EMOTION AS A DETERMINANT OF INTEGRATIVE LEARNING: AN EXPERIMENTAL STUDY

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Summary—Twenty emotionally reactive and twenty non-reactive rats were tested under two conditions of shock. The rats were required to learn the "rule" that food in a trough must not be eaten for 3 sec after delivery, under pain of being shocked; after this period the food could be eaten without any punishment being incurred. Eating without punishment was called the "normal" reaction; eating with shock was called the "psychopathic" reaction, and not eating, even when safe, was called the "dysthymic" reaction. These terms were applied because of an explicit analogy with human behaviour along the lines of the writer's general theory of personality. It was predicted on the basis of this theory that non-emotional rats should show more "normal" reactions, emotional rats more "abnormal" reactions, under both levels of shock. It was found that emotional rats did in fact show more "dysthymic" and more "psychopathic" reactions than did non-emotional rats. Strong shock reduced both types of "abnormal" reaction in both strains equally, as compared with weak shock. It was considered that the results supported the theory, and that alternative theories did not suffice to explain the observed facts.

INTRODUCTION

THE writer has developed a nosological and aetiological theory of neurotic behaviour which emphasizes two independent factors (Eysenck, 1957). The first of these is emotionality or neuroticism; this is conceived as a largely inherited lability of the autonomic nervous system (Eysenck, 1960a; Eysenck and Prell, 1951; Shields, 1962). The second factor is extraversion, conceived as a pattern of behaviour based on a largely inherited tendency of the central nervous system to generate inhibitory potentials speedily and lastingly (Eysenck, 1957; Eysenck, 1960a; Shields, 1962). This two-dimensional system is related to traditional psychiatric nosology through the postulate that dysthymic disorders (anxiety states, phobias, obsessions, reactive depressions) are predominantly found in the high-neuroticism, high-introversion quadrant, while hysterical and particularly psychopathic disorders are found predominantly in the high-neuroticism, high-extraversion quadrant (Eysenck and Claridge, 1962). Normal control groups, randomly sampled, would of course be found to cluster round the origin.

The prediction relating type of neurotic behaviour to extraversion is derived along the following lines. (1) Inhibition impedes the development of conditioned responses; consequently extraverts, who generate strong cortical inhibition, will condition poorly, while introverts, who generate weak cortical inhibition, will condition well (Eysenck, 1957). The evidence in favour of this hypothesis is reasonably impressive and extends both to normal and to neurotic groups; a discussion of the general theory and of the evidence relating to it, has been given elsewhere (Eysenck, 1962).

Anxieties, phobias and other dysthymic symptoms are regarded as conditioned fear reactions; it follows from this that (2) introverts are more liable than extraverts to form these conditioned reactions, being the more easily conditionable group. Here the assumption is made, of course, that events in the external world, which produce the traumatic happenings

which constitute the UCS in this connexion, are distributed randomly over extraverts and introverts alike; undue concentration of such events on one group or the other would seriously disturb this prediction, but is not perhaps very likely on *a priori* grounds. (It is curious that so little is known about the actual distribution of traumatic events in the life histories of neurotics.)

It is also argued, following Mowrer (1950), that the process of socialization is based fundamentally on a conditioning paradigm; social mores are acquired through Pavlovian conditioning, i.e. the acquisition of anxiety responses to socially disproved acts (Eysenck, 1960b). It follows from this conception (3) that extraverts are less liable than introverts to form these social conditioned responses, being the less easily conditioned group. Psychopaths, moral imbeciles of all kinds, and some kinds of criminals would therefore be expected to be extraverted in their behaviour pattern, and to condition poorly in specially arranged experimental situations. (This hypothesis should not be over-extended to apply to all criminals; the argument has been well presented by Trassler (1962) and will not here be repeated. Eysenck (1960b) has also discussed this point.)

Many deductions are possible from this general framework. The general evidence on the relation between extraversion-introversion, on the one hand and dysthymia-psychopathy, on the other, is sufficiently strong to suggest that the theory is not very vulnerable on this point.* Another type of deduction, also already mentioned, relates to the high conditionability of introverts and dysthymics, as compared with extraverts and psychopaths/ hysterics; here also a considerable body of evidence supports the prediction. A third type of prediction follows from the writer's drug postulate (Eysenck, 1963a), according to which C.N.S. stimulant drugs have introverting properties, while C.N.S. depressant drugs have extraverting properties. It would follow that psychopaths and patients suffering from other types of behaviour disorders, if given stimulant drugs for any length of time, should be shifted in the introverted direction, and thus become more "normal" and loose their anti-social behaviour patterns. Studies by Shorvon (1945, 1947), Hill (1947), Bradley and Bowen (1941), Lindsley and Henry (1942), all support this prediction, as well as the corollary that depressant drugs should have an adverse effect. A fourth type of prediction relates to the type of therapy best suited to neurotic patients; the arguments in favour of certain forms of behaviour therapy, and the evidence relating to its superiority over alternative methods, suggest that here also the theory is not falsified (Eysenck, 1960c; 1963b). These are only some of the lines of evidence on which empirical support is available, but it is not the main purpose of this paper to discuss this body of evidence; we are more concerned with the solution of a theoretical problem posed by the interaction of emotionality and extraversion.

It is easy to see that dysthymics are pre-destined to fall prey to autonomic conditioned responses, not only because of their introversion, which makes them condition more readily, but also because of their neuroticism (emotional lability) which leads to their responses to traumatic situations (and of course to subtraumatic situations as well) being particularly strong. Savage and Eysenck (1963) have argued that differences in emotionality

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* Apart from the Anglo-American literature summarized by KNAPP (1962), it has also been found in other cultures that similar relations obtain. Thus BOLADOS (1962) in Chile studied 19 hysterics and 32 dysthymics, as well as a control group of 60 normals. The scores of the 3 groups were as follows.

	N	*E*
Normals	17·2	24·9
Hysterics	34·5	27·8
Dysthymics	32·8	17·9

All the relevant differences were fully significant statistically.

in organisms confronted with identical stimulus situations have equal behavioural effects to differences in strength of stimuli when presented to organisms of equal emotionality; thus in two animals equal in emotionality a strong shock produces greater effects than a weak shock and similarly a shock of given strength produces greater effects in an emotional than in an unemotional animal. Experimental evidence presented by Savage and Eysenck (1963), Levine and Broadhurst (1963) and Owen (1963) supports this hypothesis. It follows that for people high on emotionality, events which would not be traumatic to people low on emotionality, would prove to be traumatic, thus making them more liable to the acquisition of conditioned autonomic responses.

With extraverts and psychopaths the position is not quite as simple. It might be argued that for people high on extraversion and also high on emotionality these two propensities would pull in opposite directions. High extraversion, and the accompanying lack of conditionability, would make the conditioning of socially desirable responses more difficult, thus contributing the essential causal feature to the anti-social behaviour of the hysteric and the psychopath. High emotionality, however, for the reasons just given, would facilitate conditioning, thus pushing the organism away from the psychopathic position. We would thus be led to discriminate between two kinds of extraversion. One of these (E_C) refers to the constitutional component, which would not be affected by different degrees of emotionality; this can be measured in terms of such fundamental measures of inhibition as reminiscence, satiation, vigilance etc. The other component (E_B) refers to the behavioural manifestations in every-day life, as measured and recorded in questionnaires like the M.P.I., or in case histories. This component would be expected to be profoundly influenced by events in the individual's history (his reinforcement schedule), and could hardly fail to show the influence of high or low degrees of emotionality. This distinction, which recalls Pavlov's stress on differentiating genotypic and phenotypic personality (Gray, 1963) has been elaborated in detail elsewhere (Eysenck, 1960d); it leads to certain testable predictions.

One such prediction would lead us to expect that measures of E_C would show the hysteric/psychopathic group as far removed from the normal in the extraverted direction as the dysthymic group is in the introverted direction; measures of E_B, however, should show a displacement of the hysteric/psychopathic group in the direction of lesser extraversion, i.e. towards the normal. This follows from our hypothesis that emotionality and extraversion are pulling in opposite directions in psychopaths and hysterics, the former increasing the effects of experiences conducive to conditioning, the latter decreasing them. For introverts, however, no such contradiction exists, both emotionality and introversion pulling in the direction of greater conditioning. It is certainly true that on the M.P.I. hysterics and psychopaths are much less clearly differentiated from normals in the extraverted direction, than are dysthymics in the introverted direction (Eysenck, 1959; Knapp, 1962). Similarly, the evidence suggests that when measures of E_C are used this disproportion disappears; under these conditions the clinically diagnosed groups are equidistant from the normal controls (Eysenck and Claridge, 1962).

This theory may be further developed along the following lines. It has often been argued that anxiety has drive properties (Spence, 1956) and in view of the high correlation between such measures of anxiety as the M.A.S., and measures of neuroticism, such as the M.P.I., it seems that the experimental support for this notion would also apply to slightly different conceptions like emotionality and neuroticism. If we accept this possibility, then we would be justified in arguing in this fashion: drives multiply with existing habits to produce behaviour; in the psychopath the existing habits are antisocial. Consequently, emotionality

(=high drive) should potentiate these antisocial habits to produce even more strongly psychopathic behaviour than would be found in persons with lower degrees of emotionality. We may put this whole conception rather naively in the following manner. Behaviour is a function of the relative strength of temptation and conscience. Conscience is the (conditioned) product of the socialization process; temptation is a combination of primary and secondary drives. In a conflict situation, emotion is aroused and increases the existing drive level (Brown, 1961). This increased drive potentiates whatever habits are predominant in the habit family hierarchy. In other words, where anti-social responses are habitual (as in the psychopath) added drive will make his behaviour even more psychopathic; where highly conforming responses are habitual (as in the dysthymic) added drive will make his behaviour even more conforming. The function of emotionality, then, would be to exaggerate the conforming or antisocial behaviour of an organism beyond that which would be demonstrated at lower levels of drive. If overly conforming and antisocial behaviour are both non-integrative (as defined below), then the effect of emotion should be to make behaviour less integrative. The same argument would apply to a situation in which an attempt was being made to develop conforming behaviour through conditioning; "introverted" rats should acquire overly conforming responses, "extraverted" rats, through failure to develop socialized responses, should show anti-social behaviour. Emotion should increase both types of non-integrative behaviour. The purpose of the experiment described below is to test this hypothesis.

Experimental design†

The apparatus used in this experiment has been described in detail by Mowrer and Miller (1942). It consisted of a box-like compartment, 33 in. long, 20 in. high, and 6 in. wide, with a glass front covered with gauze to form a one-way screen and a floor consisting of a metal grill through which electric shock could be administered. Light was provided by two 40 W bulbs mounted 8 in. from each end and 18 in. above the grid, giving an illumination measured at 25 candles/ft^2. Food, in the form of pellets containing equal amounts of rat diet and sucrose, and weighing 0·05 g each could be made available in a small trough at the left end of the apparatus. The experimental animals, which will be described later, were subjected to a procedure directly copied from Mowrer and Ullman (1945); in describing this procedure I shall paraphrase their own account. The animals, maintained on a feeding schedule so that they were 22½ hr hungry, were put into the apparatus and taught to go to the food trough whenever a buzzer, whose intensity at floor level was 88·5 dB (ref. 0·0003 dynes/cm^2), sounded. This buzzer lasted for 2 sec, and just as it terminated a pellet of food was dropped into the trough. Buzzer and food were presented at regular minute intervals, 10 times per day over a period of 10 days. All rats learned to run to the trough as soon as the buzzer sounded, as shown in Fig. 1.

At this point of training a "Rule" was introduced, to the effect that the rats were henceforth not to touch the food for a period of 3 sec after it appeared in the trough. "One may think of this as a kind of rat 'etiquette', according to which it was not 'polite' to eat until the prescribed length of time had elapsed. We could not, of course, 'tell' our subjects

about this rule, but we established conditions which were calculated to teach it to them" (Mowrer and Ullman, 1945). On the day immediately following the 10 day training period just described, each of the rats was put into the apparatus as usual; but the conditions were now such that if a rat took the food within the forbidden 3 sec interval, it received 2 sec of shock (either 0·1 or 0·3 mA through a matched impedance power source) from the floor of the apparatus. "In other words, the rats were 'punished' for eating within the tabu period but were free to eat, without punishment, if they waited a minimum of 3 sec after the food appeared" (Mowrer and Ullman, 1945). The punishment came immediately after the tabu period ended, i.e. 3 sec after the food was presented. The buzzer, which during the preliminary training had the single function of calling the animals to the food trough and which terminated just as the food appeared, now remained on until the end of the tabu period. If the animal did not take the pellet during this period, the buzzer was turned off, its termination serving as an "all-clear" signal. On the other hand, if an animal sinned and took the food during the tabu period, the buzzer remained on throughout this period and until the shock was administered, i.e. the buzzer stayed on until the shock had been applied for 2 sec. The buzzer and shock then went off together. (A detailed explanation of the reasons for this particular arrangement is given in the Mowrer and Ullman article referred to above). Each animal received 10 trials per day for 10 days, with an inter-trial interval of 60 sec.

Animals can react in three ways to this experimental situation. (1) They can take the food within the danger period and get shocked; Mowrer calls this the "delinquent" pattern, but we shall prefer to call it the "psychopathic" reaction. (2) They can avoid the shock by not eating at all: Mowrer calls this the "neurotic" pattern, but we shall prefer to call it the "dysthymic" reaction. (3) They can wait the 3 sec and then eat, thus avoiding the shock, but nevertheless obtaining the food. Mowrer calls this the "normal" reaction, or the "integrative" reaction; the psychopathic and dysthymic reactions he calls "nonintegrative". A discussion of the nomenclature adopted here will be given later in this paper.

Mowrer studied the behaviour of his animals as a function of the length of time elapsing between violation of the tabu and shock administered as a punishment; in addition to the 3 sec interval also used in the present experiment he used a 6 sec and a 12 sec interval. In this experiment we did not vary the time element, but varied instead two other parameters: (1) strength of shock, as noted, and (2) constitutional emotionality of the rat. This second variable was controlled by using the Maudsley Reactive and Non-Reactive Strains bred in the Animal Psychology Laboratories and numbered 163f and 163g, respectively, in the Catalogue of Uniform Strains (Laboratory Animals Centre, 1958). An account of this psychogenetic experiment has been given by Broadhurst (1960) who describes how the strains were selected on the basis of their emotional defecation in the open-field test (Hall, 1934) and gives details of their husbandry. The particular animals here used came from the 19th generation of this selection experiment: approximately half of them had served as subjects some 50 days previously in a short experiment in which their responses to noise stimulation under the influence of various steroid hormones had been observed. We thus have four groups of 10 animals each, viz. strong shock (S) × emotionally reactive (R); weak shock (s) × emotional (R); strong shock (S) × non-emotionally reactive (r); weak shock (s) × non-emotional (r), making a total of 40 animals. The four groups of animals will be referred to as RS, Rs, rS and rs. Age and previous experience were randomly distributed over the four groups. Within each group, half the animals were male, half female; average age was $160·0 \pm (SD)$ 2·9 days at the start of the experiment which was run in two successive batches.
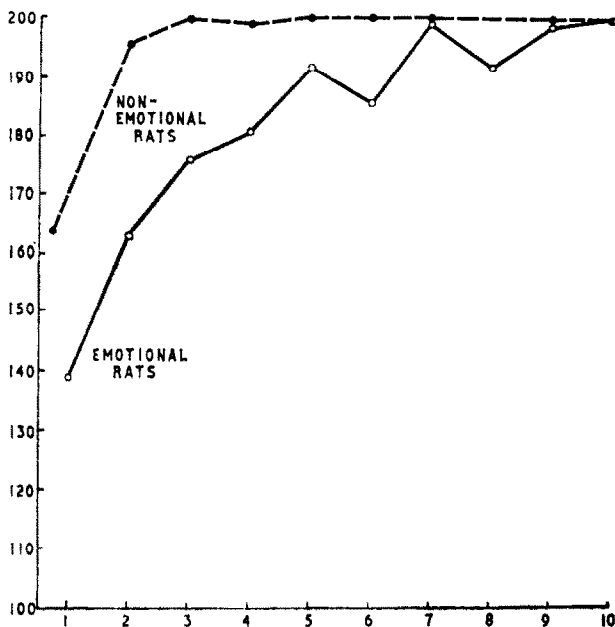
FIG. 1. Speed of acquisition of food-eating habits by emotional and non-emotional rats.
Ordinate shows the total number of pellets eaten on ten successive days (abscissa).

Results

Figure 1 shows the rate of acquisition of the food eating habit for the emotional and non-emotional rats. A non-eating response was defined in terms of a delay of 53 sec: after this period the food was removed and the next trial initiated. It will be seen that the emotional rats eat less than do the non-emotional ones; the former eat on 1819 occasions out of 2000, the latter on 1959 occasions. In order to test this difference, an angular transformation was undertaken of the proportions (in order to obviate the manifest inhomogeneity of variance); an analysis of variance showed the differences to be $P < 0.01$ level. (In view of the curious statistical difficulties to which the experimental design gives rise, all statistical calculations are discussed in the Appendix specially prepared by Dr. P. Slater. In the body of the paper only P levels will be cited, to obviate duplication).

Figure 2 shows the development of the "normal" reactions in the four sub-groups over the 10 days of testing. It will be seen that the non-emotional strain (r) shows a larger number of normal reactions than the emotional strain (R), and that strong shock (S) as compared with weak shock (s) produces more normal reactions. Starting from much the same level of reactivity, the four groups end in the order: $r, S; r, s; R, S$; and R, s. Figure 3 shows the the inverse of this, i.e. the development of the "abnormal" reactions. Here the order of the four groups at the end of the experiment is of course inverted.

Analysis of variance shows that both the "strength of shock" effect and the "emotionality" strain effect are significant, while their interaction is not. It might be argued that as the two groups of animals $(R$ and $r)$ are differentiated in terms of their original learning of the food taking response, analysis of covariance might be more appropriate. This is a doubtful point; it is not that the R animals learn the "normal" reactions more slowly than the r animals, but rather that they do not learn at all, or even unlearn this type of reaction.
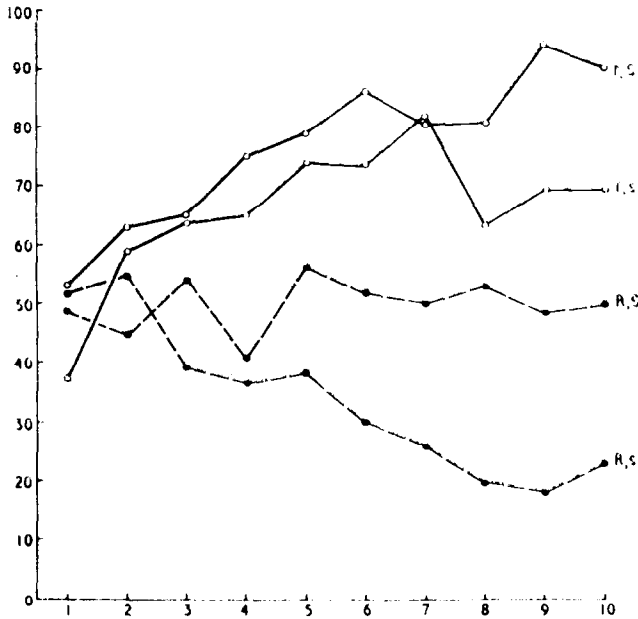
FIG. 2. Development of the integrative reaction in the four sub-groups used. (*R* and *r* refer to emotionally reactive animals; *S* and *s* to strong and weak shock respectively). Ordinate shows the number of responses in the four sub-groups on ten successive days (abscissa).
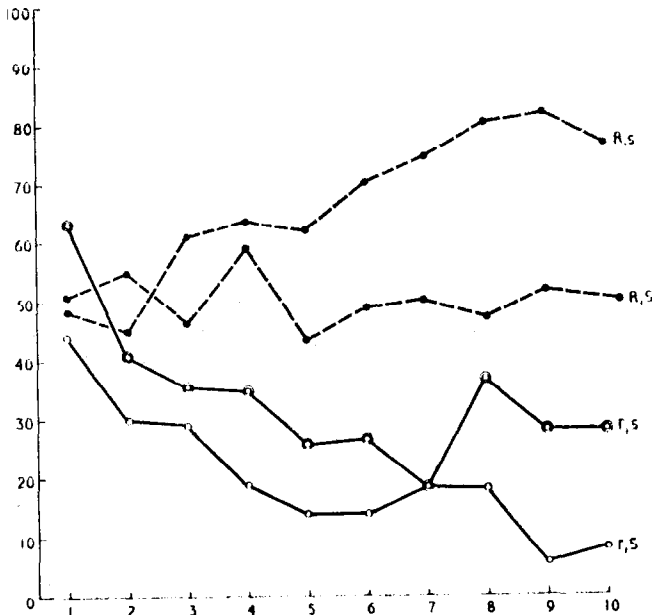

FIG. 3. Development of the non-integrative reaction in the four sub-groups used. Ordinate shows the number of responses in the four sub-groups on ten successive days (abscissa).

And on the other hand, they do in fact learn the "abnormal" reactions, while the *r* animals unlearn these reactions. Nevertheless, an analysis of covariance was in fact undertaken, demonstrating that even when original learning was held constant, emotionality and shock still emerged as significant variables at the 1 per cent level, and without interaction. These results may therefore be accepted as clearly demonstrated in this experiment.

We have demonstrated that "abnormal" responses occur more frequently in emotional than in non-emotional animals. Figures 4 and 5 show in detail the breakdown of these responses into the dysthymic and the psychopathic ones, at shock levels of 0·1 and 0·3 mA respectively. At the former level, it will be seen that psychopathic reactions remain at their original level (non-emotional rats) or increase dramatically (emotional rats). Dysthymic reactions disappear in the non-emotional and remain fairly steady in the emotional rats. At this level of shock, then, training favours psychopathic over dysthymic reactions.
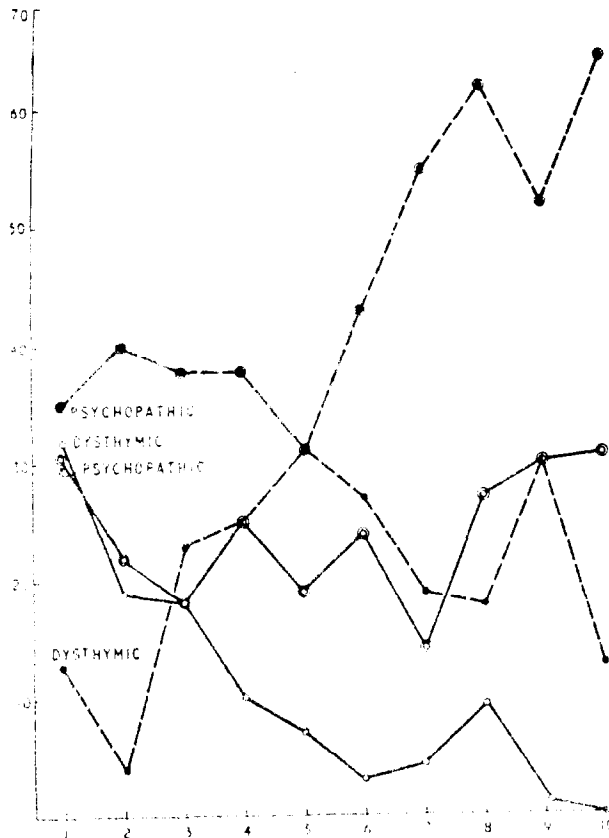

FIG. 4. Development of dysthymic and psychopathic reactions of *R* (broken lines) and *r* (unbroken lines) groups under weak shock. Ordinate shows the number of responses on ten successive days (abscissa).
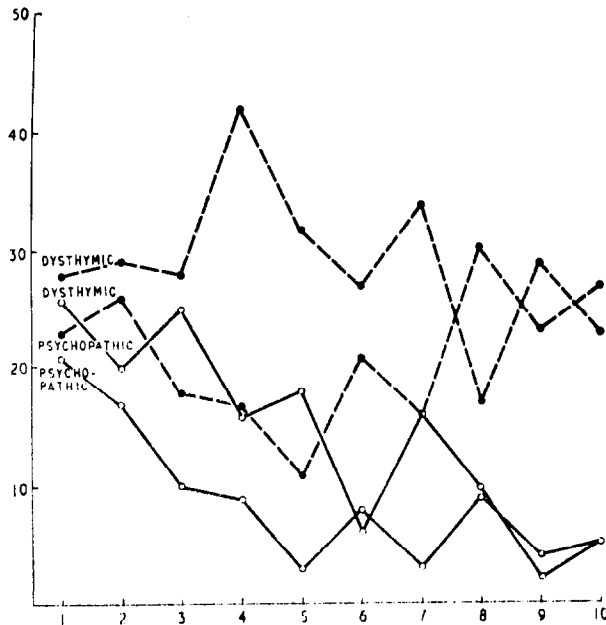
FIG. 5. Development of dysthymic and psychopathic reactions of R (broken lines) and r (unbroken lines) groups under strong shock. Ordinate shows the number of responses on ten successive days (abscissa).

At the higher shock level, both types of reaction remain at the same level for the emotional rats, while both decline for the non-emotional rats. These results are unexpected from at least one point of view. It might have been thought that dysthymic reactions would have been pre-eminent among emotional animals, shock being more traumatic for the animals (Eysenck, 1963); after all, the increase in shock level has the effect of lowering dysthymic reactions more than psychopathic reactions. The expectation, however, is clearly falsified; psychopathic reactions are if anything more prominent among emotional then among non-emotional rats. The statistical significance of these trends is assessed in the Appendix.

Discussion

Our experiment has demonstrated the following facts. (1) Emotional rats acquire normal, "integrative" reactions more slowly, and abnormal, "non-integrative" reactions more quickly than do non-emotional rats. (2) "Psychopathic" reactions are more easily acquired than are "dysthymic" reactions, both by emotional and by non-emotional rats. (3) Shock level does not interact with these trends, which are observed at both the shock levels used. (4) Strong shock promotes the acquisition of "normal" reactions as compared with weak shock. (5) Strong shock interferes with psychopathic rather than with dysthymic reactions, as compared with weak shock. (6) Emotional rats are somewhat slower in acquiring simple food-eating habits in the experimental training period.

These results speak rather strongly against a type of interpretation which might on *a priori* grounds have much in its favour. It might have been thought that rats learn the "normal" reaction because of the reinforcement applied; the greater the reinforcement,

the better the learning. So far results are in agreement. It might then have been thought that emotional animals, reacting more to the shock, would acquire the "normal" habit better; for them the weak shock should, roughly speaking, have the same "punishment value" as the strong shock for the non-emotional rats. But the opposite is true; the emotional rats learn the "normal" reaction much less well than do the non-emotionals. One might of course here bring in the Yerkes-Dodson Law (Broadhurst, 1957; 1959) and suggest that the learning, being difficult, was beyond the point on the drive/complexity curve where increase in drive increased efficiency of learning. But this would be difficult to maintain; increase in the severity of shock improves learning in both emotional and non-emotional animals to an equal extent. Also in the extremely simple original learning situation (Fig. 1) the emotional animals are significantly slower, although this task is surely well short of the point of inflection on the Yerkes-Dodson curve. For this situation, some fear-interference hypothesis is obviously more appropriate.

Along the same lines of thought, one might have imagined that dysthymic reactions would be characteristic of the emotional animals, psychopathic ones of the non-emotionals. This, too, is not true; if anything the analysis shows the opposite. Clearly, therefore, no single-factor theory along orthodox lines can account for the facts; what is required is a two-factor theory. Such a theory has been outlined at the beginning of this article; it posits effectively that rats in both the emotional and the non-emotional groups differ from each other along the dimension of extraversion-introversion (E_C, of course, not E_B, although it may become possible in due course to obtain measurements of E_B also in rat populations). "Introverted" rats are predisposed to react with dysthymic behaviour, "extraverted" rats are predisposed to react with psychopathic behaviour. (By "extraverted" and "introverted", in this context, we mean animals situated on the factor continuum to one side or the other, respectively, of an arbitrary point which roughly divides the continuum into two equal parts.) Emotionality is conceived as a drive factor which multiplies with the existing predisposition and the acquired habit systems and thus makes performance in one direction or the other more vigorous; this would be our explanation of the fact that high emotionality actually lowers the number of "normal" reactions, as was indeed predicted when the experiment was planned.

The explanation given above might of course be attacked as being circular were it not that our general theory makes it possible to make other predictions which can be confirmed. Thus "extraverted" rats should show alternation behaviour to a stronger degree than "introverted" rats (Sinha, Franks and Broadhurst, 1958). Rats which in this experiment show "psychopathic" behaviour should show much alternation, while rats showing "dysthymic" behaviour should show little alternation. This and other similar predictions are at the moment being followed up, and it is hoped eventually to establish strains by bidirectional selection for "extraversion" and "introversion" in rats, very much in the same way that it has been possible to do with respect to "emotionality" or "neuroticism" (Broadhurst, 1960; 1962). Furthermore, a direct application of the writer's drug postulate (Eysenck, 1963a) should give predictable results, in that stimulant drugs should promote dysthymic behaviour, depressant drugs, psychopathic behaviour. Our theory, therefore, is by no means circular; it generates several classes of testable predictions, and is thus subject to falsification. Whether it does in truth mediate a connexion between human conduct and rat behaviour, or whether we are here merely dealing with a far-fetched analogy, cannot of course, be decided on the basis of available data; it will require much concentrated work before any decision become possible.

STATISTICAL APPENDIX

P. SLATER

The training period

DURING this period the rats could either A eat the pellet or B not eat it while it is in the trough. The records give the number of A and B responses per rat in 10 trials for 10 successive days and the total of the latencies of the A responses per rat per day. Averages of the crude measures are:

	Strain	
	r	R
Proportion of A responses per rat over the entire training period	98·0%	91·0%
Average latency on the last day	1·92 sec	3·45 sec.

The two measures used for comparing the strains—the proportion of A responses, $\phi(A) = A/(A+B)$, during the entire training period, and the mean latency, 1, for the ten trials on the last day—both have extremely skew distributions. Accordingly the angular transformation $\phi = \sin^{-1}\sqrt{p(A)}$ was used for the proportions, and the logarithmic transformation $t = \log 1$ for the latencies when proceeding to test significance. The results are combined in Table A 1.

TABLE A 1. ANALYSIS OF THE VARIANCE OF ϕ AND t

Source	Sums of squares		Degrees of freedom
	ϕ	t	
Total observed variation	2885·3	1·0752	39
Between strains	910·1	0·1061	1
Between sexes	2·8	0·0102	1
Interaction sex : strain	32·8	0·0109	1
Residual variance			
between sub-groups	267·1	0·0474	4
within sub-groups	1672·5	0·9006	32

Both measures show significant differences between the two strains, but not between the sexes; and there is no significant sex : strain interaction. The residual variance between the sub-groups is also insignificant, showing that the animals given different levels of shock during testing were evenly matched.

The testing period as a whole

During this period the rats could either a take the pellet after the buzzer stops, b take it without waiting, or c leave it. The records give the number of each kind of response per rat in 10 trials for 10 successive days as before.

The r rats gave a much higher proportion of a responses than the R rats, but the proportion of b to c responses is approximately the same in both strains. It varies in the same way with the shock level. The averages are:

	r	R
Proportion of a responses, $p(a)$ per rat over the entire training period	71·1%	41·8%
Proportion of b responses, $p(b)$ at shock level 0·1	69·9%	69·2%
at shock level 0·3	38·2%	42·3%

Here $p(a)$ is defined as $a/(a+b+c)$ and $p(b)$ as $b/(b+c)$. The significance of the differences is tested in the analysis of variance in the following section.

The differences between the two strains in ϕ and t observed during the training period do not account for the difference in $p(a)$ observed during the testing period. To investigate the connexion $p(a)$ was transformed analogously with $p(A)$ into $\psi = \sin^{-1}\sqrt{p(a)}$ though the transformation is not so necessary as $p(a)$ varies to about the same extent in both strains and does not have a skew distribution.

The correlations between ϕ, t and ψ within the strains are:

	ϕ	t	ψ
t		0·757	0·287
			0·088

The two correlations involving ψ are not significant, nor is the multiple correlation, 0·349, of ψ with ϕ and t combined. These findings virtually preclude the possibility that the difference between the strains in ψ can be attributed to the previously noted differences in ϕ and t. A more precise proof of independence can be obtained by making two analyses of the regression of ψ on ϕ and t, firstly ignoring the differences between the strains and secondly taking them into account, i.e. using a test of the significance of the difference between the adjusted means. The residual left by the first analysis as the variance of ψ independently of ϕ and t is 4790·0 with 37 d.f.; the residual from the second is 3706·5 with 36 d.f., mean square 103·0. The difference, 1083·5, which is highly significant (F = 10·52, P < 0·01) demonstrates that strain affects ψ independently of ϕ and t.

Progressive changes during the testing period

The important general changes to be found in the performance of the rats during the ten days of testing are shown in Table A 2.

TABLE A 2. TOTAL NUMBER OF RESPONSES OF DIFFERENT KINDS GIVEN BY RATS OF EACH
STRAIN DURING THE 10 DAYS OF TESTING

Strain:	Response					
	a		b		c	
	r	R	r	R	r	R
Day						
1	90	101	52	58	58	41
2	122	100	39	66	39	34
3	129	93	28	56	43	51
4	140	78	34	55	26	67
5	153	95	22	42	25	63
6	159	82	32	64	9	54
7	163	76	17	71	20	53
8	144	73	36	92	20	35
9	163	66	34	75	3	59
10	159	73	36	91	5	36

The three measures a, b and c cannot vary independently: changes in one are compensated by changes in the others, for they are connected by the relationship $a+b+c = n$ in any set of n trials.

Thus the 20 rats of the r strain give 200 responses altogether on the first day: 90 are a, 52 b and 58 c. In the following days, as their a responses increase, their b and c responses both decline; but after the seventh day, when there is no further increase in a, the b responses rise while the c responses continue to fall. Their behaviour may be interpreted as evidence that as a group they become more expert at obtaining food throughout the period. They either learn relatively quickly how to obtain it without a shock, by waiting till the buzzer stops; or else more slowly to tolerate the shock and obtain the food without waiting.

But the rats of the R strain are on the whole no more successful in obtaining food at the end of the period than at the beginning. The major change is from a to b behaviour, while c behaviour fluctuates unsteadily. It seems as if they gradually become inured to the noise and the shock and give up waiting.

The counts of the three modes of behaviour a, b or c per rat per day form three variables which can be included in one analysis because they are commensurate empirically and by definition. As they are connected by the linear relationship $a+b+c = 10$ each set of three such entries has only two degrees of freedom. So the complete set of 1200 entries (3 per rat per day for 40 rats on 10 successive days) has a general mean fixed a priori at 10/3 and a variance about it with 800 degrees of freedom.

These modes of behaviour provide the only direct source of variance; the other main sources—strain, sex, shock level, the remaining differences between rats and the differences between days—only contribute to the variation through their interactions with the modes.

TABLE A 3. ANALYSIS OF THE VARIANCE IN MODES OF BEHAVIOUR DURING THE TESTING PERIOD

Part 1. Differences between rats over the period as a whole

Source	Mean square	d.f.
Total observed variation between rats:	105·14	80
1. Between modes	1648·54*	2
First order interactions of modes with:		
2. Strain	647·31*	2
3. Sex	65·98	2
4. Shock level	310·70*	2
Second order interactions of modes with:		
5. Strain and sex	117·50	2
6. Strain and shock level	16·58	2
7. Sex and shock level	3·69	2
Third order interactions of modes with:		
8. Sex, strain and shock level	69·42	2
Residual variance between rats of the:		
same strain and sex tested under the same conditions	41·43	64

Part 2. Variations in their behaviour on different days

	Mean square	d.f.
Total observed	54·64	720
9. First order interactions of days with modes	12·74*	18
Second order interactions of days and modes with:		
10. Strain	24·69*	18
11. Sex	5·97	18
12. Shock level	7·06	18
Third order interactions of days and modes with:		
13. Strain and sex	6·29	18
14. Strain and shock level	6·26	18
15. Sex and shock level	8·18†	18
Fourth order interactions of days and modes with:		
16. Strain, sex and shock level	4·46	18
Residual variance between days in the records of individual rats	4·46	576

* P < 0·01.
† 0·05 > P > 0·01.

The complete analysis of variance, Table A 3, falls into two parts. The first relates to the variation between the individual means of the rats over the whole period, and the second to their variation about their own means from day to day. They need to be separated because their residual errors differ.

The variances in Part 1 which are significantly higher than the residual arise from sources 1, 2 and 4. The means to which they relate are shown in Table A 4.

TABLE A 4. MEAN PROPORTION OF EACH KIND OF RESPONSE IN:

Mode	(1) All Cases	(2) Strain R	r	Shock level 0·1	0·3
a	56·48	41·80	71·10	49·65	63·30
b	25·00	33·50	16·50	34·95	15·05
c	18·52	24·65	12·40	15·40	21·65

(1) Demonstrates that there are significant differences in the proportions of a, b and c responses, (2) that the proportions in the two strains differ significantly, and (4) that the proportions at the two shock levels differ also. To show that the strain : mode interaction depends on the difference in the proportion of a responses and not on the relative proportion of b to c responses in the two strains the sum of squares 1294·6 can be separated into its appropriate parts, 1283·3 for the interaction of a with (b+c) and 11·3 for the interaction of b with c, of which only the first is significant.

The variances in Part 2 of Table A 3 which are significant at the 0·01 level are (9) and (10). They show that the frequencies of a, b and c responses vary significantly from day to day and that their fluctuations do not follow the same course for both strains. These are the frequencies given in Table A 2 and discussed above.

Two further sources of variance (12) and (15) are on the borderline of significance, one first within the 0·05 limit and one just beyond. The nature of these interactions is shown in Table A 5.

TABLE A 5. PROPORTION OF a RESPONSES

In sex	At shock level	During the first 3 days	During the last 3 days
M	0·1	49·7	39·0
M	0·3	46·0	68·3
F	0·1	52·3	48·3
F	0·3	63·7	70·3

There is an increase in a responses at shock level 0·3 which is not paralleled at level 0·1; and it is more marked among the male rats than among the females. Apart from here, the only significant effect of shock level is the one shown at (4), and sex has no significant effects.

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