

*O PAPEL DO TIPO DE RESPOSTA NA FORMA DO CONTRASTE NEGATIVO OU DA
INDUÇÃO POSITIVA EM RATOS*

*THE ROLE OF TYPE OF RESPONSE IN THE APPEARANCE OF NEGATIVE CONTRAST
OR POSITIVE INDUCTION IN RATS*

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RESUMO

Ratos podem diminuir (contraste negativo) ou aumentar (indução positiva) sua taxa de respostas reforçadas com solução de sacarose a 1% quando reforçamento com solução de sacarose a 32% é iminente, em diferentes condições. Pesquisa anterior sugere que o efeito que ocorrerá pode depender de qual resposta motora (lamber *versus* pressionar a barra, por exemplo) é requerida para obter a solução de sacarose. O presente estudo investigou esse problema fazendo os sujeitos emitirem respostas diferentes em cada uma das metades das sessões. Os sujeitos ou lambiam ou pressionavam uma barra e produziam reforçamento de solução de sacarose a 1% na primeira metade da sessão. Eles emitiam, então, a resposta alternativa, reforçada por solução de sacarose a 1% ou 32%, em condições diferentes, na segunda metade da sessão. No Experimento 1, ambos, lamber e pressionar a barra eram respostas operantes. No Experimento 2, lamber foi uma resposta estritamente consumatória. Os resultados mostraram que a solução de sacarose a 32% iminente tendeu a diminuir o responder por solução de sacarose a 1% na primeira metade da sessão, independentemente de qual era a resposta requerida na outra metade. Indução positiva nunca foi observada. Os resultados presentes questionam se o tipo de resposta motora seria um fator chave para a observação de contraste ou de indução, sugerindo, ao contrário, que o local em que as substâncias são liberadas e consumidas seja crítico. Compreender quando um efeito ou outro vai ocorrer aumentará nossa compreensão do comportamento relacionado com alimentar-se.

Palavras-chave: Contraste negativo, indução positiva, reforçamento, pressão à barra, rato.

ABSTRACT

Rats may decrease (negative contrast) or increase (positive induction) their rate of responding for 1% sucrose reinforcement when 32% sucrose reinforcement is upcoming under different conditions. Previous research suggests that which effect occurs may depend on what motor response (i.e., licking vs. press a lever) is required to obtain the sucrose. The present study investigated this idea by having subjects make different responses in different halves of the session. Subjects either licked or pressed a lever for 1% sucrose reinforcement in the first half of the session. They then made the alternative response for 1% or 32% sucrose reinforcement, in different conditions, in the second half. In Experiment 1, both licking and lever pressing were operant responses. In Experiment 2, licking was strictly a consummatory response. Results showed that upcoming 32% sucrose tended to decrease responding for 1% sucrose in the first half of the session regardless of the response required in either half. Positive induction was never observed. The present results question whether type of motor response is a key factor in whether contrast or induction is observed. Instead, they suggest that the location that the substances are delivered and consumed is critical. Ultimately, understanding when one effect or the other will occur will enhance our understanding of eating-related behavior.

Key words: negative contrast, positive induction, reinforcement, lever press, rat.

Factors which control behaviors related to eating and obtaining food have become of special interest to researchers because of the human population's growing trend toward

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obesity. If the causal factors for such behavior are identified, then they could potentially be used in developing new treatments for overeating and/or by altering societal practices. Controlled studies employing animal subjects will likely play a large role in determining those factors.

One reason to be optimistic is that such research has proven to be successful in the past. For instance, a long line of research studies has demonstrated that the amount of food an animal will consume varies as a function of that food's hedonic value relative to the hedonic value of other foods which may be available in other situations (e.g., see Flaherty, 1996, for a review). Perhaps the most well-known of such effects is negative anticipatory contrast (Flaherty & Checke, 1982). Negative anticipatory contrast occurs when an organism decreases its consumption of a low-valued appetitive substance because it will soon have access to a high-valued substance, with the decrease compared against consumption in a situation in which the upcoming period will allow access to either the same low-valued substance or to no substance at all. Colloquially, the organism is "saving room for dessert."

Although negative anticipatory contrast is a reliable effect, it is interesting that the seemingly opposite effect can be observed by slightly altering the procedure used to produce contrast. Research from our lab has demonstrated that if a rat presses a lever for a low-valued appetitive reinforcer (e.g., 1% liquid sucrose) delivered by an intermittent schedule of reinforcement in the first half of an experimental session, the rat will increase the rate at which it presses the lever if the rat will have the opportunity to press the lever

for a high-valued reinforcer (e.g., a food pellet) in the second half of the session, with the increase compared to when the same low-valued reinforcer will be available in the second half of the session (e.g., Weatherly, Stout, Rue, & Melville, 2000) or in which there will be no second half (Weatherly, Plumm, Smith, & Roberts, 2002). This effect can be called positive induction and it has also shown to be reliable.

Although both effects have shown to occur reliably, it is not yet known which factors lead to the observance of one or the other effect. Determining when negative anticipatory contrast or positive induction will occur would seem important for our understanding of eating-related behavior. Whereas the former contrast effect appears to represent a situation in which the organism is regulating its food intake, the latter induction effect appears to represent a situation in which the organism could potentially consume a greater amount of the low-valued food than it would consume otherwise. If positive induction is a general phenomenon, then it is possible the effect contributes to overeating and obesity.

Several studies have investigated the factors that possibly control whether an animal will display a negative contrast or a positive induction effect. Weatherly, Arthur, and Lang (2003), for instance, investigated the role of the function of the behavior (consummatory vs. operant), type of motor response (licking vs. pressing a lever), and substance availability (often vs. infrequently available) potentially play. To do so, they had two groups of rats make an operant response, either licking or pressing a lever, to earn 1% liquid-sucrose reinforcers delivered by a random-interval (RI) schedule during the first half of the 30-min

session. Subjects made the same response to earn either 1% or 32%, depending on the condition, sucrose reinforcers in the second half of the session. Across conditions, the rate of reinforcement, which was the same in both halves of the session, ranged from high (i.e., RI 7.5 s) to low (RI 60 s). The authors reasoned that if the distinction between consummatory and operant behavior was the key factor determining the appearance of contrast or induction, then both groups would display induction in the first half of the session when 32% sucrose was upcoming because operant behavior was the dependent measure for both groups (i.e., for the licking group, only licks made to earn reinforcement were analyzed). On the other hand, if the distinction between licking and pressing a lever was critical, then the rats that licked should display contrast whereas the rats that pressed a lever should display induction. Finally, if frequency of substance availability was the key factor, then both groups might display contrast at the highest rate of reinforcement and induction as reinforcement was delivered more intermittently. Results demonstrated that the rats that licked displayed a negative contrast effect at each rate of reinforcement whereas rats that pressed the lever displayed a positive induction effect at each rate. The authors thus concluded that the type of motor response, licking or pressing a lever, was a determining factor in whether negative contrast or positive induction would be observed.

The present experiments were designed as an extension of the Weatherly et al. (2003) study. Although the results reported by Weatherly et al. (2003) support the idea that whether rats lick a spout or press a lever influences which effect is observed, the results

do not isolate the influence. That is, because subjects in both groups made the same response (i.e., either licking or pressing a lever) in both halves of the session, it is not possible to identify whether making the response in the first half of the session for the low-valued reinforcer or in the second half of the session for the high-valued reinforcer is the critical factor. To make such determinations, one needs to vary the type of response required of subjects in the different halves of the session and record which effect was observed.

The present experiments did this. In Experiment 1, subjects emitted an operant response in the first half of the session to obtain 1% sucrose reinforcement delivered on a RI schedule. The required response was either licking a spout or pressing a lever. The rats then emitted the alternative response in the second half of the session for either 1% or 32% sucrose reinforcement, in different conditions, which was delivered by the identical RI schedule. If making a particular response in the first or second half of the session determines which effect is observed, then the procedure of Experiment 1 should produce a contrast effect in some conditions and an induction effect in others. Experiment 2 was a systematic replication of Experiment 1. It followed the identical procedure with the exception that licking was strictly a consummatory rather than an operant response.

EXPERIMENT 1

METHOD

Subjects

The subjects were five experimentally experienced male Sprague-Dawley rats

originally obtained for the Center for Biomedical Research on the campus of the University of North Dakota. Subjects' experimental histories included lever pressing and licking for liquid-sucrose reinforcers delivered by a RI schedule of reinforcement. They were approximately 14 months of age at the start of the present experiment. Subjects were maintained at approximately 85% of their free-feeding body weights by supplemental daily feedings, when necessary, which occurred after all subjects had been run. As subjects were experimentally experienced, their 85% weights had previously been established. Those weights were continuously maintained. Subjects were individually housed and had free access to water (only) in the home cage. They experienced a 12/12 h light/dark cycle, with lights on at 0700. All sessions were conducted during the light portion of the cycle. Maintenance of the animals complied with the ethical guidelines for the care and use of animal subjects (National Research Council, 1996).

Apparatus

Subjects responded in a Coulbourn Instruments experimental chamber which measured 30.5 cm (L) x 25 cm (W) x 28.5 cm (H) and was equipped with one response lever and one optical lickometer. The lever was 3.5-cm wide x 0.1-cm thick. It extended 2 cm into the chamber and required a force of approximately 0.25 N to depress. The lever was located 6.5 cm above the grid floor, 2.5 cm from the left wall. A panel containing three stimulus lights (red, yellow, and green from left to right) was located above the lever. The lights were 0.6 cm in diameter, with the center light being 5 cm above the lever and the other lights 0.6 cm to the left and right. A 3.3-cm

(W) x 3.8-cm (H) x 2.5-cm (D) opening was centered on the front panel, 2 cm above the grid floor. The opening allowed access to a trough into which sucrose reinforcers which were earned by pressing the lever were delivered. The sucrose reinforcers were delivered to the trough via a syringe pump located outside of the apparatus and attenuating chamber. The optical lickometer was located 2.5 cm from the right wall and 5 cm above the grid floor. It consisted of an opening which measured 3.0 cm (W) x 4.0 cm (H) x 3.6 cm (D) that housed a 1-cm-diameter drinking spout centered 2 cm inside the opening. Directly in front of the spout, on both sides, was a photo cell that recorded each lick of the spout. The lickometer was capable of measuring up to 10 licks/s. The spout was directly connected to a second syringe pump also located outside of the apparatus. Five cm above each lickometer was a panel of three colored stimulus identical to that above the lever. A 1.5-cm diameter houselight that provided general illumination in the chamber was centered on the back wall of the chamber, 2.5 cm below the ceiling.

The chamber was located in a sound-attenuating cubicle with a ventilation fan which masked noise from the outside. The experimental events were programmed and data were recorded by an IBM-compatible desktop computer running Graphic State Software and was connected to a Coulbourn Instruments Universal Linc. The experimental chamber and control equipment were located in adjacent rooms.

Procedure

As subjects were experimentally experienced, they were immediately placed on the procedure. Subjects responded in 30-min sessions in which 0.2-ml 1% liquid-sucrose (v/

v mixed with tap water) reinforcers were available on a RI 30-s schedule in the first half of the session. The reinforcer in the second half of the session was either 0.2 ml of 1% or 32% liquid sucrose, in different conditions, also available on a RI 30-s schedule. Reinforcers were programmed at a probability of 0.01 every 0.6 s, unless a reinforcer had been programmed but not yet collected. In such an instance, the inter-reinforcer interval did not advance until the subject had collected the programmed reinforcers. In sessions in which a switch in reinforcers type occurred at the midpoint of the session, a new inter-reinforcer interval began timing at the midpoint of the session. That is, if a reinforcer had been programmed but not collected in the first half of the session, it was canceled. The type of response required to earn reinforcement differed between halves. Subjects pressed the left lever in one half of the session and licked the right spout in the second half. As in Weatherly et al. (2003), when licking was the response, only operant licks were recorded. That is, although subjects consumed sucrose reinforcers for licking from the same spout licked to earn the reinforcers, licks which occurred during reinforcement were excluded from data collection/analysis. The left/red stimulus light was illuminated over the active operandum in each half of the session. The houselight was continuously illuminated throughout the session.

Thus, subjects responded in a total of four conditions. In the first (L-LP 1%-32%), licking was reinforced with 1% sucrose in the first half of the session and lever pressing was reinforced with 32% sucrose in the second half. In the second (LP-L 1%-1%), lever pressing and licking were reinforced with 1% sucrose

in the first and second halves, respectively. In the third (L-LP 1%-1%), licking and lever pressing were reinforced with 1% sucrose in the first and second halves, respectively. In the fourth (LP-L 1%-32%), lever pressing was reinforced with 1% sucrose in the first half of the session and licking was reinforced with 32% sucrose in the second half.

All subjects experienced the conditions in the order listed. Although counterbalancing the order of conditions across subjects would have been ideal, doing so would have required physically altering the experimental chamber twice daily. Because doing so was not feasible, the above order of conditions was randomly determined prior to the experiment and all subjects experienced the same order. Each condition was conducted for 20 consecutive sessions, with sessions conducted 5 to 6 days per week. Twenty sessions were conducted per condition because research from our lab has indicated that 20 sessions is sufficient to produce steady-state responding and because past research (e.g., Weatherly et al., 2003) has used a similar number of sessions per condition.

RESULTS AND DISCUSSION

Figure 1 presents the results from the four conditions. Presented are the rates of responding (responses/min) in each half of the session for the mean of all subjects responding in each condition. Response rates are plotted on a logarithmic ordinate so that differences in responding at low rates of responding are visually apparent. The top graph presents the results from the two conditions in which licking was reinforced in the first half of the session and lever pressing was reinforced in the second half. The bottom graph presents the

TYPE OF RESPONSE

results from the two conditions in which lever pressing was reinforced in the first half of the session and licking was reinforced in the second half. The solid bars represent conditions in which 1% sucrose was the reinforcer in both halves of the session. The striped bars represent conditions in which 32% sucrose was the reinforcer in the second half of the session. The error bars represent one standard error of the mean across all subjects responding in that half of the session. The results in Figure 1 were calculated using data from the final five sessions of each condition. Mean data are presented because they are representative of results for individual subjects. Data for individual subjects responding in each half of each condition (of each experiment) can be found in Appendix A.

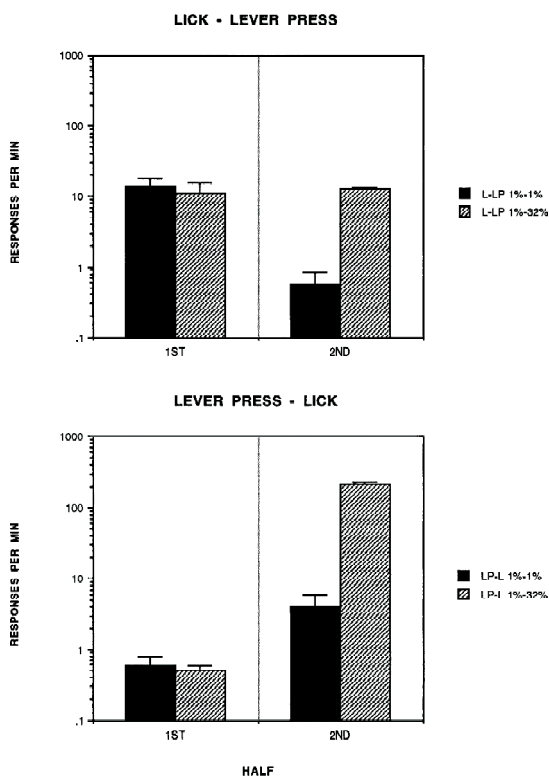


Figure 1. Presented are the rates of responding (responses/min) for the mean of all subjects in both halves of the session in each of the four conditions in Experiment 1. Note the logarithmic ordinate.

The results in Figure 1 question whether type of response in either half of the session determines whether contrast of induction is observed in the first half. Responding in the first half of the session decreased slightly when 32% sucrose reinforcement was upcoming relatively to when 1% sucrose would be available in the second half of the session regardless of which combination of response was required in that particular condition. This negative contrast effect, however, was small and not statistically significant. Responding in the first half of the session was analyzed by conducting a two-way (Type of response x Upcoming reinforcer) repeated measures analysis of variance (ANOVA) on response rates (not logarithms) in the first half of the session for individual subjects in each condition. This analysis resulted in a significant main effect of type of response ($F(1, 4) = 8.78$), indicating that subjects licked at a higher rate than they pressed the lever. However, the main effect of upcoming reinforcer ($F(1, 4) = 1.11$) and interaction between type of response and upcoming reinforcer ($F < 1$) were not significant. Results for this analysis and all which follow were considered significant at $p < .05$.

Finding non-significant differences in response rates for 1% sucrose in the first half of the session when 32% sucrose reinforcement was or was not upcoming would suggest that type of response required in either half of the session does not determine whether a contrast or an induction effect will be observed. Unfortunately, non-significant differences represent null results and thus it is not possible to firmly conclude that type of response in either half of the session plays no role. One could argue that the non-significant differences in responding in the first half of the session

may have occurred because competing forces (e.g., one promoting contrast and one promoting induction) cancelled out each other. For instance, licking in either half of the session might promote a contrast effect whereas lever pressing might promote induction. As both responses were required in each condition, neither contrast nor induction was observed.

EXPERIMENT 2

The implication of the results of Experiment 1 are limited because no significant contrast or induction effect was found. Thus, although it is possible that the results question that a licking or lever-pressing response in either half of the session influences which effect is observed, it remains possible that the different responses promote opposing effects. Experiment 2 was therefore designed to systematically replicate the procedure of Experiment 1 by enhancing the difference between the licking and lever-press response. It did so by making licking a consummatory response (i.e., each lick of the spout produced sucrose). If the type of response contributes to which effect is observed, then by making the lick and lever-press response as different as possible should facilitate one or both effects.

METHOD

Subjects and Apparatus

The subjects were the same five subjects which served in Experiment 1. They were maintained as described in Experiment 1 and responded in the same experimental chamber.

Procedure

The procedure was identical to that described in Experiment 1, with one exception.

When the lickometer was the active operandum, each lick of the spout delivered 0.00625 ml of sucrose to the spout. All other procedural aspects, including order of conditions, were identical to Experiment 1.

RESULTS AND DISCUSSION

Figure 2 presents the results from Experiment 2. It was constructed as was Figure 1. The results in Figure 2 indicate that converting licking to a consummatory response produced lick rates which exceeded those observed when licking was an operant response (see Figure 1). The results in Figure 2 also suggest that a negative contrast effect was observed with each combination of responses. A two-way (Type of response x Upcoming

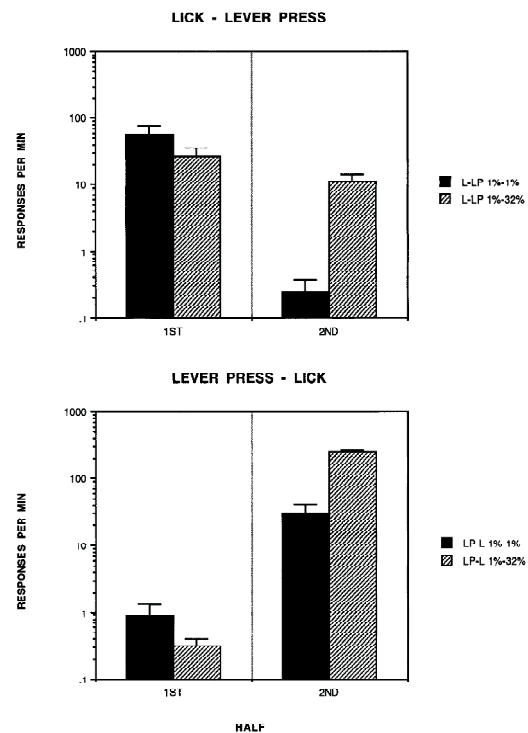


Figure 2. Presented are the rates of responding (responses/min) for the mean of all subjects in both halves of the session in each of the four conditions in Experiment 2. Note the logarithmic ordinate.

reinforcer) repeated measures ANOVA conducted on the response rates in the first half of the session for individual subjects produced a significant main effect of type of response ($F(1, 4) = 12.65$) and of upcoming reinforcer ($F(1, 4) = 10.57$), suggesting that subjects licked at a higher rate than they pressed the lever and that they responded at a lower rate when 32% sucrose reinforcement was upcoming versus when it was not, respectively. The interaction between type of response and upcoming reinforcer was also significant ($F(1, 4) = 10.02$). Follow-up analyses conducted on responding in the first half of the session for each response combination indicated that upcoming 32% sucrose produced a significant decrease in responding in the Lick - Lever Press conditions ($F(1, 4) = 10.31$). The decrease was not significant for the Lever Press - Lick conditions ($F(1, 4) = 1.61$).

The results of Experiment 2 further support the conclusion that type of response (i.e., licking or pressing a lever) required in either half of the session does not appear to be the major determinant of whether a negative contrast or positive induction effect is observed. As in Experiment 1, response rates for 1% sucrose in the first half of the session decreased when 32% sucrose was upcoming regardless of the combination of required response. Indeed, this contrast effect was significant in Experiment 2. By finding contrast in Experiment 2, the results also further the conclusion of Weatherly et al. (2003) that the function of the response (i.e., consummatory vs. operant) is also not a critical factor. Similar results were observed regardless of whether licking was a consummatory or operant behavior (Experiment 1 vs 2) or whether the

consummatory behavior occurred in the first half of the session (top graph of Figure 2) or in the second half (bottom graph of Figure 2).

GENERAL DISCUSSION

The goal of the present study was to investigate whether or not upcoming 32% sucrose reinforcement produced a negative contrast or a positive induction effect in responding for 1% sucrose depends on whether subjects lick a spout or press a lever for reinforcement in one or the other half of the session. It did so by requiring subjects to make one of those responses in the first half of the session to earn 1% sucrose and to make the other response in the second half of the session to earn, in different conditions, either 1% or 32% sucrose. The results question whether type of response in either half of the session is a critical factor in which effect is observed. Across both experiments, upcoming 32% sucrose never produced a positive induction effect. In fact, upcoming 32% sucrose tended to produce a decrease in responding for 1% sucrose in both experiments regardless of type of response required in the different halves of the session. However, this negative contrast effect was only statistically significant in Experiment 2 when press a lever was intermittently reinforced in the first half of the session and licking served as a consummatory response in the second half.

Although both of the present experiments failed to produce an induction effect, the results may actually shed light on the conditions that produce induction, as well as potentially explain the results of Weatherly et al. (2003). Specifically, the present results and those of Weatherly et al. (2003) would

appear to support the idea that the location to which the sucrose is delivered may in fact be the key factor in whether contrast or induction is observed. In the present experiment, sucrose earned by pressing the lever was delivered to a trough adjacent to the lever whereas sucrose earned by licking was consumed from the spout that was licked to earn it. Positive induction was not observed in the present experiments; the results of both experiments trended toward contrast. In Weatherly et al. (2003), the subjects that licked did so by licking separate spouts in the two halves of the session, with the sucrose rewards being delivered directly to each spout. These subjects displayed a negative contrast effect when 32% sucrose was upcoming. The subjects that pressed levers pressed separate levers in the two halves of the session, but the sucrose reinforcers earned in both halves were delivered to the same trough (and thus were consumed from the same location). These subjects displayed positive induction. In fact, of the studies from our laboratory that have reported the finding of positive induction (e.g., Weatherly et al., 2000, 2002), all of them have employed a procedure in which the low-valued reinforcer in the first half of the session was delivered to and consumed from the same location as was the high-valued reinforcer in the second half of the session. Such an explanation would also appear consistent with previous research on anticipatory contrast. Flaherty, Coppotelli, Grigson, Mitchell, and Flaherty (1995), for instance, argued that delivering the different substances to different locations promoted the appearance of negative anticipatory contrast.

Future research will need to pursue the idea that location of substance delivery is the

critical factor in determining whether negative contrast or positive induction is observed. Such research will not only enhance our understanding of these different effects, but as noted above might also help our understanding and treatment of eating behavior. It may be the case that where one consumes food, and what foods are consumed in that location, may play a significant role in weight regulation and overeating.

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TYPE OF RESPONSE

Appendix A

Response rates (response/min) of individual subjects in each half of each condition of each experiment. Rates were calculated using the final five sessions of each condition.

Subject	Condition							
	L-LP 1%-1%		L-LP 1%-32%		LP-L 1%-1%		LP-L 1%-32%	
	1st	2nd	1st	2nd	1st	2nd	1st	2nd
Experiment 1								
61	1.07	0.00	0.37	12.13	0.08	0.00	0.57	223.00
62	12.53	0.15	4.76	15.20	0.24	0.07	0.41	249.59
64	27.08	1.60	17.99	11.64	1.21	2.08	0.79	199.29
65	18.76	0.51	24.61	13.41	0.73	8.53	0.36	158.91
66	10.44	0.63	8.53	11.27	0.69	9.43	0.35	223.92
Experiment 2								
61	1.77	0.00	0.75	1.72	0.20	0.00	0.28	263.44
62	47.89	0.04	12.83	9.05	0.25	0.00	0.41	251.49
64	75.59	0.61	43.23	21.00	2.59	42.99	0.79	260.76
65	76.87	0.21	50.88	12.54	0.56	47.17	0.36	229.15
66	91.52	0.41	29.64	10.57	0.77	58.45	0.35	269.72