University of Kansas.

References

1. Cox WM. A review of recent incentive contrast studies involving discrete-trial procedures. The Psychological Record. 1975; 25:373.
2. Flaherty CF. Incentive contrast: A review of behavioral changes following shifts in reward. Animal Learning & Behavior. 1982; 10:409–440.
3. Flaherty CF. Incentive contrast and selected animal models of anxiety. 1991
4. Flaherty, CF. Incentive relativity. Vol. 15. Cambridge University Press; 1999.
5. Papini MR, Wood M, Daniel AM, Norris JN. Reward loss as psychological pain International Journal of Psychology and Psychological Therapy. 2006; 6:189–213.
6. Hu K, Padmala S, Pessoa L. Interactions between reward and threat during visual processing. Neuropsychologia. 2013; 51:1763–1772. [PubMed: 23770538]
7. Bower GH. A contrast effect in differential conditioning. Journal of Experimental Psychology. 1961; 62:196.
8. Spear NE, Hill WF. Adjustment to new reward: simultaneous-and successive-contrast effects. Journal of Experimental Psychology. 1965; 70:510. [PubMed: 5833673]
9. Flaherty CF, Checke S. Anticipation of incentive gain. Animal Learning & Behavior. 1982; 10:177–182.
10. Reynolds GS. Behavioral contrast. Journal of the Experimental Analysis of Behavior. 1961; 4:57–71. [PubMed: 13741096]
11. Crespi LP. Quantitative variation of incentive and performance in the white rat. The American Journal of Psychology. 1942; 55:467–517.

12. Flaherty CF, Rowan GA. Rats (Rattus norvegicus) selectively bred to differ in avoidance behavior also differ in response to novelty stress, in glycemic conditioning, and in reward contrast. Behavioral and Neural Biology. 1989; 51:145–164. [PubMed: 2649069]
13. Morales A, Torres MDC, Megias JL, Candido A, Maldonado A. Effect of diazepam on successive negative contrast in one-way avoidance learning. Pharmacology Biochemistry and Behavior. 1992; 43:153–157.
14. Pellegrini S, Wood M, Daniel AM, Papini MR. Opioid receptors modulate recovery from consummatory successive negative contrast. Behavioural Brain Research. 2005; 164:239–249. [PubMed: 16135386]
15. Rosen AJ, Tessel RE. Chlorpromazine, chlordiazepoxide, and incentive-shift performance in the rat. Journal of Comparative and Physiological Psychology. 1970; 72:257. [PubMed: 5530814]
16. Wood M, Daniel AM, Papini MR. Selective effects of the δ-opioid receptor agonist DPDPE on consummatory successive negative contrast. Behavioral Neuroscience. 2005; 119:446. [PubMed: 15839790]
17. Mitchell C, Flaherty C. Temporal dynamics of corticosterone elevation in successive negative contrast. Physiology & Behavior. 1998; 64:287–292. [PubMed: 9748095]
18. Becker HC, Jarvis M, Wagner G, Flaherty CF. Medial and lateral amygdala lesions differentially influence contrast with sucrose solutions. Physiology & Behavior. 1984; 33:707–712. [PubMed: 6522490]
19. Flaherty CF, Coppotelli C, Hsu D, Otto T. Excitotoxic lesions of the hippocampus disrupt runway but not consummatory contrast. Behavioural Brain Research. 1998; 93:1–9. [PubMed: 9659981]
20. Leszczuk MH, Flaherty CF. Lesions of nucleus accumbens reduce instrumental but not consummatory negative contrast in rats. Behavioural Brain Research. 2000; 116:61–79. [PubMed: 11090886]
21. Liao RM, Chuang FJ. Differential effects of diazepam infused into the amygdala and hippocampus on negative contrast. Pharmacology Biochemistry and Behavior. 2003; 74:953–960.
22. Pecoraro N, Dallman MF. c-Fos after incentive shifts: Expectancy, incredulity, and recovery. Behavioral Neuroscience. 2005; 119:366. [PubMed: 15839784]
23. Perone M, Courtney K. Fixed-ratio pausing: Joint effects of past reinforcer magnitude and stimuli correlated with upcoming magnitude. Journal of the Experimental Analysis of Behavior. 1992; 57:33–46. [PubMed: 16812647]
24. Perone M. Negative effects of positive reinforcement. The Behavior Analyst. 2003; 26:1. [PubMed: 22478391]
25. Everly JB, Holtyn AF, Perone M. Behavioral functions of stimuli signaling transitions across rich and lean schedules of reinforcement. Journal of the Experimental Analysis of Behavior. 2014; 101:201–214. [PubMed: 24446283]
26. Baron A, Mikorski J, Schlund M. Reinforcement magnitude and pausing on progressive-ratio schedules. Journal of the Experimental Analysis of Behavior. 1992; 58:377–388. [PubMed: 16812671]
27. Galuska CM, Yadon KA. The effect of prefeeding on fixed-ratio pausing is jointly determined by past and upcoming reinforcer magnitudes. Behavioural Processes. 2011; 86:156–159. [PubMed: 20804830]
28. Wade-Galuska T, Perone M, Wirth O. Effects of past and upcoming response-force requirements on fixed-ratio pausing. Behavioural Processes. 2005; 68:91–95. [PubMed: 15639389]
29. Galuska CM, Wade-Galuska T, Woods JH, Winger G. Fixed-ratio schedules of cocaine self-administration in rhesus monkeys: Joint control of responding by past and upcoming doses. Behavioural Pharmacology. 2007; 18:171–175. [PubMed: 17351424]
30. Bejarano R, Williams DC, Perone M. Pausing on multiple schedules: Toward a laboratory model of escape-motivated behavior. Experimental Analysis of Human Behavior Bulletin. 2003; 21:18–20.
31. Hayashi Y, Hall SE, Williams DC. Effect of signaled reinforcer magnitude on delayed matching-to-sample performance in individuals with intellectual disabilities. Behavioural Processes. 2013; 96:88–92. [PubMed: 23523782]

32. Williams DC, Saunders KJ, Perone M. Extended pausing by humans on multiple fixed-ratio schedules with varied reinforcer magnitude and response requirements. Journal of the Experimental Analysis of Behavior. 2011; 95:203–220. [PubMed: 21541121]
33. Jessel J, Hanley GP, Ghaemmaghami M. A translational evaluation of transitions. Journal of Applied Behavior Analysis. 2016
34. Flaherty CF, Rowan GA. Rats (Rattus norvegicus) selectively bred to differ in avoidance behavior also differ in response to novelty stress, in glycemic conditioning, and in reward contrast. Behavioral and Neural Biology. 1989; 51:145–164. [PubMed: 2649069]
35. Rosas JM, Callejas-Aguilera JE, Escarabajal MD, Gómez MJ, de la Torre L, Agüero Á, et al. Torres C. Successive negative contrast effect in instrumental runway behaviour: A study with Roman high-(RHA) and Roman low-(RLA) avoidance rats. Behavioural Brain Research. 2007; 185:1–8. [PubMed: 17764760]
36. Rowan GA, Flaherty CF. Behavior of Maudsley reactive and nonreactive rats (Rattus norvegicus) in three consummatory contrast paradigms. Journal of Comparative Psychology. 1991; 105:115. [PubMed: 1860305]
37. Freet CS, Tesche JD, Tompers DM, Riegel KE, Grigson PS. Lewis rats are more sensitive than Fischer rats to successive negative contrast, but less sensitive to the anxiolytic and appetite-stimulating effects of chlordiazepoxide. Pharmacology Biochemistry and Behavior. 2006; 85:378–384.
38. Grigson PS, Freet CS. The suppressive effects of sucrose and cocaine, but not lithium chloride, are greater in Lewis than in Fischer rats: Evidence for the reward comparison hypothesis. Behavioral Neuroscience. 2000; 114:353. [PubMed: 10832796]
39. Kosten TA, Ambrosio E. HPA axis function and drug addictive behaviors: insights from studies with Lewis and Fischer 344 inbred rats. Psychoneuroendocrinology. 2002; 27:35–69. [PubMed: 11750769]
40. Chaouloff F, Kulikov A, Sarrieau A, Castanon N, Mormède P. Male Fischer 344 and Lewis rats display differences in locomotor reactivity, but not in anxiety-related behaviours: Relationship with the hippocampal serotonergic system. Brain research. 1995; 693:169–178. [PubMed: 8653405]
41. Glowa JR, Sternberg EM, Gold PW. Differential behavioral response in LEW/N and F344/N rats: Effects of corticotropin releasing hormone. Progress in Neuro-Psychopharmacology and Biological Psychiatry. 1992; 16:549–560. [PubMed: 1641498]
42. Haile CN, Hiroi N, Nestler EJ, Kosten TA. Differential behavioral responses to cocaine are associated with dynamics of mesolimbic dopamine proteins in Lewis and Fischer 344 rats. Synapse. 2001; 41:179–190. [PubMed: 11391778]
43. Katzev RD, Mills SK. Strain differences in avoidance conditioning as a function of the classical CS-US contingency. Journal of Comparative and Physiological Psychology. 1974; 87:661. [PubMed: 4426989]
44. Pryce CR, Lehmann J, Feldon J. Effect of sex on fear conditioning is similar for context and discrete CS in Wistar, Lewis and Fischer rat strains. Pharmacology Biochemistry and Behavior. 1999; 64:753–759.
45. Stöhr T, Szuran T, Welzl H, Pliska V, Feldon J, Pryce CR. Lewis/Fischer rat strain differences in endocrine and behavioural responses to environmental challenge. Pharmacology Biochemistry and Behavior. 2000; 67:809–819.
46. Madden GJ, Smith NG, Brewer AT, Pinkston JW, Johnson PS. Steady-state assessment of impulsive choice in Lewis and Fischer 344 rats: Between-condition delay manipulations. Journal of the Experimental Analysis of Behavior. 2008; 90:333–344. [PubMed: 19070340]
47. Webb AA, Gowribai K, Muir GD. Fischer (F-344) rats have different morphology, sensorimotor and locomotor abilities compared to Lewis, Long–Evans, Sprague–Dawley and Wistar rats. Behavioural Brain Research. 2003; 144:143–156. [PubMed: 12946605]
48. Azrin NH. Time-out from positive reinforcement. Science. 1961; 133:382–383. [PubMed: 13685461]
49. Kobre KR, Lipsitt LP. A negative contrast effect in newborns. Journal of Experimental Child Psychology. 1972; 14:81–91. [PubMed: 5061607]

50. Stanton M, Amsel A. Adjustment to reward reduction (but no negative contrast) in rats 11, 14, and 16 days of age. Journal of Comparative and Physiological Psychology. 1980; 94:446.

51. Stanton ME, Lobaugh N, Amsel A. Age of first appearance of simultaneous and successive negative contrast in infant rats. Journal of Experimental Psychology: Animal Behavior Processes. 1984; 10:376. [PubMed: 6747555]

52. Spencer RE, Shanab ME. Contrast effects as a function of delay and shifts in magnitude of water reward in thirsty rats. Bulletin of the Psychonomic Society. 1979; 13:93–96.

53. Shanab ME, Spencer RE. Positive and negative contrast effects obtained following shifts in delayed water reward. Bulletin of the Psychonomic Society. 1978; 12:199–202.

54. Hamilton KR, Potenza MN, Grunberg NE. Lewis rats have greater response impulsivity than Fischer rats. Addictive behaviors. 2014; 39:1565–1572. [PubMed: 24613059]

55. Grossbard CL, Mazur JE. A comparison of delays and ratio requirements in self-control choice. Journal of the Experimental Analysis of Behavior. 1986; 45:305–315. [PubMed: 3711777]

Research Highlights

Negative incentive contrast is characterized by increased response latencies for an upcoming small reward when preceded by a larger reward.

We evaluated the aversive properties of negative incentive contrast using an operant, simultaneous contrast paradigm.

Fischer 344 and Lewis rats were exposed to incentive shifts across a range of fixed-ratios (costs).

Fischer 344 rats showed greater negative incentive contrast than Lewis rats and cost-modulated effects.

Negative incentive shifts may elicit negative affective responses in line with emotionality accounts of negative incentive contrast.

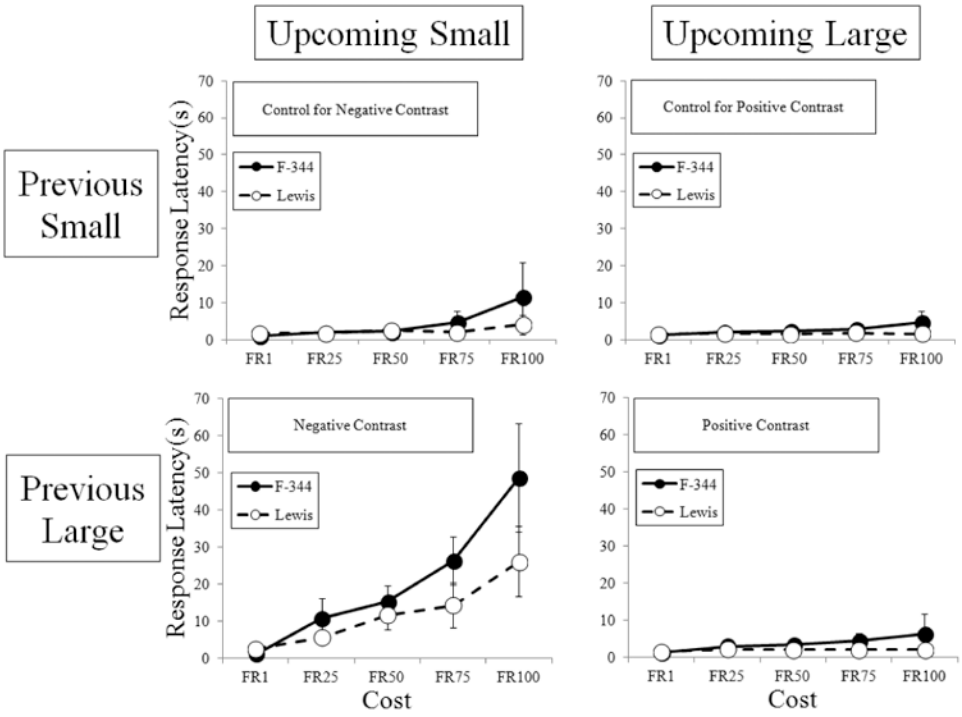

Figure 1.

Response latencies for Fischer 344 and Lewis rats. Plots show time taken to respond after receiving a large/small reward in the presence of a cue signaling an upcoming large/small reward. Response latencies are plotted as a function of increasing fixed-ratio (FR) cost requirements ranging from 1 to 100. Cost was manipulated between sessions. (Bars represent 95% confidence intervals).

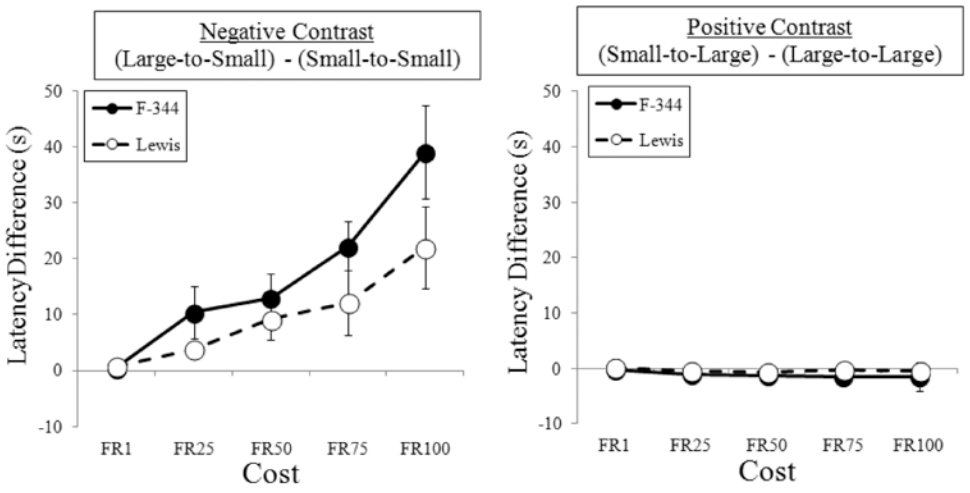

Figure 2.

Response latency differences for Fischer 344 and Lewis rats. The left plot highlights negative contrast effects in the form of latency differences between the large-to-small and small-to-small shifts. A significant interaction was observed with Fischer 344 rats exhibiting longer response latencies with increasing cost. In contrast, the right plot shows positive contrast effects in the form of latency differences between the small-to-large and large-to-large shifts; no significant findings were found. Results suggest a larger negative contrast effect in Fisher 344 rats, lending support for the emotionality account of negative contrast. (Bars represent 95% confidence intervals).