

THE PSYCHOPHYSIOLOGICAL BASIS OF INTROVERSION-EXTRAVERSION

JEFFREY A. GRAY

Institute of Experimental Psychology, Oxford, England

(Received 4 February 1970)

Summary—On both psychological and physiological grounds it is suggested that the hypothesis in Eysenck's theory of introversion-extraversion attributing greater conditionability to the introvert should be replaced by the hypothesis that the introvert is relatively more sensitive to punishment and to frustrative nonreward. The data on which this conclusion is based stem chiefly from the study of eyeblink conditioning in Man as a function of personality, and from the study of the physiological locus of action of the extraverting drug, sodium amobarbital, in animals. It is suggested that the physiological basis of introversion includes, besides the Ascending Reticular Activating System, an inhibitory system comprising the orbital frontal cortex, the medial septal area and the hippocampus. This system is able to carry out the essential psychological functions believed by Eysenck to underlie introversion-extraversion. A new conception of neuroticism as reflecting degree of sensitivity to both reward and punishment is also proposed.

THE PURPOSE of this paper is to suggest a new conception of the nature of the psychological variables underlying the dimensions of personality of introversion-extraversion and neuroticism (Eysenck, 1957, 1967; Cattell, 1966; Cattell and Scheier, 1961), and to propose a new hypothesis as to the physiological basis of introversion.

It is, of course, impossible to discuss the psychological and physiological nature of introversion without taking as one's starting point the extensive and important contributions to this field of study by Eysenck (1957, 1967) and his collaborators. Unfortunately, the sheer volume of this work precludes any but the simplest summary of it. In attempting such a summary, I shall begin with what I take to be the problems to which Eysenck has addressed himself, sketch the main lines of his solution to these problems, and point out what seems to me to be a link in this solution which requires alteration.

EYSENCK'S THEORY OF INTROVERSION AND NEUROTICISM

The starting point for Eysenck's theory of introversion and neuroticism lies in the relation of these two dimensions of personality to each other and also to a cluster of psychiatric disorders, called by Eysenck (1957) "dysthymic", and a second cluster of offences against society which he calls "psychopathic". These relations are set out in Fig. 1. The problems they pose for the student of personality, and to which Eysenck has repeatedly addressed himself over a period of more than twenty years (e.g. Eysenck, 1947, 1957, 1960, 1964, 1967; Eysenck and Rachman, 1965; Eysenck and Eysenck, 1968), are these: (1) What are the psychological and/or physiological variables which result in the high susceptibility of individuals with high degrees of neuroticism *both* to dysthymic disorders *and* to the commission of psychopathic offences? (2) What are the psychological and/or physiological variables which differentiate neurotic individuals along the dimension of introversion-extraversion (which is quite independent of the dimension of neuroticism) and which cause

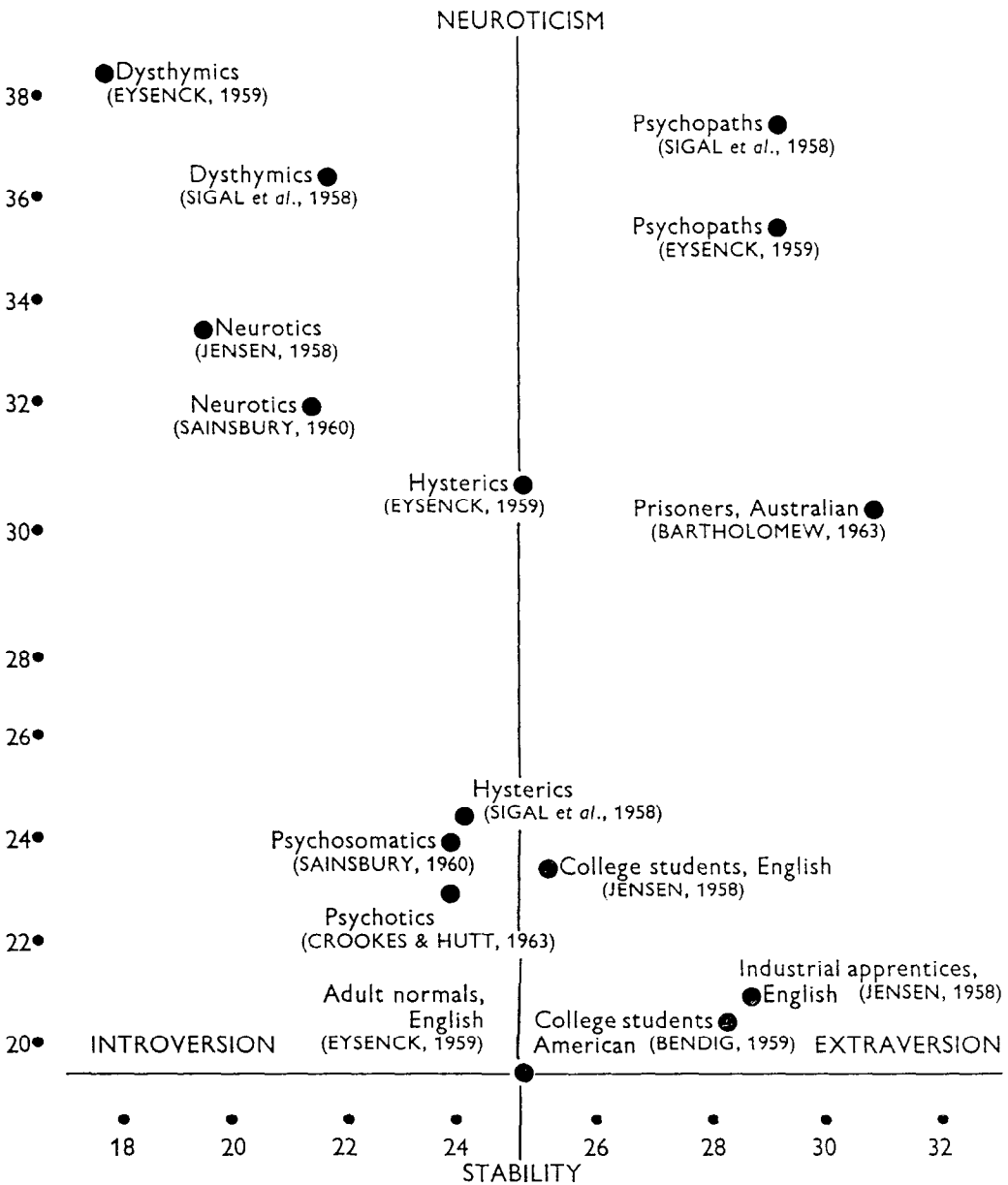


FIG. 1. Relationship of dimensions of introversion–extraversion and neuroticism to dysthymic neuroses and psychopathic behaviour. From Eysenck (1967).

the *introverted* neurotic to be susceptible to the *dysthymic* disorders, but the *extraverted* neurotic to display anti-social behaviour of a *psychopathic* kind? Although there have been many changes in detail, the broad lines of Eysenck's solutions to these problems have remained fairly constant over the years; they are set out, in a highly simplified manner, in Fig. 2.

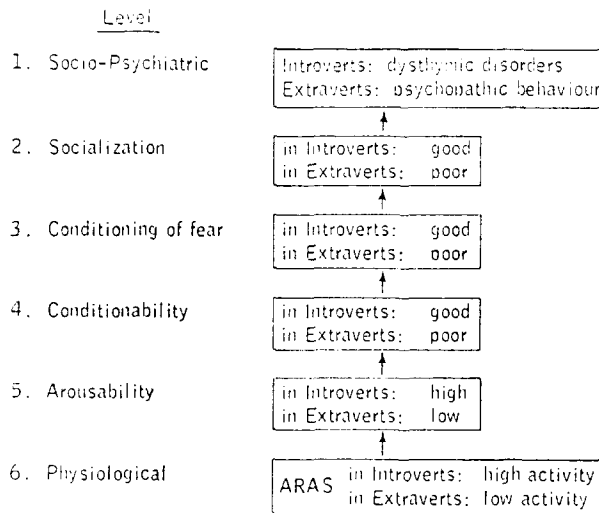


FIG. 2. Basic structure of Eysenck's theory of introversion-extraversion. See text for further explanation.

In brief commentary on Fig. 2, the following points must be made.

(1) The first link in Eysenck's chain of explanation is to describe dysthymic neuroses as disorders of *over*-socialisation and psychopathic behaviour as a disorder of *under*-socialisation (e.g. Eysenck and Rachman, 1965). In the introverted neurotic the establishment of the conscience (treated by Eysenck, e.g. 1964, as a cluster of classically conditioned fear reactions) has proceeded so effectively that the individual concerned is disabled in adulthood by a variety of manifestations of his conditioned fears (in the form of phobias, obsessions and compulsions, frank anxiety states, reactive depression, or other dysthymic symptoms). In the extraverted neurotic, by contrast, there has been a failure of socialisation, resulting in a lack of feeling of responsibility towards society and the various forms of anti-social behaviour (juvenile delinquency, sexual delinquency, lying, careless or drunken driving, or more serious breaches of the law: Eysenck, 1964) displayed by the psychopath.

(2) The role of neuroticism in this process is to raise the general intensity of emotional reactions. Neuroticism is treated by Eysenck (e.g. 1967) as equivalent to degree of emotionality. It is the combination of strong emotions with the neurotic introvert's over-socialised conscience which leads him into hospital; and, correspondingly, the combination of strong emotions with the lack of a conscience which leads the extraverted neurotic into trouble with the law.

(3) Psychologically speaking, Eysenck supposes that, under conditions likely to produce emotional activation, highly neurotic subjects will have higher levels of general drive (Hull, 1943). This is a move also employed by Spence (1956) in his treatment of the personality trait of manifest anxiety (Taylor, 1956).

(4) Physiologically speaking, Eysenck (e.g. 1967) suggests that degree of neuroticism is a direct function of the reactivity of the autonomic nervous system.

A similar dual level of explanation—psychological and physiological—is used by Eysenck (1957, 1967) to deal with introversion.

(5) He proposes that introverts form the conditioned reflexes composing the conscience with greater ease than do extraverts because they are, in general, more highly conditionable.

The greater *conditionability* of the introvert is in turn attributed by Eysenck either to a relatively lower susceptibility to processes of *inhibition* or to a relatively higher level of general *arousal* or to both (Eysenck, 1957, 1967).

(6) Recently, Eysenck (1963, 1967) has also offered a physiological hypothesis as to the nature of introversion: he proposes that degree of introversion is a direct function of the level of activity in the ascending reticular activating system (ARAS: Moruzzi and Magoun, 1949; Magoun, 1963).

Figure 2, then, attempts to set out, in summary form, these various levels of Eysenck's important theoretical edifice: the problems with which he has been concerned, his description of the relevant dimensions of personality, his hypotheses as to the psychological variables underlying these dimensions, and finally his hypotheses as to the physiological systems responsible for the psychological phenomena. The evidence he has marshalled for these various levels of explanation, impressive as it is in both scope and quality, can be found in the various works of his which have been cited.

CONDITIONABILITY

The present analysis takes as its point of departure Eysenck's assumption that the introvert forms the conditioned fear reactions composing the conscience with especial ease because he is in general more readily conditionable. This assumption, which is of central importance in Eysenck's account of the behavioural differences between introverted and extraverted neurotics, has been subjected to a considerable amount of experimental investigation (Eysenck, 1965). Much of this work has been equally concerned with the similar hypothesis advanced by Spence (1956, 1964), according to which those high on the trait of "manifest anxiety" would form conditioned responses more easily than those low on this trait. As pointed out by Eysenck (1965), the trait of susceptibility to anxiety, measured by the Manifest Anxiety Scale (Spence, 1956, 1964; Taylor, 1956) is loaded on both the Eysenckian dimensions of introversion and neuroticism, though the correlation with neuroticism is somewhat higher (Fig. 3). Thus Eysenck would agree with Spence (though for different reasons) in expecting those high in anxiety to form conditioned responses with particular ease.

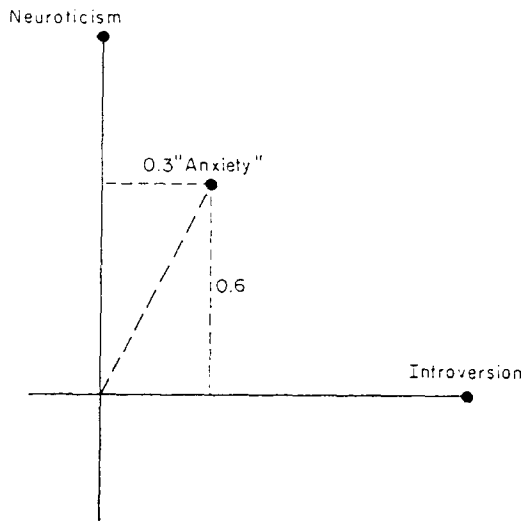


FIG. 3. Relation of dimensions of introversion-extraversion, neuroticism and anxiety.

These different conceptions have been the cause of considerable controversy, both theoretical and empirical in content (Spence, 1964; Jones, 1960; Eysenck, 1965), but recently the picture has become a little clearer. As far as the dimension of introversion is concerned, it appears that introverts do form conditioned responses (in particular, the conditioned eyeblink response) more easily than extraverts, *but only under certain conditions* (Eysenck and Levey, 1967; Eysenck, 1967). Exactly the same is true in the case of the trait of manifest anxiety: those high on this trait also form conditioned eyeblink responses more readily than those low on it, but under some conditions only (Spence, 1964; Ominsky and Kimble, 1966). The nature of these conditions is, in the case of both sets of results, crucial for the arguments that follow.

In the case of introversion, the important experiments were conducted by Eysenck and Levey (1967) in a study of eyeblink conditioning in groups of extreme introverts and extraverts. Three variables were investigated: reinforcement schedule (50 per cent random vs. 100 per cent), UCS intensity (an air-puff of 3 p.s.i. vs. one of 6 p.s.i.) and CS-UCS interval (400 msec vs. 800 msec). In the case of each of these three variables, Eysenck (1966, 1967) predicts that the first-named alternative should favour the introvert.

For the variable of reinforcement schedule, this prediction follows from Eysenck's (1957, 1967) use of the concept of inhibition. He supposes that the nonreinforced trials on the partial reinforcement schedule will cause an increment of inhibition, and that this will be greater in the extravert owing to his postulated greater susceptibility to inhibitory phenomena. In this way, the extravert's level of performance should fall below that of the introvert. However, Eysenck and Levey's (1967) results did not support this prediction: reinforcement schedule did not have significantly different effects on introverts and extraverts. Given the difficulties attached to the concept of inhibition as it is used in Eysenck's theory of extraversion (Gray, 1967a), the failure of this one of Eysenck's predictions is not altogether surprising. The remaining two predictions were both successful, and both were based on the construct of arousal (Eysenck, 1963, 1967; Gray, 1964b, 1967a): it is therefore on this construct that we shall concentrate for the rest of this paper.

In making these two predictions, Eysenck (1966, 1967) followed arguments which have been successfully used to make predictions for the Soviet dimension of strength of the nervous system (Gray, 1964a) and which have been related by the writer (Gray, 1964b) to Western ideas of arousal. In the case of UCS intensity the argument runs as follows. The more highly aroused introvert will, relative to the extravert, act as though he amplifies stimulation. His conditioning with a UCS of an objective intensity which is lower than that necessary for optimal performance will, therefore, fall below optimal to a smaller extent than will the conditioning shown by the extravert. Figure 4, taken from Eysenck and Levey's (1967) work, bears this prediction out. The argument for CS-UCS interval makes direct use of the findings from Teplov's laboratory on reaction time as a function of strength of the nervous system. As reported by Nebylitsyn (see Gray, 1964a), the increase in reaction time which occurs as stimulus intensity decreases is smaller in individuals with a weak nervous system, who *ex hypothesi* (Gray, 1964b, 1967a) are individuals of high arousability. Therefore, the highly arousable introvert should be less hampered than the extravert if CS-UCS interval is made smaller than the optimum for good conditioning. Again, Fig. 4 shows that this prediction was borne out by the facts of Eysenck and Levey's (1967) experiment.

In the case of Spence's (1956) theory of anxiety, the important experiments are those from Kinible's laboratory (Ominsky and Kimble, 1966; see also Spence, 1956, 1964). These

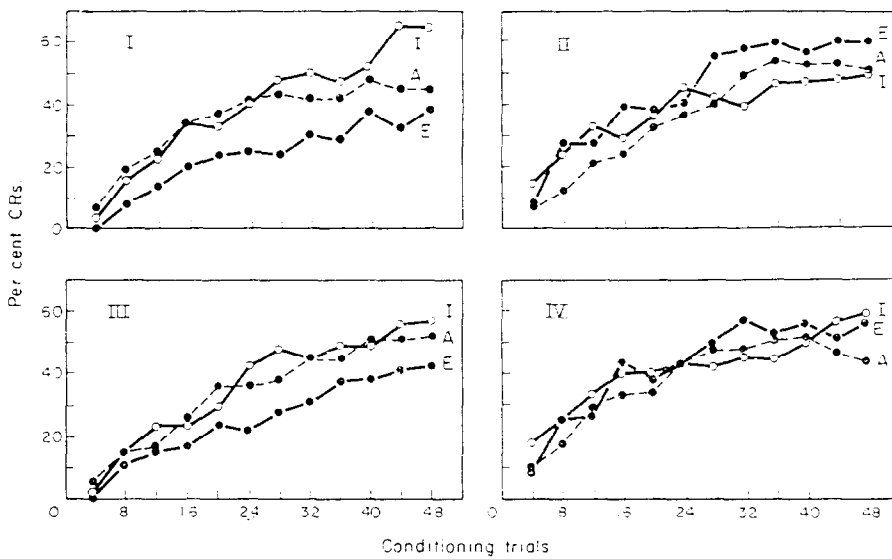


FIG. 4. Eyeblink conditioning in introverts (I), ambiverts (A) and extraverts (E). I, with low (3 p.s.i.) UCS intensity; II, with high (6 p.s.i.) UCS intensity; III, with short (400 msec) CS-UCS interval; IV, with long (800 msec) CS-UCS interval. From Eysenck and Levey (1967).

show that individuals scoring high on the Manifest Anxiety Scale form conditioned eyeblink responses more easily than low scorers on this scale only if the environment in which the experiments are conducted is relatively threatening. Notice that, since the trait of anxiety is about an equal mixture of introversion and neuroticism (Eysenck, 1965), it is difficult to see how Ominsky and Kimble's (1966) result could have been obtained if either neuroticism or introversion is related to ease of conditioning in a way which is *not* dependent on the degree of threat encountered by the experimental subject. This is a point which will be important in the later development of this paper.

In summary, the eyeblink conditioning experiments just reviewed establish the following points:

- (1) Introverts are better than extraverts at eyeblink conditioning under some conditions, but not all;
- (2) These conditions can be predicted on the hypothesis that introverts are relatively more highly aroused in the experimental situation than extraverts;
- (3) The superiority of the individual high on anxiety—and therefore the *superiority of the introvert*—at eyeblink conditioning depends on the degree of threat he encounters in the experimental environment. (Data contradicting this conclusion have, however, been reported by Piers and Kirchner, 1969.)

It is the first of these conclusions which has most importance for Eysenck's general theory of introversion. The idea that introverts are more highly conditionable than extraverts has to bear a heavy burden within this theory: it is by way of this assumption that the vital behavioural and psychiatric differences between introverted and extraverted neurotics are accounted for (Fig. 2). It is not at all clear that this burden can be carried by the weaker assumption (demanded now by the experimental facts) that introverts condition better than extraverts only *under some conditions*. It is true that, in Eysenck and Levey's

experiment, introverts conditioned better than extraverts under those conditions which were less than optimal for the group as a whole; and one might well argue that, in real life, parental conditioning techniques are unlikely to be optimal very often. But, of course, the non-optimal conditions in Eysenck and Levey's (1967) experiment favoured introverts because they were especially chosen to do so. Had they been *over*-arousing non-optimal conditions rather than under-arousing ones, Eysenck's theory predicts that it is the *extravert* who would have fared relatively well. Thus, since there is no reason to suppose that parental conditioning techniques are more often under-arousing than over-arousing, there is equally no reason to predict the over-socialisation of the introvert which is critical to the whole of Eysenck's theoretical super-structure (Fig. 2).

SENSITIVITY TO PUNISHMENT AND NONREWARD

Faced with this impasse, let us retreat one step. If we accept Eysenck's description of introvert behaviour as over-socialised and of extravert behaviour, correspondingly, as under-socialised; and if we accept his view that the process of socialisation consists in the formation of a cluster of conditioned fear reactions; then we must agree that Eysenck has asked the right question: why do introverts form conditioned fear reactions more strongly than extraverts? We have just rejected the answer: "because they are better at *conditioning*". The only alternative answer is: "because they are more susceptible to *fear*"; and that is the hypothesis proposed in this paper.

Notice that we already have support for this hypothesis in the conclusion, deriving from the Spence and Kimble experiments, that individuals high on anxiety, and therefore also introverted, only form conditioned eyeblink responses better than those low on this trait if the environment in which they are investigated contains some element of threat. Notice also that all the data favouring the hypothesis that introverts are in general more conditionable than extraverts (Eysenck, 1965, 1967) also favour the present hypothesis, since they have all been obtained in *aversive* conditioning situations, mainly that of eyeblink conditioning. The crucial test between the two hypotheses would be, of course, an investigation of the conditioning of introverts and extraverts using non-aversive reinforcement in a definitely unthreatening environment; but, to the writer's knowledge, no such experiment has yet been carried out.

The hypothesis that introversion involves a heightened susceptibility to fear (or to express the same point differently, a heightened sensitivity to punishment and warnings of punishment) has a great deal of face validity. Psychopathic behaviour in the extraverted neurotic is easily regarded as a tendency to take a reward (by, say, stealing, lying or sexual gratification) without thought for the consequences, i.e. with no fear of punishment*. The recidivism which is such a feature of psychopathic behaviour (Eysenck, 1964) is also most simply regarded precisely as a relative insensitivity to punishment. Conversely, the symptoms of the dysthymic neuroses are in many cases perfectly clear expressions of fear, as for example in the phobias and the anxiety state. In other cases it requires very little skill to discern the fear which lies less obviously behind the neurotic symptoms. A good example is the obsessional ritual or rumination. This may be performed in a state of apparent calm, but it is usually sufficient to prevent the patient from complying with the urge to perform the ritual for overt signs of fear, often intense, to become evident. Indeed, the obsessive-compulsive symptoms bear all the marks of an active avoidance response (Gray, in press, a).

* A number of writers have made similar suggestions concerning psychopathy, but not necessarily in connection with extraversion, see Hare (1968) for references; and also Hetherington and Klinger (1964).

The occurrence of ulcers, among other psychomatic symptoms, in persons of an introverted neurotic disposition (Fig. 1) is also not unexpected on the present hypothesis, since it is known from animal studies (Sawrey, Conger and Turrell, 1956; Gray, in press, a) that ulcers may be induced in conflict situations.

The only syndrome among the dysthymic neuroses requiring more complicated analysis in the light of the hypothesis advanced here is the neurotic or "reactive" depression (Mayer-Gross, Slater and Roth, 1960; Eysenck, 1960). In fact, however, one of the main strengths of the present position is that it can make very good sense out of the fact that individuals suffering from this illness have personality profiles which are identical with those of individuals suffering from the other major dysthymic neuroses, i.e. phobias, anxiety state and obsessive-compulsive neurosis (Cattell and Scheier, 1961). This strength arises from the "fear = frustration" hypothesis (Gray, 1967b, in press, a), according to which the behavioural effects of punishment and of the omission of anticipated reward ("frustrative nonreward") are functionally and physiologically very similar, and perhaps identical. The evidence for this hypothesis is rather strong (Gray, 1967b, in press, a; Wagner, 1966; Miller, 1964), and it derives from sources quite independent of the arguments offered here. Now Mayer-Gross *et al.* (1960) note that "as a rule such states (i.e. reactive depression) are produced by a sudden critical change, the death of a wife, the breaking of a love-affair, and are much less frequently precipitated by a gradual accumulation of miseries." These conditions are naturally described as the removal of accustomed sources of reward. If we accept the fear = frustration hypothesis, we would expect that those individuals who are most susceptible to punishment would also be most susceptible to the effects of frustrative nonreward. There is, in fact, direct evidence (Savage and Eysenck, 1964) from animal experiments that rats which are particularly susceptible to the effects of punishment (in this case, Maudsley Reactive rats; Broadhurst, 1960) also show a bigger frustration effect in the Amsel and Roussel (1952) double runaway. On the hypothesis advanced here, in Man it is the introvert who is particularly susceptible to punishment. It is also the introvert, therefore, who should be particularly susceptible to the effects of frustrative nonreward and who, among other things, should be likely to develop a reactive depression.

Notice that the present hypothesis does not rely as heavily as Eysenck's on differences in the course of socialisation in introverts and extraverts: in the foregoing, we have had regard to the presumed effects of differing degrees of sensitivity to punishment *in the adult*. Differences in conditionability, as postulated by Eysenck, do not obviously mediate predictions for the adult (that is, without calling on the process of socialisation) in the same way. However, the present hypothesis continues to predict the same socialisation differences as are postulated by Eysenck, since greater sensitivity to punishment in the introverted neurotic child should lead to a firmer development of the conscience to the extent that punishment or withdrawal of reward are used as parental techniques of control of undesirable behaviour.

In further considering the hypothesis advanced here, we must bear in mind that the extraversion factor is in fact made up of two highly correlated sub-factors (Eysenck and Eysenck, 1963), one of "impulsiveness" and one of "sociability" or "social extraversion". In the light of the present hypothesis we would propose that the extravert acts on the spur of the moment because his behaviour is relatively more determined by potential rewards in his environment, and he is relatively less likely to operate the "stop" of passive avoidance in the face of potential punishment. His greater liking for people can be understood if we recall that people are the most important dispensers of both rewards and punishments for other people; therefore, those who are less sensitive to punishment are more likely to seek

them out. The optimism of the extravert, contrasted with the introvert's pessimism, is equally understandable as an example of insensitivity to potential punishment.

Relatively direct evidence for differences between introverts and extraverts in their modes of reaction to threatening stimuli comes from experimental work on personality differences on the "repression-sensitisation" trait (Byrne, 1964; Eriksen, 1966). It has been found that there are rather consistent individual differences in the perception, recognition, learning and recall of threatening stimuli. Some individuals (called "repressors") do worse in all these tasks when threatening stimuli are used than when neutral stimuli are involved; others ("sensitisers") do better with threatening than with neutral ones. The former appear to be extraverts and optimists; the latter, introverts and pessimists (Eriksen, 1966). Thus it seems that the introvert is more likely to notice threatening stimuli, recognise them subsequently, learn about them, and recall them.*

THE PHYSIOLOGICAL BASIS OF INTROVERSION

But the strongest support for the present hypothesis comes from a re-consideration of what is known about the *physiological* basis of introversion. As we have seen (Fig. 2), Eysenck (1963, 1967) has proposed that it is variation in the degree of activity taking place in the ARAS which underlies degree of introversion; and this is a very natural suggestion if one supposes that, psychologically speaking, introversion depends on the level of general arousal. But consider the significance of two of the major experimental facts known about the physiological basis of introversion: (1) that the barbiturate drugs (in particular, sodium amylobarbitone) and alcohol have an extraverting effect on behaviour (Eysenck, 1967), and (2) that lesions to the frontal cortex have a similar effect (Willett, 1960). Consider in particular what is known about the effects of these treatments on the behaviour of animals.

It is clear from a large number of experimental studies that the behavioural effects of both amylobarbitone ("amytal") and alcohol are specific with respect to the reinforcement contingencies governing the animal's behaviour. The effects of amytal have been studied in more detail, so we shall confine the discussion to this drug. Amytal is known to reduce the effects of punishment (Miller, 1959) and of frustrative nonreward (Miller, 1964; Wagner, 1966; Gray, 1967b, 1969, in press a; Ison and Pennes, 1969) on behaviour. This has been shown for passive avoidance, extinction and the partial reinforcement acquisition and extinction effects. There is no impairment, however, of simple reward learning, nor of active avoidance in the Miller-Mowrer shuttle-box, which is actually improved (Kamano, Martin and Powell, 1966).

The nature of active avoidance learning requires some further discussion. It has been proposed elsewhere (Gray, in press, a) that this kind of learning is in fact reinforced by activity in the same positive reinforcing brain system which is involved in ordinary reward learning, a view which has also been expressed by Olds and Olds (1964). Furthermore, the two-way active avoidance involved in the shuttle-box is in fact a conflict between approach to the now-safe side of the apparatus and passive avoidance of this same side, since the animal has just been shocked there. Thus it is to be expected that amytal will enhance active avoidance in the shuttle-box in exactly the same way that it increases the likelihood that

* Dana and Cocking (1969) have recently reported that the correlation between a repression-sensitization scale and extraversion (-0.38) is lower than that with neuroticism (+0.89), both the latter being measured by the Maudsley Personality Inventory. As will appear subsequently (see Fig. 7) the fact that sensitizers are both introverted *and* neurotic is to be expected on the theory advanced here.

literature (e.g. Killam, 1962) that this *is* the chief site of action of the barbiturates. It is, of course, likely that action at the level of the midbrain reticular formation is important in producing the anaesthetic and sedative effects of the barbiturate drugs. But in a typical psychological experiment in which a rat is injected with 15–20 mg/kg of sodium amytal, and in which the behavioural effects of the drug discussed above are manifested, the experimental animal is not normally sedated. If it is, for example, running an alley towards a food or water reward, it continues to run fast and perform in an alert and well-motivated manner, sometimes even better than placebo-injected controls. In the study of human personality, too, it is the extraverting effect of amytal in doses well short of those needed for sedation or anaesthesia which has attracted the attention of experimental psychologists (Eysenck, 1967). Thus the interesting behavioural effects of small doses of amytal may well arise because of an action at a different level of the nervous system than that which is responsible for the sedative and anaesthetic effects of relatively large doses of the barbiturate drugs.

I have proposed elsewhere (Gray, in press, c) that this other level is to be found in the hippocampus and in the cluster of cells in the medial septal area which acts as the pace-maker for the hippocampal theta rhythm (Stumpf, 1965); and I have summarised there the evidence for this suggestion. Included in this evidence are some of my own recent experiments which indicate that the behavioural effects of frustrative nonreward are critically mediated by the occurrence of a hippocampal theta rhythm, and that amytal blocks the behavioural effects of frustrative nonreward by raising the threshold for this hippocampal theta response (Gray, in press, c).

One important feature of this proposal for the site of action of amytal is that it immediately offers a rationale for the similarity between the effects of this drug in Man and the effects of damage to the frontal cortex in Man. This is because, in primates, the highest controlling centre for the septo-hippocampal system just delineated appears to lie in the orbital frontal cortex. Lesions to the frontal cortex in rats and monkeys, for example, produce the same pattern of improved shuttle-box active avoidance (Albert and Bignami, 1968), impaired passive avoidance and impaired extinction of once-rewarded behaviour which is produced by lesions to the septal area and lesions to the hippocampus (see reviews by Grossman, 1967; McCleary, 1966; Douglas, 1967), as well as, of course, by injections of sodium amytal. Furthermore, in a specific comparison between the effects of septal and frontal lesions in the rhesus monkey, Butters and Rosvold (1968) showed that lesions to the *medial* septal area (containing the pace-maker cells for the hippocampal theta rhythm) were similar in their effects on behaviour to lesions to the orbital frontal cortex.

Thus the extraverting effects of both injections of amytal and frontal lesions readily fall into place if we make the following assumptions:

(1) High degrees of introversion represent high levels of sensitivity to punishment and to frustrative nonreward, as reflected experimentally by strong tendencies towards passive avoidance and extinction of once-rewarded behaviour;

(2) Physiologically, sensitivity to punishment and to nonreward reflects the degree of activity in the system just described, involving the orbital frontal cortex, the medial septal area, and the hippocampus, and the occurrence of the hippocampal theta rhythm;

(3) Amytal mimics the effects of damage to the orbital frontal cortex in virtue of a depressant action on the medial septal cells which act as the pace-maker for the hippocampal theta rhythm.

Thus we arrive at the conclusion that *it is activity in this frontal cortex-medial septal area-hippocampal system which determines the degree of introversion*: the more sensitive or the more active this system is, the more introverted will the individual be.

AROUSABILITY AND SENSITIVITY TO PUNISHMENT

Now, as we saw above, Eysenck derives the notion of higher conditionability in the introvert from a more fundamental difference in the excitation-inhibition balance postulated to underlie the dimension of introversion-extraversion: that is to say, the introvert may be conceived of as relatively more highly aroused than the extravert. There is good evidence in support of the view that introverts and extraverts do, in fact, differ in their chronic level of arousal, or arousability (Eysenck, 1967; Gray, 1967a); so that it would be in the interests of parsimony if we could now relate differences in susceptibility to punishment to differences in arousability in the same way that Eysenck relates conditionability to arousability.

One way of doing this is to start from the fact that any stimulus, if it is made sufficiently intense, may act as a punishment; and then to recall that differences in arousability may be regarded as differences in the degree to which individuals amplify (if they are at the high arousal pole of the continuum) or dampen (at the low arousal pole) stimulation (Gray, 1964b 1967a). It must follow that, as any physical stimulus is increased in intensity, the point at which it becomes punishing will be reached sooner, the more highly aroused the individual, i.e. (*ex hypothesi*), the more introverted he is. Direct evidence for the introvert's tendency to avoid intense stimulation is reviewed by Eysenck (1967). In this way, then, the greater susceptibility to punishment of the introvert, relative to the extravert, proposed in this paper, may be derived from the same fundamental substrate of introversion-extraversion which is postulated in Eysenck's theory: the introvert is more highly aroused than the extravert and is *therefore* more susceptible to punishment.

The derivation of heightened susceptibility to punishment from the introvert's postulated higher level of arousal may be matched very naturally at the physiological level. I have argued above that the physiological basis of introversion consists in activity in the frontal cortex-medial septal area-hippocampal system whose chief function appears to be that of inhibiting maladaptive behaviour, i.e. behaviour followed by punishment or frustrative nonreward. But the links between this system and the ARAS are very close:

(1) There is good evidence that the occurrence of a theta rhythm in the hippocampus depends on input from the midbrain reticular formation to the medial septal area (Stumpf, 1965); and also good evidence that the hippocampus exerts an inhibitory influence on activity ascending from the midbrain reticular formation to the thalamic level of the ARAS (Adey, Segundo and Livingston, 1957; Livingston, 1959) and to the cerebral cortex (Redding, 1967). It seems very likely, therefore, that the ARAS and the septo-hippocampal system responsible for the hippocampal theta rhythm (Gray, *in press*, c) function as a negative feedback loop. That is to say, increased activity in the ARAS results in an increase in hippocampal activity (indicated first by the initiation of a theta rhythm and then by an increase in the frequency of this theta rhythm as reticular input increases: Stumpf, 1965), and one result of the increased hippocampal activity is to inhibit any further increase in activity in the ARAS. In this way, for a given sensory input and under given conditions, a temporary equilibrium between reticular activation and hippocampal inhibition is reached.

(2) At the same time, the evidence suggests that the effects of hippocampal inhibition are not confined to the ARAS. Lesions to the medial septal area, which controls the theta

rhythm, and to the hippocampus itself, as well as to the orbital frontal cortex, impair passive avoidance and extinction of once-rewarded behaviour (see Gray in press, c, for review). As suggested elsewhere (Gray, in press, c), the experimental results are best understood on the assumption that these kinds of behavioural inhibition are exerted by the hippocampus and the septal area at times when the hippocampus is displaying a theta rhythm, i.e. at times when it is receiving an important input from the ARAS.

(3) As well as what might be called the "act" inhibition which is involved in passive avoidance and extinction of appetitive behaviour, there is good evidence that the hippocampus and the medial septal area exert an inhibitory influence on sensory input. For the hippocampus, relevant data are reviewed by Douglas (1967) and Kimble (1969). In the case of the septal area, it is clear that loss of sensory inhibition is an important feature of the hyper-irritability syndrome, which follows lesions to this part of the brain (see Grossman, 1967, for review). Rats displaying this syndrome have greater sensitivity to tactile stimuli and a lower threshold for electric shock (Lints, cited by Lorens and Brown, 1967). Septal lesioned rats also show increased reactivity to light (Schwartzbaum, Green, Beatty and Thompson, 1967) and to gustatory stimuli (Beatty and Schwartzbaum, 1967). A connection between the septal hyper-irritability syndrome and disruption of the normal hippocampal theta rhythm is strongly suggested by some experimental results of my own. A total of 21 rats were given small electrolytic lesions in the medial septal area. In most cases the lesion caused some disruption of the hippocampal theta rhythm, which was recorded through chronically implanted bipolar electrodes, both before and after the lesion; but only two rats showed a complete absence of the theta rhythm after the lesion. These were also the only two rats to display hyper-irritability, and to an extremely marked degree.

We see, then, that an increase in the activity of the ARAS is likely to increase the probability that the septo-hippocampal system will initiate inhibitory influences of three kinds: (1) on the ARAS itself; (2) on behavioural acts leading to punishment or frustrative non-reward; and (3) on sensory inputs.* But point (2) is an exact physiological parallel to the hypothesis that susceptibility to punishment and to frustrative nonreward will be greater under conditions of high arousal.

Furthermore, the general architecture of this set of interactions between the ARAS and the septo-hippocampal system—increased arousal leading to both behavioural and sensory inhibition—is remarkably similar to the psychological relationship postulated by Eysenck (e.g. 1957) to lie at the root of the personality dimension of introversion-extraversion. Eysenck has consistently presented a picture of increased *cortical* arousal in the introvert leading to increased *behavioural* inhibition, though he has sometimes used the vocabulary of "arousal" or "excitation" (higher in the introvert) and sometimes that of "cortical inhibition" (higher in the extravert). If we now substitute for "cortical" arousal, the degree of activity in the feedback loop constituted by the ARAS, the orbital frontal cortex, the medial septal area and the hippocampus, we see that there is indeed a considerable amount of evidence that activity in this system leads precisely to the kind of behavioural and sensory (selective*) inhibition so emphasised by Eysenck and his group (e.g. Eysenck, 1957, 1967).

The modified theory of introversion at which we have now arrived is presented in Fig. 6, which should be compared to Fig. 2, displaying Eysenck's theory, whose basic structure we have retained.

* It seems likely that the inhibition of sensory input which results from septo-hippocampal activity is functionally part of a selective attention mechanism. But there is not space to discuss this issue here.

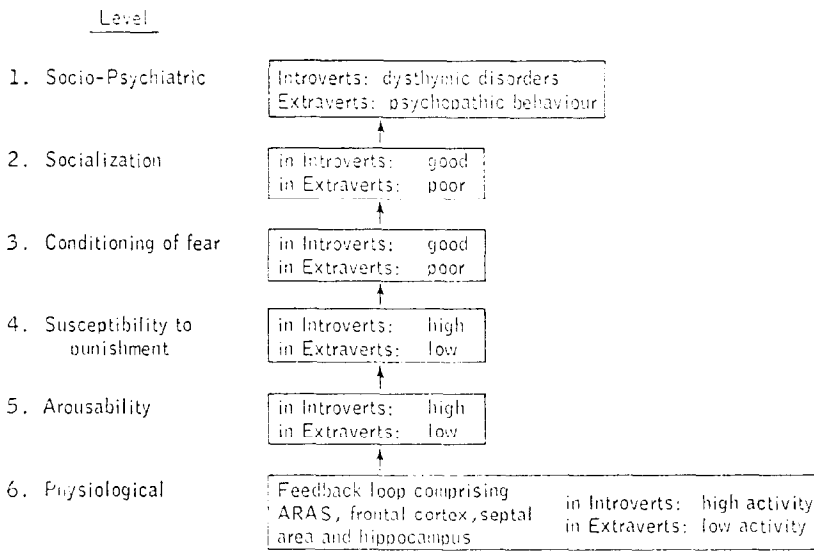


FIG. 6. Proposed modification of Eysenck's theory of introversion-extraversion. Compare with Fig. 2.

THE NATURE OF NEUROTICISM AND ANXIETY

The view of the nature of introversion presented in this paper rather naturally suggests a corresponding view of the nature of neuroticism. As we have seen, Eysenck equates this with emotionality; that is, the more neurotic a person is, the more intense are his emotional reactions of all kinds. There seems to be no reason to quarrel with this formulation. It is at the next step that I would like to propose a second modification to Eysenck's theory. This step concerns the translation of emotionality into terms of the theory of learning. Eysenck (1957, 1967) suggests that we may conceive of emotional arousal as the equivalent of the Hullian construct of drive. However, in recent years there has emerged within learning theory a view of the emotions as essentially modes of reaction to various classes of reinforcers (e.g. Mowrer, 1960; Millenson, 1967; Gray, in press, a, b). In this way, they become different from drives (such as hunger, thirst, sexual arousal, etc.) while no doubt being dependent on drives for their initial formation. Thus, rather than equate emotionality with general drive, as do Eysenck (1957) and Spence (1956), we might be tempted to treat emotionality as degree of sensitivity to *both* reward (including the omission of anticipated punishment) *and* punishment (including the omission of anticipated reward) (Gray, in press a, b).

Such a view has the advantage that it can account very neatly for the relations which exist between position on the Manifest Anxiety Scale (Taylor, 1956) and Eysenck's dimensions of neuroticism and introversion-extraversion (Fig. 3). It is a natural supposition that proneness to anxiety reflects the individual's sensitivity to punishment and threats of punishment (and to nonreward and warnings of nonreward). But, if increasing degrees of neuroticism represent increasing degrees of sensitivity to all classes of reinforcement, and if increasing degrees of introversion represent *increasing sensitivity to punishment as compared with sensitivity to reward* (which we now offer as a more precise statement of the present hypothesis concerning the nature of introversion), then it is precisely the diagonal line between

the dimensions of introversion and neuroticism which will indicate the most rapid increase in absolute level of sensitivity to punishment (Fig. 7); and this is where the Manifest Anxiety Scale in fact lies.* By the same token, of course, the presence of high-anxiety syndromes in the neurotic-introvert quadrant of the Eysenck dimensional map is exactly what we would expect to find.

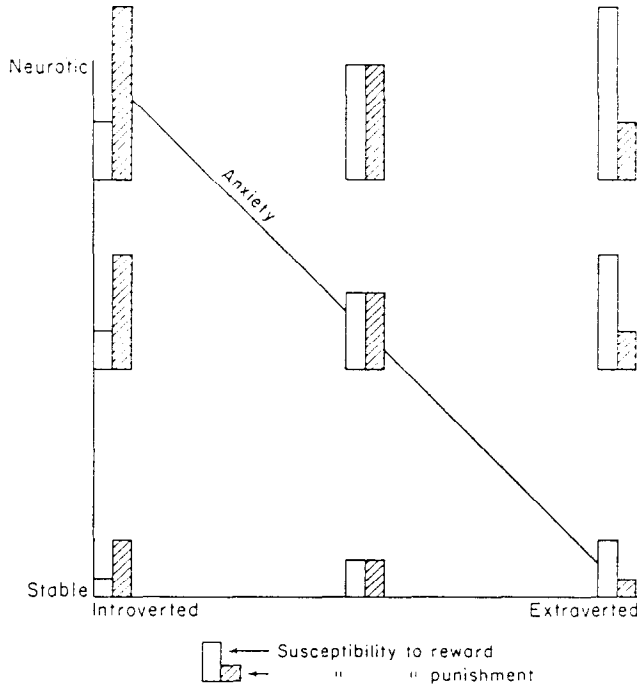


FIG. 7. Proposed relationships of (a) susceptibility to reward and susceptibility to punishment to (b) the dimensions of introversion-extraversion and neuroticism. The dimension of anxiety (diagonal line) represents the steepest rate of increase in susceptibility to punishment. See text for further explanation.

CONCLUSION

Figures 6 and 7 provide a summary of the hypotheses as to the psychophysiological nature of introversion-extraversion and the psychological nature of neuroticism which have been presented in this paper. Essentially the modifications in Eysenck's theory which have been proposed are the following:

- (1) The substitution of the hypothesis that, relative to extraverts, introverts are more susceptible to punishment and frustrative nonreward for the hypothesis that introverts are, in general, more readily conditioned; while continuing to derive susceptibility to punishment from the more basic factor of general level of arousal (Eysenck, 1967; Gray, 1967a).

* Figure 7 has been drawn as though the increase in sensitivity to punishment due to increasing degrees of introversion is in exact step with the increase in sensitivity to punishment due to increasing degrees of neuroticism. In fact, if the Manifest Anxiety Scale (Taylor, 1956) is an efficient measure of sensitivity to punishment and if the relation between this scale and the dimensions of introversion-extraversion and neuroticism is truly as shown in Fig. 3, we must suppose that sensitivity to punishment grows more rapidly with increasing neuroticism than with increasing introversion. This would also agree with Dana and Cocking's (1969) results mentioned in an earlier footnote.

(2) The proposal that the physiological basis of introversion consists, not in activity in the ascending reticular activating system alone, but both in this and in the negative feedback loop, involving the orbital frontal cortex, the medial septal area and the hippocampus, to which the ARAS is coupled.

(3) The suggestion that neuroticism be conceived of as degree of sensitivity to reinforcing events in general, rather than in terms of general drive.

Acknowledgements—This paper was prepared while I held a Medical Research Council Travelling Fellowship in Dr. N. E. MILLER's laboratory, The Rockefeller University, New York. I am grateful to H. J. EYSENCK and C. BRAND for their comments on an earlier version of the manuscript.

REFERENCES

- ADEY W. R., SEGUNDO J. P. and LIVINGSTON R. B. (1957) Corticifugal influences on intrinsic brainstem conduction in cat and monkey. *J. Neurophysiol.* **20**, 1-16.
- ALBERT M. and BIGNAMI G. (1968) Effects of frontal, median cortical and caudate lesions on two-way avoidance learning by rats. *Physiol. Behav.* **3**, 141-147.
- AMSEL A. and ROUSSEL J. (1952) Motivational properties of frustration: I. Effect on a running response of the addition of frustration to the motivational complex. *J. exp. Psychol.* **43**, 363-368.
- BEATTY W. W. and SCHWARTZBAUM J. S. (1967) Enhanced reactivity to quinine and saccharine solutions following septal lesions in the rat. *Psychonom. Sci.* **8**, 483.
- BROADHURST P. L. (1960) Applications of biometrical genetics to the inheritance of behaviour. In *Experiments in Personality*, Vol. I *Psychogenetics and Psychopharmacology* (Ed. H. J. EYSENCK), pp. 3-102. Routledge & Kegan Paul, London.
- BUTTERS N. and ROSVOLD H. E. (1968) Effect of caudate and septal nuclei lesions on resistance to extinction and delayed alternation. *J. comp. physiol. Psychol.* **65**, 397-403.
- BYRNE D. (1964) Repression-sensitization as a dimension of personality. *Progr. exp. Pers. Res.* **1**, 169-220.
- CATTELL R. B. (1966) Anxiety and motivation: Theory and crucial experiments. In *Anxiety and Behavior* (Ed. C. D. SPIELBERGER). Academic Press, London.
- CATTELL R. B. and SCHEIER I. H. (1961) *The Meaning and Measurement of Neuroticism and Anxiety*. Ronald Press, New York.
- DANA R. H. and COCKING R. R. (1969) Repression-sensitization and Maudsley Personality Inventory scores: response sets and stress effects. *Brit. J. soc. clin. Psychol.* **8**, 263-269.
- DOUGLAS R. J. (1967) The hippocampus and behavior. *Psychol. Bull.* **67**, 416-442.
- ERIKSEN C. W. (1966) Cognitive responses to internally cued anxiety. In *Anxiety and Behavior* (Ed. C. D. SPIELBERGER). Academic Press, New York.
- EYSENCK H. J. (1947) *Dimensions of Personality*. Praeger, New York.
- EYSENCK H. J. (1957) *The Dynamics of Anxiety and Hysteria*. Praeger, New York.
- EYSENCK H. J. (1960) Classification and the problem of diagnosis. In *Handbook of Abnormal Psychology* (Ed. H. J. EYSENCK), pp. 1-31. Pitman, London.
- EYSENCK H. J. (1963) *Experiments with Drugs*. Pergamon, New York.
- EYSENCK H. J. (1964) *Crime and Personality*. Houghton Mifflin, Boston.
- EYSENCK H. J. (1965) Extraversion and the acquisition of eyeblink and GSR conditioned responses. *Psychol. Bull.* **63**, 258-270.
- EYSENCK H. J. (1966) Conditioning, introversion-extraversion and the strength of the nervous system. *Proc. Eighteenth Int. Congr. exp. Psychol.* Moscow. Ninth Symposium, pp. 33-34.
- EYSENCK H. J. (1967) *The Biological Basis of Personality*. Charles C. Thomas, Springfield, Illinois.
- EYSENCK H. J. and EYSENCK S. B. G. (1968) *Personality Structure and Measurement*. R. R. Knapp, San Diego.
- EYSENCK H. J. and LEVEY A. (1967) Konditionierung, Introversion-Extraversion und die Stärke des Nervensystems. *Zeitschrift für Psychologie* **174**, 96-106.
- EYSENCK H. J. and RACHMAN S. (1965) *The Causes and Cures of Neurosis*. R. R. Knapp, San Diego.
- EYSENCK S. B. G. and EYSENCK H. J. (1963) On the dual nature of extraversion. *Brit. J. Soc. clin. Psychol.* **2**, 46-55.
- GRAY J. A. (1964a) Strength of the nervous system as a dimension of personality in Man: a review of work from the laboratory of B. M. Teplov. In *Pavlov's Typology* (Ed. J. A. GRAY), pp. 157-287. Pergamon Press, Oxford.
- GRAY J. A. (1964b) Strength of the nervous system and levels of arousal: a reinterpretation. In *Pavlov's Typology* (Ed. J. A. GRAY), pp. 289-364. Pergamon Press, Oxford.

- GRAY J. A. (1967a) Strength of the nervous system, introversion-extraversion, conditionability and arousal. *Behav. Res. & Therapy* 5, 151-169.
- GRAY J. A. (1967b) Disappointment and drugs in the rat. *Advan. Sci.* 23, 595-605.
- GRAY J. A. (1969) Sodium amobarbital and effects of frustrative nonreward. *J. comp. physiol. Psychol.* 69, 55-64.
- GRAY J. A. (in press, a) *The Psychology of Fear and Stress*. Weidenfeld and Nicholson, London; McGraw-Hill, New York.
- GRAY J. A. (in press, b) Learning theory, the conceptual nervous system and experiments in personality. In *Handbook of Modern Personality Theory* (Ed. R. B. CATTELL). Aldine, Chicago.
- GRAY J. A. (in press, c) Sodium amobarbital, the hippocampal theta rhythm and the partial reinforcement extinction effect. *Psychol. Rev.*
- GRAY J. A. and SMITH P. T. (1969) An arousal-decision model for partial reinforcement and discrimination learning. In *Animal Discrimination Learning* (Eds. R. GILBERT and N. S. SUTHERLAND). Academic Press, London. pp. 243-272.
- GROSSMAN S. P. (1967) *A Textbook of Physiological Psychology*. Wiley, New York.
- HARE R. D. (1968) Psychopathy, autonomic functioning, and the orienting response. *J. abnorm. Psychol. Monog. Suppl.* 73, 1-24.
- HETHERINGTON E. M. and KLINGER E. (1964) Psychopathy and punishment. *J. abnorm. soc. Psychol.* 69, 113-115.
- HULL C. L. (1943) *Principles of Behavior*. Appleton-Century, New York.
- ISON J. R. and PENNES E. S. (1969) Interaction of amobarbital sodium and reinforcement schedule in determining resistance to extinction of an instrumental running response. *J. comp. physiol. Psychol.* 68, 215-219.
- JONES H. G. (1960) Learning and abnormal behaviour. In *Handbook of Abnormal Psychology* (Ed. H. J. EYSENCK). Basic Books, New York.
- KAMANO D. K., MARTIN L. K. and POWELL B. J. (1966) Avoidance response acquisition and amobarbital dosage levels. *Psychopharmacologia* 8, 319-323.
- KILLAM E. (1962) Drug action on the brainstem reticular formation. *Pharmacol. Rev.* 14, 175-223.
- KIMBLE D. P. (1969) Possible inhibitory functions of the hippocampus. *Neuropsychologia* 7, 235-244.
- LIVINGSTON R. B. (1959) In *Central Nervous System and Behavior, 2nd Conference* (Ed. M. A. B. BRAZIER), pp. 153-156. Josiah Macy, Jr. Foundation.
- LORENS S. A. and BROWN T. S. (1967) Influence of stimulation of the septal area on visual evoked potentials. *Exp. Neurol.* 17, 86-90.
- MCCLEARY R. A. (1966) Response-modulating functions of the limbic system: Initiation and suppression. In *Progress in Physiological Psychology* (Eds. E. STELLAR and J. M. SPRAGUE), Vol. I, pp. 209-272. Academic Press, New York.
- MAGOUN H. W. (1963) *The Waking Brain*. 2nd edn. Charles C. Thomas, Springfield, Illinois.
- MAYER-GROSS W., SLATER E. T. O. and ROTH M. (1960) *Clinical Psychiatry*. Williams and Wilkins, Baltimore.
- MILLENSON J. R. (1967) *Principles of Behavioral Analysis*. Macmillan, New York.
- MILLER N. E. (1959) Liberalization of basic S-R concepts: Extensions to conflict behavior, motivation and social learning. In *Psychology: A Study of a Science* (Ed. S. KOCH), Study 1, Vol. 2, pp. 196-292. McGraw-Hill, New York.
- MILLER N. E. (1964) The analysis of motivational effects illustrated by experiments on amyobarbitone. In *Animal Behaviour and Drug Action* (Ed. H. STEINBERG), pp. 1-18. Churchill, London.
- MORUZZI G. and MAGOUN H. W. (1949) Brain stem reticular formation and activation of the EEG. *Electroenceph. clin. Neurophysiol.* 1, 455-473.
- MOWRER O. H. (1960) *Learning Theory and Behavior*. Wiley, New York.
- OLDS J. and OLDS M. E. (1964) The mechanisms of voluntary behavior. In *The Role of Pleasure in Behavior* (Ed. R. G. HEATH), pp. 23-29. Harper, New York.
- OMINSKY M. and KIMBLE G. A. (1966) Anxiety and eyelid conditioning. *J. exp. Psychol.* 71, 471-472.
- PIERS E. V. and KIRCHNER E. P. (1969) Eyelid conditioning and personality: positive results from non-partisans. *J. abn. Psychol.* 74, 336-339.
- REDDING F. K. (1967) Modification of sensory cortical evoked potentials by hippocampal stimulation. *Electroenceph. clin. Neurophysiol.* 22, 74-83.
- SAVAGE R. D. and EYSENCK H. J. (1964) The definition and measurement of emotionality. In *Experiments in Motivation* (Ed. H. J. EYSENCK), pp. 292-314. Pergamon Press, Oxford.
- SAWREY W. L., CONGER J. J. and TURRELL E. S. (1956) An experimental investigation of the role of psychological factors in the production of gastric ulcers in rats. *J. comp. physiol. Psychol.* 49, 457-461.
- SCHWARTZBAUM J. S., GREEN R. H., BEATTY W. W. and THOMPSON J. B. (1967) Acquisition of avoidance behavior following septal lesions in the rat. *J. comp. physiol. Psychol.* 63, 95-104.
- SPENCE K. W. (1956) *Behavior Theory and Conditioning*. Yale Univ. Press, New Haven.

- SPENCE K. W. (1964) Anxiety (drive) level and performance in eyelid conditioning. *Psychol. Bull.* **61**, 129-139.
- STUMPF CH. (1965) Drug action on the electrical activity of the hippocampus. *Intern. Rev. Neurobiol.* **8**, 77-138.
- TAYLOR J. (1956) Drive theory and manifest anxiety. *Psychol. Bull.* **53**, 303-320.
- WAGNER A. R. (1966) Frustration and punishment. In *Current Research on Motivation* (Ed. R. N. HABER), pp. 229-239. Holt, Rinehart and Winston, New York.
- WILLETT R. (1960) The effects of psychosurgical procedures on behaviour. In *Handbook of Abnormal Psychology* (Ed. H. J. EYSENCK), pp. 566-610. Pitman, London.