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Contrast effects using intracranial self-stimulation in a runway situation.

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Contrast Effects using Intracranial Self-Stimulation in a Runway Situation

A Thesis Presented

by

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CONTRAST EFFECTS USING INTRACRANIAL SELF-STIMULATION IN A RUNWAY SITUATION

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Abstract

A runway situation was designed whereby animals receiving electrical stimulation to the brain (ESB) as reward would be subjected to the same response requirements as animals running to sucrose reward. An incentive contrast paradigm was employed that equated current intensity changes for ESB reward to concentration changes for sucrose reward. It was predicted that behavior controlled by ESB reward would be similar to that obtained under sucrose reward conditions in such aspects as rate of postshift performance changes and positive and negative contrast effects for measures of both instrumental and consummatory responses. Results showed that intensity changes produced behavior identical to that observed with concentration changes except in one crucial area, negative contrast. In this one instance behavioral results indicated that animals may have been responding to a quantity change rather than to a change in quality of reward. The data support the idea that ESB is a high incentive reinforcer operating in the presence of low or no deprivation.

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The author wishes to thank the members of his thesis committee, Dr. Jay A. Trowill, Dr. Ernst Dzendolet, and Dr. Theodore Sargent for their cooperation in the completion of this research. I am particularly grateful to Dr. Jay A. Trowill for his encouragement and his excellent theoretical and technical advice throughout the course of this investigation. I am also indebted to my wife Butler for typing the initial drafts and the final manuscript.

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The discovery that short bursts of electrical stimulation to certain areas of the brain can control behavior (Olds and Milner, 1954) has stimulated research attempting to elucidate the nature of the reinforcing and motivating properties of the electrical stimulation. To date, one of the most complete theoretical statements on the manner in which electrical stimulation of the brain (ESB) acts to control behavior is the drive decay hypothesis of Deutsch and Howarth (1963). This hypothesis assumes that each burst of stimulation simultaneously stimulates two systems in the brain, a reward system and a drive system, thus furnishing an immediate reward and a brief source of drive for the next response. Deutsch and Howarth have used the peculiarities of ESB controlled behavior (e.g. priming, fast extinction, failure to maintain partial reinforcement schedules, and extinction without responding) as support for their drive decay model.

However, recent findings have contradicted the implication that ESB simultaneously rewards and energizes behavior. Olds (1956) and Scott (1967) have shown that performance for ESB is maintained even when rewards are separated by long intertrial intervals. Other investigators (Pliskoff, Wright, and

Hawkins, 1965; Gibson, Reed, Sokai, and Porter, 1965) have shown that the peculiarities of ESB performance are more a function of the training and testing conditions than of any drive properties of ESB itself.

Olds (1956) compared groups of food-rewarded rats to rats rewarded with ESB in both runway and maze performance. He found ESB groups superior in runway performance and only slightly slower in learning the maze than food rewarded rats, although speeds at the end of forty-five trials were virtually identical in the two groups. Olds concluded that ESB may become a strong incentive if given each day for a number of days. In another study, Scott (1967) ran rats down a straight alley for a single 0.25 sec. train of rewarding brain stimulation delivered to lateral hypothalamic areas. He found that such animals, when run at fifteen minute intervals, still demonstrated typical acquisition curves although induced drive from the previous reinforcement should not have affected subsequent trials.

Pliskoff et. al. (1965) have found that when response requirements and scheduling for ESB reward was equated to that normally found in a typical food reward paradigm that ESB reward could be used to establish and maintain partial reinforcement schedules in the range of parameter values used with conventional reinforcers. In a direct comparison of ESB and food-reward situations, Gibson et. al. (1965) found comparable resistance to extinction when the delay of reward was made equivalent for the ESB and food reward conditions. Panksepp and Trowill (1967a) replicated this result but failed to find comparably low resistance to extinction in a group of rats that were reinforced for bar pressing with an immediate injection, via an intra-oral fistula, of a highly preferred chocolate milk solution. However, intra-orally rewarded Ss, maintained under *ad libitum* conditions, behaved essentially identically to animals responding for ESB, i.e., they exhibited fast acquisition, fast extinction, fast reacquisition (priming), agitated behavior, and extinction without responding. This crucial study indicated not only that a high incentive reward could duplicate ESB produced behavior, but also that many of the differences in behavior produced by conventional rewards and ESB could be explained by the differences in response requirements at the time of testing (Panksepp and Trowill, 1967b) and not by the delay of reward.

These and other results apparently in conflict with the drive decay hypothesis have recently been reviewed by Trowill, Panksepp, and Gandelman (in press) who have proposed that ESB performance can best be understood as a high incentive condition operating in the presence of low or no deprivation.

The purpose of the present study was to further test the theory that ESB reward contains a strong incentive component. A runway was employed whereby the S could obtain a standardized number of reinforcements in the goal box by lever pressing on a CRF schedule. Incentive levels were varied by changing the intensity of the rewarding stimulation delivered to the animal. It was hypothesized that if ESB is a high incentive reward then results obtained with intensity shifts in a runway would essentially replicate the trends of the sucrose shift studies in such aspects as rate of postshift performance change and contrast effects (undershooting or negative contrast and overshooting or positive contrast as described by Crespi in 1942).

Method

Subjects

Ten naive male rats from the Charles River Breeding Company were used in the present experiment. The Ss were approximately three to four months old at the time of electrode implantation. Ss were individually housed and maintained on ad libitum food and water throughout the experiment.

Surgery

Ss were implanted bilaterally, under sodium nembutal anesthesia (40 mg/kg), with stainless steel monopolar electrodes with a tip diameter of 0.25 mm. Krieg coordinates (Krieg,1946) were used, aiming at the lateral hypothalamus in or near the medial forebrain bundle. Coordinates of 1.7 mm. posterior to bregma, 1.4 mm. lateral to the midline, and 8.2 mm. deep, as measured from skulltop at the site of implantation, were used. Two weeks were allowed for recovery before screening tests began.

Apparatus

The experimental chamber was a short runway, 17 in. long, 7.5 in. wide, and 15 in. high. A lever was installed on the far wall of the runway. There was no discrete goal box. The start box was an additional 7 in. long and 5 in. wide with a hinged floor set on a microswitch. A Standard electric timer (0.01 sec. accuracy) started when the animal exited into the chamber proper. The timer was stopped when the S made his first response on the lever. This first response also started a running time meter which counted the number of seconds required for the animal to make a predetermined number of responses, i.e. 75 lever presses per trial. Thus, two dependent variables were recorded, running time and time to complete bar pressing (response time).

Two electrode leads, 20 in. long, were attached to the S from an overhead mercury swivel. Sixty Hz. sine-wave current in 0.3 sec. bursts were delivered to the animal through one of the implanted electrodes and a ground electrode attached to the skull. The current was stepped down from 110 V house current by a transformer and regulated by a micropotentiometer used as a voltage divider. Current readings were inspected visually by a microammeter wired in series with the S.

Pretraining

Two days prior to screening, each animal was handled 10 to 15 min. per day and then placed into the experimental chamber for 15 min. without electrode leads attached.

Screening consisted of placing the animal into the experimental chamber with electrode leads attached and arbitrarily setting the stimulation at 40 uA (rms). The S was then shaped to lever press. If the S did not acquire the response at this intensity, he was removed from the chamber and returned to his home cage. The following day S was tested again with an increase of 20 uA. This process was repeated until the animal (a) learned to lever press, (b) showed overt motor reactions to the stimulation, or (c) reached intensity ranges beyond the limits of the micropotentiometer (230 uA) with no signs of being positively rewarded. At no time during pretraining or training did the S receive two different intensities in one day. After screening was completed, all non-contingent reinforcements were discontinued.

When the lever-press response was acquired, rate-intensity curves were obtained for each animal. These points were tested using one intensity setting per day. Response rates were recorded in two consecutive 10 min. sessions. The number of responses in the second 10 min. interval was used in plotting responses per hour *versus* intensity in uA. Intensity settings were randomly tested over days in 5 uA steps from subthreshold levels to a point where further increases in intensity produced motor reactions or no responding.

Plots from each animal showed inverted U-shaped functions. Two intensity settings were selected on the ascending arm of the curve, the highest intensity being arbitrarily designated as the most favorable (MF). The MF was chosen several uA below the maximum point to minimize response time ceiling effects (Bower, 1961), with the assumption that response ceiling effects would also be minimized for running time measures. The lower intensity setting (least favorable or LF) was generally selected 10 to 15 uA below the MF, but in all cases exceeded threshold responding by 10 uA.

Experimental Procedure

The *S*s were randomly assigned to one of two groups, negative contrast (NC) or positive contrast (PC), and run on consecutive days. Each *S* received ten daily training trials and a total of 75 response-produced reinforcements per trial. The Ss of the experimental condition of the negative contrast group was trained to aymptote with the MF intensity and then switched to the LF intensity. Ss in the experimental condition of the positive contrast group were initially trained on the LF intensity and subsequently shifted to the MF intensity. The ten daily trials were separated by an intertrial interval of 30 sec., the S being returned to his home cage (placed adjacent to the runway) during this periods. Acquisition curves were not obtained, but each S was run to a criterion asymptote determined by four consecutive days at a stable running speed (randomization test for matched pairs, Siegel, 1956). On the next day, intensity settings were changed prior to the initial trial and remained at this level for a total of six days.

Separate control groups were not run due to the large amount of individual variation in both dependent measures found in pilot work. Therefore, each S served as his own control. After postshift trials were completed, a rest period of one week was instituted. At the end of this period the S was allowed a session of 1,000 responses at the control intensity setting (i.e. at the postshift value), allowed to rest one additional week, and then brought back to run 100 trials (10 per day) at the control intensity. Thus, each contrast group had two conditions, an experimental (NC-E; PC-E) and a control condition (NC-C; PC-C).

Results

Reciprocals of both running time and response time scores were calculated and analyzed. Reciprocal running time, although not a true measure of speed in this experiment, will be referred to as such to simplify discussion. Likewise, reciprocal response time is designated as response speed.

Comparison between First and Fourth Preshift Days

The randomization test for matched pairs (two tailed) (Siegel, 1956) was employed to test for asymptotic preshift running speeds for the experimental conditions. Comparisons between Day 1 median scores and Day 4 median scores for both NC-E and PC-E conditions showed that there was no significant difference ($p > .05$) between these values, indicating that a stable baseline was present before the introduction of reinforcement shifts.

The same analysis was applied to response speed scores. Values obtained indicated that the preshift baseline was not stable for either experimental group and that both groups were consistently increasing their speed of lever pressing over the training days. Table 1 presents the difference scores and probability levels for this analysis.

Negative Contrast

Graphs of running speed and response speed are presented in Figures 1 and 2 respectively. Inspection of Figure 1 indicates that postshift NC-E running speed scores are well below the NC-C levels and show little evidence of a return to control values even after 60 postshift trials. It can be noted that scores for the first postshift day (Day 5) show no change from preshift levels. By the second day there is a reduction in running speed to a value significantly below control levels.

Table 1

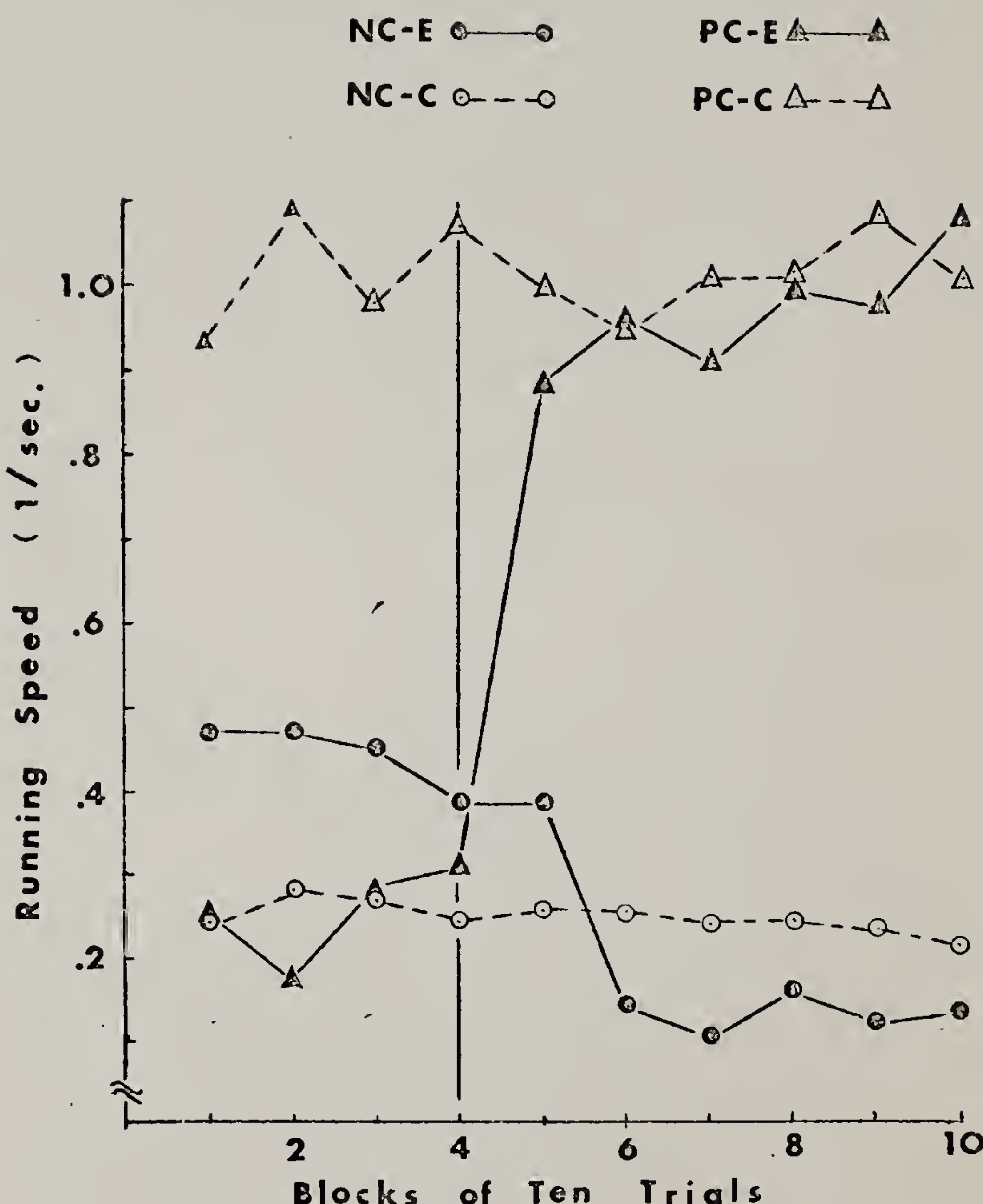
Preshift difference scores are presented for running speed and response speed measures for both contrast groups. Difference scores were obtained by subtracting fourth day scores from first day scores. Significant probability levels are also presented.

GROUP	MEASURE	d SCORES
NEGATIVE CONTRAST	Running Speed	.2392 .1734 .0720 -.0613 -.0043
	Response Speed	-.0003 -.0006 -.0011 -.0019 -.0062*
POSITIVE CONTRAST	Running Speed	.0360 .0068 -.0127 -.0455 -.2152
	Response Speed	-.0049 -.0050 -.0081 -.0084 -.0141*

$*p < .05$

Figure 1

Reciprocal median latency to respond (running speed) for both negative and positve contrast groups *versus* blocks of ten trials.



NC-E
PC-E
NC-C
PC-C
Running Speed (1/sec.)
1.0
.8
.6
.4
.2
2
4
6
8
10
Blocks of Ten Trials

The response speed graph (Figure 2) shows a somewhat different result-- i.e. an immediate and rapid postshift performance change and a return to control levels.

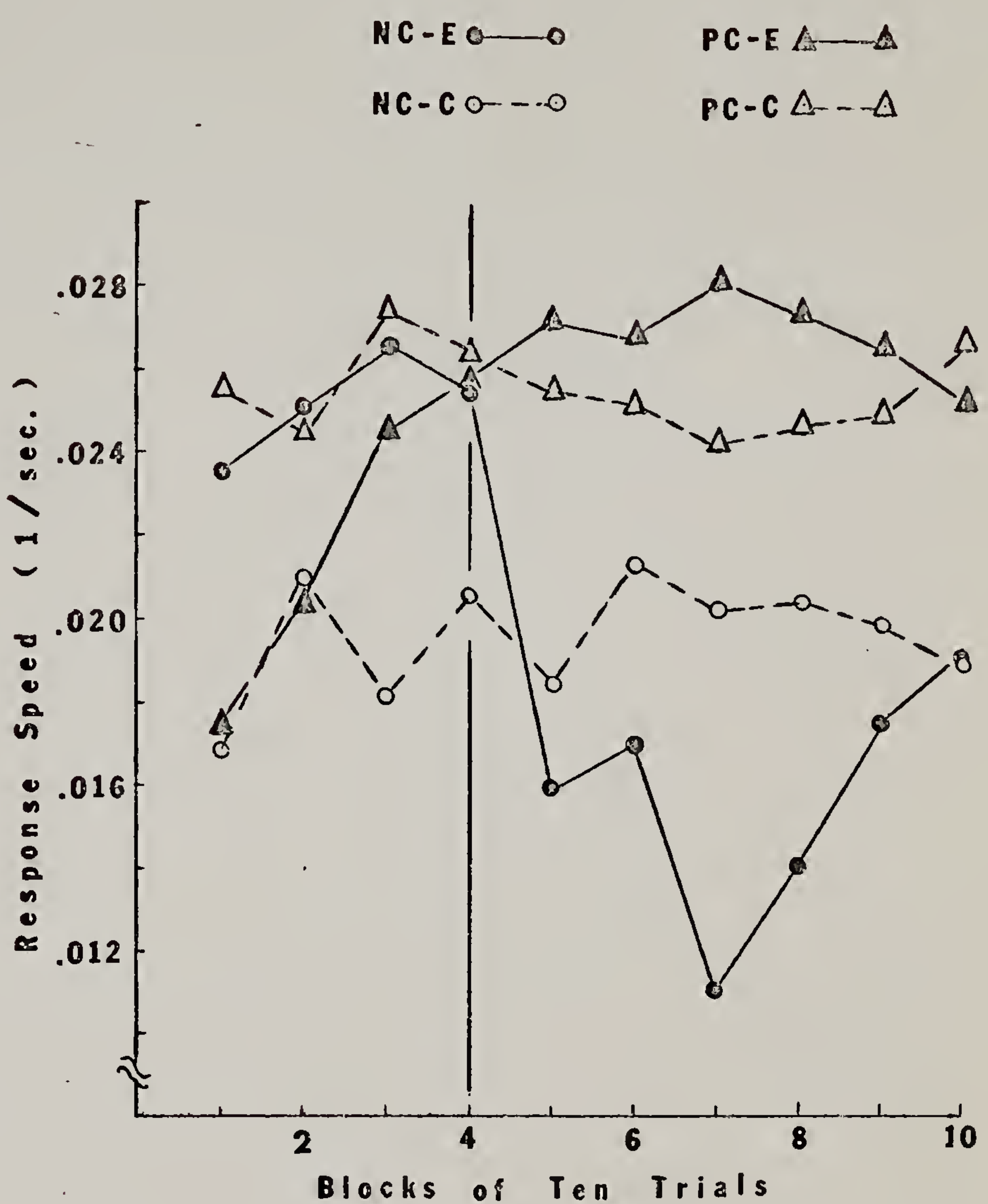
The difference scores between the NC-E and NC-C conditions obtained from the median scores of the ten daily postshift trials were analyzed using the one-tailed randomization test for matched pairs. This day by day appraisal revealed significant results for postshift Days 2,3,4,5, and 6 ($p=.031$)[1] on running speed data, whereas significance was obtained only on postshift Days 7 and 8 ($p=.031$) for response data. Difference scores and probability levels are presented in Table 2.

<u>Positive Contrast</u>

Graphs for Group PC for both running speed and response speed scores are also presented in Figures 1 and 2 respectively. Running speed scores show an immediate postshift change to control levels and generally stay equal to, or a little below, those values. Figure 2 shows

Figure 2

Reciprocal median response time (response speed) for both negative and positve contrast groups *versus* blocks of ten trials.



NC-E
NC-C
PC-E
PC-C
.028
.024
.020
.016
.012
Response Speed (1/sec.)
2
4
6
8
10
Blocks of Ten Trials

shows preshift median scores consistently rising toward control condition levels. Postshift scores are generally above control values.This trend should be interpreted with caution because of the non-asymptotic preshift response speed scores.

The same analysis was applied to Group PC scores as was applied to Group NC scores. As seen in Table 2, results of day by day analysis showed that running speed scores for the experimental and control conditions were not significantly different for any of the postshift days, and that only the third postshift day for response speed scores was significant ($p=.031$).

Trial by Trial Analysis of the First Postshift Day

The first postshift day was analyzed on a trial by trial basis for both running and response speed data. The randomization test for matched pairs indicated that none of the individual trials for Day 5 approached significance for either running speed or response speed scores in Group NC, whereas trials 3 and 4 for Group PC of that day

Table 2

Difference scores between median values of experimental and control conditions for postshift days. Running speed and response speed values for both negative and positive contrast groups are presented. Significant probability levels are also given.

GROUP	MEASURE	POST-SHIFT DAYS 1	2	3	4	5	6
NEGATIVE CONTRAST	Running Speed	.4077	-.2075	-.3003	-.1786	-.2835	-.4947
		.1644	-.2065	-.1873	-.0907	-.1864	-.0761
		.0647	-.0664	-.1314	-.0702	-.0559	-.0586
		.0442	-.0567	-.0574	-.0558	-.0262	-.0483
		-.0190	-.0414*	-.0434*	-.0154*	-.0057*	-.0091*
	Response Speed	-.0185	-.0181	-.0251	-.0201	-.0091	.0073
		.0076	-.0084	-.0143	-.0099	-.0087	-.0066
		.0074	.0053	-.0028	-.0014	.0078	-.0027
		-.0064	-.0045	-.0027	-.0012	-.0034	.0026
		-.0015	.0040	-.0016*	-.0002*	.0015	.0003
POSITIVE CONTRAST	Running Speed	-.3592	.3415	-.1640	-.2799	-.2826	.2737
		-.1927	-.3251	-.1253	.1649	.2426	-.2230
		-.1518	.0386	-.1056	.0602	-.2409	.1651
		.0846	.0360	-.0888	.0454	-.2143	.1391
		.0646	-.0055	-.0262	-.0400	-.0391	.0631
	Response Speed	-.0067	.0082	.0070	.0081	.0084	-.0058
		.0049	.0052	.0053	.0043	-.0063	-.0041
		.0044	-.0049	.0042	-.0016	.0049	.0029
		.0033	-.0008	.0020	.0014	.0009	-.0006
		.0019	-.0002	.0005*	.0012	-.0001	.0004

* p=.031

Table 3

Difference scores for the trial by trial analysis of the first postshift day for running speeds. Significant probability levels are presented.

		TRIALS									
		1	2	3	4	5	6	7	8	9	10
NC	S_1	-.2502	.4728	.1997	.2826	.6146	.7613	.9922	.4303	.2945	-.2151
	S_2	-.0654	.1171	-.0718	.1903	.0979	.0934	.1189	-.1376	-.0002	.0861
	S_3	.1037	-.0041	.1767	.0934	.0753	.0724	.0691	.0315	-.0241	.0027
	S_4	.3648	-.2579	.1243	-.3277	.0908	-.1357	.5696	.2381	.7002	.4477
	S_5	-.0039	.3654	.3089	.2588	.0031	-.0674	-.0002	-.1105	-.0867	-.0788
PC	S_1	-.4830	-.0963	-.3802	.0000	-.0441	-.6639	-.2169	-.8766	-.3784	-.4048
	S_2	.5042	-.1455	-.7624	-.7177	.1905	-.2107	.1729	-.2932	-.3382	.5024
	S_3	-.4986	.2984	-.3636	-.4540	-.1327	-.0939	.1866	.2020	-.3707	-.2060
	S_4	.0922	-.6732	-.4055	-.1890	.3086	-.1178	-.2500	.1030	-.2588	.0000
	S_5	-.1767	.4537	.0685	-.2470	-.1896	.2594	-.3781	.2205	.0566	-.1378

Table 4

Difference scores for the trial by trial analysis of the first postshift day for response speeds.

		TRIALS									
		1	2	3	4	5	6	7	8	9	10
NC	S_1	-.0164	-.0169	-.0101	-.0089	-.0045	-.0083	.0000	.0000	-.0034	.0000
	S_2	.0054	.0069	.0062	.0103	.0039	.0059	.0056	.0181	.0075	.0126
	S_3	.0058	.0072	.0058	-.0059	-.0053	-.0153	-.0008	.0012	-.0064	-.0065
	S_4	-.0033	.0052	-.0053	.0073	.0116	.0098	.0012	.0129	-.0047	.0057
	S_5	-.0098	-.0041	-.0183	-.0226	-.0188	-.0185	-.0207	-.0159	-.0161	-.0230
PC	S_1	-.0003	-.0113	-.0105	-.0109	-.0066	-.0067	.0033	-.0037	.0004	-.0110
	S_2	.0049	.0014	.0014	-.0021	.0058	.0018	.0032	.0024	.0035	.0000
	S_3	-.0028	.0106	.0006	.0067	.0084	.0089	.0029	.0074	.0012	.0065
	S_4	.0061	.0030	.0055	.0031	.0078	.0066	.0016	.0034	-.0029	.0017
	S_5	.0123	.0096	.0031	.0044	.0030	.0063	.0077	.0006	.0045	-.0011

were significant (p_3=.063; p_4=.031) for running speed scores and Trial 7 (p_7=.031) for response speed scores. The difference scores for this analysis are presented in Tables 3 and 4.

Reanalysis using Trials 2-10

Inspection of individual trial scores versus the median score for that day revealed that the first trial of the day remained reasonably constant for both dependent measures regardless of the reinforcement conditions, while the second trial and the tenth trial of the day followed reinforcement levels in the same manner as did median scores.

A re-analysis of the data utilizing only Trials 2 through 10 to establish the median scores for the day was performed. Significant results were not changed for either group in both running speed and response speed scores. Difference scores and probability levels for this analysis are presented in Table 5.

Comparisons between Negative and Positive Contrast Groups

Cross comparisons between running speed graphs

Table 5

Difference scores between median values of experimental and control conditions for postshift days. This analysis was done utilizing only trials two through ten for each day. Running speed and response speed values for both negative and positive contrast groups are presented. Significant probability levels are also given.

GROUP	MEASURE	POST-SHIFT DAYS					
		1	2	3	4	5	6
NEGATIVE CONTRAST	Running Speed	.4097	* -.2229	* -.3476	* -.0824	* -.2710	* -.3339
		.0659	-.0577	-.1314	-.0625	-.0569	-.0471
		.0399	-.0384	-.0484	-.0135	-.0259	-.0053
		.1939	-.2066	-.1936	-.1038	-.1808	-.0780
		.0287	-.0667	-.0583	-.0738	.0040	-.0725
	Response Speed	-.0083	-.0091	-.0033	-.0005	-.0046	-.0028
		.0069	.0035	-.0144	-.0096	.0094	.0070
		-.0016	.0058	-.0018	-.0019	.0014	-.0005
		.0067	-.0053	-.0039	-.0005	-.0093	.0013
		-.0185	-.0183	-.0241	-.0200	-.0057	-.0062
POSITIVE CONTRAST	Running Speed	-.3255	-.3297	* -.0812	* -.2877	-.0641	.4009
		-.1905	.1970	-.0277	-.2004	-.2004	-.2241
		-.1709	.0087	-.1768	-.2565	-.2565	.1613
		-.2222	-.0143	-.0710	-.2521	-.2521	.1359
		.1459	.0598	-.1204	.1682	.1682	.0321
	Response Speed	-.0067	-.0043	* .0019	-.0012	-.0062	-.0040
		.0018	.0060	.0057	.0043	.0046	.0035
		.0042	-.0005	.0048	.0017	.0004	-.0058
		.0031	-.0002	.0000	.0009	.0000	.0003
		.0044	.0079	.0072	.0081	.0089	-.0005

* p .031

(Figure 1) using the Mann-Whitney U test (Siegel, 196) suggest that these speeds may be partially determined by prior reinforcement conditions. Comparisons between preshift Days 1 through 4 for the PC-E condition and Days 7 through 10 for the NC-C condition revealed no significant differences for any of the four days (p_1=.421; p_2=.345; p_3=.579; p_4=.500). However, the same analysis for the NC-E and PC-C conditions showed a significant difference for all four comparison days (p_1=.028; p_2=.048; p_3=.016; p_4=.008). The results are summarized in Table 6.

Table 7 shows the results obtained from response speed scores for the same analysis. Only Day 1 for the PC-E condition when compared to Day 7 of the NC-C condition was significantly different (p=.028). All other comparisons were non-significant.

Discussion

The major results of the present study were (1) durable negative contrast effects with a

Table 6

Comparison between Days 1 through 4 for the PC-E condition and Days 7 through 10 for the NC-C condition, and for Days 1 through 4 (NC-E) *versus* Days 7 through 10(PC-C). The Mann-Whitney U-test was applied to these running speed differences.

	DAYS			
	1 (7-1)	2 (8-2)	3 (9-3)	4 (10-4)
PC-E (1-4) - NC-C (7-10)	u=11 p=.421	u=10 p=.345	u=13 p=.579	u=12 p=.500
NC-E (1-4) - PC-C (7-10)	u=3 p=.028	u=4 p=.048	u=2 p=.0160	u=1 p=.008

Table 7

Comparison between preshift Days 1 through 4 for the PC-E condition and Days 7 through 10 for the NC-C condition, and for Days 1 through 4 (NC-E) *versus* Days 7 through 10 (PC-C). The Mann-Whitney U-test was applied to the response speed scores.

	DAYS			
	1 (7-1)	2 (8-2)	3 (9-3)	4 (10-4)
PC-E (1-4) – NC-C (7-10)	u=3 p=.028	u=7 p=.155	u=9 p=.274	u=11 p=.421
NC-E (1-4) – PC-C (7-10)	u=11 p=.421	u=8 p=.210	u=8 p=.210	u=5 p=.075

shift from MF to LF intensities in both running and response speed measures, (2) no positive contrast effect for running speed, (3) a questionable positive contrast effect for response speed scores, and (4) a rapid rate of change for both behavioral measures for the upshifted condition while for the downshifted condition only the response speed measure changed rapidly.

Prior to the reinforcement shifts, running speeds were asymptotic for both experimental groups. However, the response speed data indicated that this measure was not at asymptote prior to the shift for either contrast condition. The interpretation of the negative contrast effect should not be questioned on this basis, however, since preshift differences were in the direction opposite to post-shift performance changes. On the other hand, for the PC-E condition, response speed scores consistently rose over the four preshift days in the direction of the expected postshift performance changes. Although the third postshift day showed a significant positive contrast effect, this result may merely reflect the non-stable preshift baseline (Spence, 1956) and should therefore be interpreted with caution.

The experimental situation used in this study with ESB was designed to duplicate the procedures found in sucrose reward situations, whereby results from the present study were expected to be consonant with the sucrose reward data in such measures as rate of performance changes with reinforcement shifts and negative and positive contrast effects.

In one of the recent sucrose reward studies, Homzie and Ross (1962) shifted the concentration of sucrose from high to low. Performance changes (running speed) were slow, requiring up to twenty trials or more to reach running speeds of a control group. No evidence was obtained for a negative contrast effect.

Rosen and Ison (1965), in an attempt to replicate parts of the Homzie and Ross study, also ran rats in a runway to a sucrose reward. Animals shifted from high concentrations to low concentrations showed the same slow running speed changes (up to

30 trials to reach control levels) as found by Homzie and Ross and like the Homzie and Ross results, there was no evidence of a negative contrast effect. A significant additional finding was that postshift lick rate measures did not differ from preshift levels, although both pre- and postshift rates for the three groups were different. Guttman (1953), employing successive contrasts with rats running to sucrose solutions, also obtained no evidence for a negative contrast effect.

An experiment by Collier, Knarr, and Marx (1961) may be particularly relevant to the present experiment. Collier, et.al. shifted rats from a 4% sucrose solution to a 32% sucrose solution and *vice versa*, while measuring total running speeds and rate of licking. The effect on running speed of a downshift in reward was identical to previous results, i.e. slow performance changes and no evidence of a negative contrast effect. On the other hand, the upshifted *Ss*, although never attaining control levels, did reach their postshift asymptotic running speeds within six trials.

Consummatory response measures (number of licks in 60 seconds) showed somewhat different results. The downshifted Ss dropped rapidly and significantly below the control level and then gradually returned to the control level. The upshifted group rapidly increased their number of licks to a level consistently above the controls, but significance was obtained only when the second trial of the two daily training trials was considered.

In general, available evidence from studies utilizing a successive non-differential paradigm (Dunham, 1968) with sucrose reward demonstrate slow performance changes in running speeds with downshifts and fast changes with upshifts, while neither negative nor positive contrast effects are seen. Consummatory response results remain equivocal, although the Collier, et.al. data are striking in light of the results obtained in the present experiment for the consummatory response.

Results from the present experiment indicate that running speeds for the upshifted Ss (LF to MF) change rapidly to control levels. Although analysis in terms of blocks of ten trials is fairly gross, the trial by trial analysis revealed that _S_s had reached running speeds significantly above control levels by the third postshift trial. Running speeds for the downshifted group (MF to LF) showed the same slow performance changes that are typical of sucrose reward shifts. Positive contrast was evidenced only as a transient and not a very convincing effect. Negative contrast was dramatic in that it occurred on the second day and carried through for 40 succeeding trials with no evidence of a return to control values.

Response speed data also indicate essentially identical trends to those found by Collier et.al. in that the downshifted group showed a dramatic and significant decrease in response speed, an increase in variability, and a gradual return to control levels. Upshifted _S_s rapidly increased bar press activity and consistently exceeded control values, although only one block of ten trials proved to be statistically significant.

Positive and negative contrast effects were also recently demonstrated by Panksepp and Trowill (in press) using ESB in a free-operant situation. The paradigm involved shifting animals from a high intensity to a lower one or vice versa within a single bar pressing session. Although the time courses for the effect are different in these two experiments it does give supportive evidence that positive and negative effects for bar press measures do occur in experiments where ESB is used as a reinforcer.

The first trial of each day was observed to remain relatively invariant under both postshift conditions. The few changes that did occur were not obviously correlated with the reinforcement contingencies. When the first trial was removed from the daily sessions and the data reanalyzed, the results remained unchanged. It is interesting to note that Collier et.al. (1961) also noticed a "periodicity" in their starting speed data for the downshifted group, (p.490). The first trial of each day, then, appears to be a special event and may largely be determined by preshift reinforcement conditions. Inspection of the second trial and the tenth trial of the day indicated that these trials follow the median of the day rather closely and are apparently being influenced predominantly by the reinforcement level of the preceeding trial or trials.

Finally, when making cross comparisons between running speed data for the two contrast groups, an unexpected result was observed. When the MF intensity was presented first to a group of Ss they ran significantly slower than a group of Ss given a comparable MF intensity but which had been preceeded by a LF intensity. Had control conditions not been run, and the speeds of the postshift PC-E condition been compared to extrapolated preshift NC-C curves, then positive contrast would have been significantly demonstrated. This surprising result remains unexplained. Although it may be tempting to regard this result as evidence for positive contrast, there is not yet sufficient information to regard it as such. The result could also reflect variations in placement of electrodes. However, since rate-intensity curves were not inordinately different and since experimental response speed scores did not differ, this explanation is unlikely.

In summary, ESB, when employed as a reinforcer in a standard runway situation, replicates many behaviors obtained with sucrose rewards. These behaviors include: (a) rapid running and response speed changes with upshifted reinforcement conditions; (b) slow running speed changes with downshifted reinforcement conditions; (c) 'consummatory' responses which follow reinforcement shifts and exceed control levels; (d) first trial of the day postshift behavior that is determined by preshift reinforcement levels and, finally, (e) learning and performance controlled only by the reinforcement contingencies present and not dependent upon priming effects.

On the negative side is the powerful negative contrast effect observed in running speeds. Typically, a large and lasting negative contrast effect is seen in shift studies that employ quantity changes rather than quality changes (Crespi, 1942; Zeaman, 1949; Gonzales, Gleitman, and Bitterman, 1962; Ehrenfreund and Badia, 1962; Dilollo, 1964). The magnitude and duration of the negative contrast effect obtained in the present study may indicate that ESB-rewarded animals may also be responding, in part, to shifts in the quantity of reward. This result is particularly convincing because the animals were responding within a procedure where response requirements were most similar to those demanded in a quality-shift study.

Despite this result, the evidence presented is sound for interpreting ESB as a very 'usual' reinforcer. When the response requirement conditions are equated performance changes found with ESB intensity shifts are quite similar to those found when shifting the incentive variables of natural rewards. The data from the present experiment lends strong support to the recent incentive model proposed by Trowill, et.al. (in press).

An uncontrolled variable in this and in most other studies comparing ESB to natural rewards, is, of course, that of the deprivation state existing in the animals at the time of testing (Panksepp and Trowill, 1967b; Trowill, et.al., in press). It remains to be seen what the behavioral results would be if animals under a zero drive condition were run for sucrose reward in a contrast experiment. The deprivation influences may also help explain differences between sucrose data and ESB data in the crucial area of negative contrast.

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FOOTNOTES

1. The randomization test for matched pairs with an N of 5 gives a probability of 0.031 for the most extreme case, and a probability of 0.063 for the second most extreme case. A probability of 0.063 was accepted as significant only for the data analyzed on a trial by trial basis.

APPENDIX

Program used for data analysis.

TN5,48 10/04/68

```
      PROGRAMEK
      DIMENSION XLAT(20,10,10), RLAT(20,10,10), RMLAT(20,10),
     1          RRESP(20,10,10), RMRESP(20,10), XMEDL(20,10), XMEDR(20,10)
      DIMENSION RESP(20,10,10)
    1 FORMAT (5X,10(F5.2,2X))
    2 FORMAT (10(2X,F6.2))
    3 FORMAT (15X,*RECIPROCAL  MEAN  LATENCIES*,//)
    4 FORMAT (26X,*DAYS*,//)
    5 FORMAT (4X,*1         2         3         4         5         6         7
     1  8         9         10*,//)
    6 FORMAT (10(2X,F6.4),/)
    7 FORMAT (38X,*RLAT*//)
    8 FORMAT (38X,*RRESP*//)
    9 FORMAT (15X,*RECIPROCAL MEDIAN LATENCIES*,//)
   99 NS = 5
      DO 10 I = 1,NS
      DO 10 II = 1,10
   10 READ(60,1) (XLAT(I,II,III),III = 1,10)
      DO 15 J = 1,NS
      DO 15 JJ = 1,10
      READ(60,2) (RESP(J,JJ,JJJ),JJJ = 1,10)
      IF(EOF,60)91,15
   15 CONTINUE
   92 DO 20 I = 1,NS
      DO 20 J = 1,10
      XKTR = 0.0
      DO 30 K = 1,10
      RLAT(I,J,K) = 1.0/XLAT(I,J,K)
      XKTR = XKTR + RLAT(I,J,K)
   30 CONTINUE
      RMLAT(I,J) = XKTR/10.0
   20 CONTINUE
      DO 25 L = 1,NS
      DO 25 M = 1,10
      CTR = 0.0
      DO 35 N = 1,10
      RRESP(L,M,N) = 1.0/RESP(L,M,N)
      CTR = CTR + RRESP(L,M,N)
   35 CONTINUE
      RMRESP(L,M) = CTR/10.0
   25 CONTINUE
      WRITE (61,3)
      WRITE (61,4)
      WRITE (61,5)
      DO 50 I = 1,NS
   50 WRITE (61,6)(RMLAT(I,J),J = 1,10)
      WRITE (61,3)
      WRITE (61,4)
      WRITE(61,5)
      DO 55 L = 1,NS
   55 WRITE(61,6) (RMRESP(L,M),M = 1,10)
      WRITE (61,7)
      DO 60 I = 1,NS
      DO 60 J = 1,10
   60 WRITE (61,6) (RLAT(I,J,K),K = 1,10)
      WRITE (61,8)
```

```
      DO 65 I = 1,NS
      DO 65 J = 1,10
   65 WRITE (61,5) (RRESP(I,J,K),K = 1,10)
      DO 75 J = 1,10
      CTRR = 0.0
      DO 85 I = 1,NS
      CTRR = CTRR + RMLAT(I,J)
   85 CONTINUE
      XNS = NS
      CTRR = CTRR/XNS
   75 WRITE(61,6)CTRR
      NS = XNS
      DO 70 J = 1,10
      CTRR = 0.0
      DO 80 I = 1,NS
      CTRR = CTRR + RMRESP(I,J)
   80 CONTINUE
      XNS = NS
      CTRR = CTRR/XNS
   70 WRITE (61,6) CTRR
      NS = XNS
      N = 9
  101 DO 200 I = 1,NS
      DO 300 J = 1,10
      DO 500 K = 1,N
      IF (RLAT(I,J,K) - RLAT(I,J,K+1))500,500,600
  600 C = RLAT(I,J,K)
      RLAT(I,J,K) = RLAT(I,J,K+1)
      RLAT(I,J,K+1) = C
  500 CONTINUE
  300 CONTINUE
  200 CONTINUE
      N = N-1
      IF (N)400,400,101
  400 DO 123 I = 1,NS
      DO 123 J = 1,10
      XMEDL(I,J) = 0.0
  123 CONTINUE
      DO 900 I = 1,NS
      DO 900 J = 1,10
      XMEDL(I,J) = XMEDL(I,J) + RLAT(I,J,5) + RLAT(I,J,6)
      XMEDL(I,J) = XMEDL(I,J)/2.0
  900 CONTINUE
      WRITE(61,9)
      WRITE(61,4)
      WRITE (61,5)
      DO 700 I = 1,NS
  700 WRITE (61,6)(XMEDL(I,J), J = 1,10)
      DO 812 J = 1,10
      YCTR = 0.0
      DO 813 I = 1,NS
      YCTR = YCTR + XMEDL(I,J)
  813 CONTINUE
      XNS = NS
      YCTR = YCTR/YNS
  812 WRITE (61,6)YCTR
```

```
      NS = XNS
      M = 9
  102 DO 235 I = 1,NS
      DO 335 J = 1,10
      DO 535 K = 1,M
      IF (RRESP(I,J,K) - RRESP(I,J,K+1))535,535,635
  635 C = RRESP(I,J,K)
      RRESP(I,J,K) = RRESP(I,J,K+1)
      RRESP(I,J,K+1) = C
  535 CONTINUE
  335 CONTINUE
  235 CONTINUE
      M = M-1
      IF (M)435,435,102
  435 DO 124 I = 1,NS
      DO 124 J = 1,10
      XMEDR(I,J) = 0.0
  124 CONTINUE
      DO 935 I = 1,NS
      DO 935 J = 1,10
      XMEDR(I,J) = XMEDR(I,J) + RRESP(I,J,5) + RRESP(I,J,6)
      XMEDR(I,J) = XMEDR(I,J)/2.0
  935 CONTINUE
      WRITE (61,9)
      WRITE (61,4)
      WRITE (61,5)
      DO 705 I = 1,NS
  705 WRITE (61,6)(XMEDR(I,J), J = 1,10)
      DO 814 J = 1,10
      YCTR = 0.0
      DO 815 I = 1,NS
      YCTR = YCTR + XMEDR(I,J)
  815 CONTINUE
      XNS = NS
      YCTR = YCTR/XNS
  814 WRITE (61,6) YCTR
      GO TO 99
   99 STOP
      END
```

NEGATIVE CONTRAST (Running speed)

RECIPROCAL MEDIAN LATENCIES - Control

DAYS									
1	2	3	4	5	6	7	8	9	10
0.6485	0,4860	0.6069	0.4751	0.8069	0.1002	0.0631	0.3304	0.1111	0,1574
0.1193	0,1237	0.2423	0.1236	0.1676	0.0547	0.0281	0.0193	0.0599	0,0635
0.2593	0,2806	0.1760	0.1873	0.1354	0.0419	0.0551	0.0697	0.0706	0,0743
0.8237	1,0025	0.8323	0.8850	0.7650	0.4785	0.3033	0.3165	0.2766	0,3571
0.5108	0,4628	0.3947	0.2716	0.0708	0.0366	0.0535	0.0777	0,0900	0,0359
0.4723									
0.4711									
0.4504									
0.3885									
0.3891									
0.1424									
0.1006									
0.1627									
0.1217									
0.1376									

RECIPROCAL MEDIAN LATENCIES - Control

DAYS									
1	2	3	4	5	6	7	8	9	10
0.4351	0,4892	0.4594	0,4882	0.3992	0.3077	0.3634	0.4211	0.3946	0,3686
0.0781	0,0707	0,1168	0.1020	0.1029	0.1114	0.1595	0.0751	0.1198	0,1118
0.0586	0,0759	0.0732	0.0818	0.0912	0.0833	0.0985	0.0851	0.0968	0,0834
0.5016	0,6809	0.6429	0,4892	0.6006	0.6850	0.4906	0.4951	0.4630	0,4157
0.1465	0,0860	0.0635	0,0599	0.0898	0.1030	0.1109	0.1479	0.0957	0,1063
0,2440									
0,2810									
0.2712									
0,2442									
0.2567									
0.2581									
0,2446									
0,2448									
0.2340									
0,2171									

NEGATIVE CONTRAST (Response speed)

RECIPROCAL MEDIAN LATENCIES - Experimental

DAYS

1	2	3	4	5	6	7	8	9	10
0.0271	0,0303	0.0301	0.0290	0.0056	0.0060	0.0056	0.0074	0.0060	0,0076
0.0214	0,0244	0.0223	0.0217	0.0255	0.0233	0.0056	0.0109	0.0277	0,0272
0.0152	0,0156	0.0193	0.0158	0.0107	0.0159	0.0090	0.0135	0.0148	0,0116
0.0272	0,0320	0.0313	0.0334	0.0323	0.0270	0.0272	0.0303	0.0226	0,0299
0.0267	0,0231	0.0299	0.0278	0.0056	0.0129	0.0074	0.0077	0.0166	0,0196
0.0235									
0.0251									
0.0266									
0.0255									
0.0159									
0.0170									
0.0110									
0.0140									
0.0175									
0.0192									

RECIPROCAL MEDIAN LATENCIES - Control

DAYS

1	2	3	4	5	6	7	8	9	10
0.0084	0,0083	0.0067	0.0129	0.0120	0.0144	0.0084	0.0086	0.0094	0,0103
0.0218	0,0249	0.0206	0.0191	0.0181	0.0193	0.0199	0.0208	0.0199	0,0199
0.0094	0,0097	0.0071	0.0120	0.0122	0.0106	0.0106	0.0149	0.0133	0,0113
0.0235	0,0346	0.0289	0.0313	0.0256	0.0315	0.0299	0.0305	0.0313	0,0273
0.0212	0,0277	0.0272	0.0278	0.0241	0.0310	0.0325	0.0278	0.0257	0,0262
0.0169									
0.0210									
0.0181									
0.0206									
0.0184									
0.0214									
0.0203									
0.0205									
0.0199									
0.0190									

POSITIVE CONTRAST (Running speed)

RECIPROCAL MEDIAN LATENCIES - Experimental

DAYS

1	2	3	4	5	6	7	8	9	10
0.5848	0,5135	0.7195	0.8000	0.8678	1.0649	1.2270	1.1706	1.2055	1,5090
0.3571	0,0858	0.3515	0.3503	1.1431	1.1429	1.1308	1.1242	0.9496	0,9594
0.0822	0,0487	0.0666	0.0949	0.8563	0.8673	0.8265	0,9250	0.8812	1,0309
0.1434	0,1838	0.1997	0.1889	1.0990	1.1905	1.0118	1.3487	1.0984	1,2823
0.1058	0,0555	0.1042	0.0698	0.4758	0.5459	0.3555	0.4097	0.7576	0,6391
0.2547									
0.1775									
0.2883									
0,3008									
0,8884									
0.9623									
0.9103									
0.9956									
0.9785									
1,0842									

RECIPROCAL MEDIAN LATENCIES -- Control

DAYS

1	2	3	4	5	6	7	8	9	10
1.3611	1,5877	1.3799	1.4425	1.2270	1.3900	1.3158	1.4505	1.2446	1,2353
0.7568	1,1824	1.1365	1.1123	1.0585	0.8860	1.1570	1.0640	1.1905	1,1824
0.9700	1,0310	0.9116	1.0990	1.0081	0.8728	0.9965	0.8796	1.0955	0,8658
1.0784	1,1706	1.0773	1.0994	1.2917	1.1519	1.1174	1.1838	1.3810	1,1432
0.5092	0,4808	0.3813	0.6234	0.4112	0.5099	0.4808	0.4497	0.5150	0,5760
0.9351									
1.0905									
0.9773									
1.0753									
0.9993									
0.9621									
1.0123									
1.0055									
1.0853									
1.0005									

POSITIVE CONTRAST (Response speed)

RECIPROCAL MEDIAN LATENCIES - Experimental

DAYS

1	2	3	4	5	6	7	8	9	10
0.0129	0,0118	0.0179	0,0213	0.0193	0.0212	0.0258	0,0237	0.0217	0,0247
0.0195	0,0197	0.0275	0,0276	0.0303	0.0315	0.0306	0.0286	0.0290	0,0274
0,0252	0,0161	0.0162	0,0301	0,0364	0.0325	0.0345	0.0342	0.0315	0,0299
0,0142	0,0357	0.0406	0.0283	0.0252	0.0231	0,0258	0.0250	0.0240	0,0241
0.0156	0,0190	0.0211	0.0206	0.0242	0.0255	0.0237	0.0256	0.0269	0,0205

0.0175
0.0205
0,0246
0.0256
0.0271
0,0268
0,0281
0.0274
0.0266
0,0253

RECIPROCAL MEDIAN LATENCIES - Control

DAYS

1	2	3	4	5	6	7	8	9	10
0,0235	0,0249	0.0280	0.0299	0.0260	0.0261	0.0238	0.0253	0.0280	0,0288
0.0292	0,0267	0.0296	0,0265	0.0284	0.0263	0.0253	0,0243	0.0241	0,0245
0.0339	0,0301	0,0357	0.0345	0.0315	0.0333	0.0303	0.0328	0,0306	0,0357
0.0241	0,0237	0.0222	0.0233	0.0219	0.0233	0.0253	0,0238	0.0241	0,0237
0.0170	0,0173	0.0219	0.0179	0.0198	0.0173	0.0166	0,0175	0.0185	0,0211

0.0256
0,0245
0.0275
0,0264
0,0255
0,0253
0,0243
0,0247
0.0250
0.0268