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MECHANISMS OF MOTIVATION IN AVOIDANCE BEHAVIOR

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Abstract. The mechanisms involved in avoidance behavior are discussed. It is assumed that the conditioned stimulus (CS) activates the memory pattern of associations related to the former applications of the unconditioned stimulus (US) and, as a result, produces an undesirable sensory state. This activates another memory pattern of associations related to the avoidance response and the postponement of the US. The performance of the avoidance response discontinues the CS, resulting in inactivation of the first memory pattern; this leads to a removal of the undesirable sensations, i.e., to an improvement in the sensory state. It is suggested that avoidance behavior obeys the same general rules which apply to approach (appetitive) behavior. In both approach and avoidance behavior the instrumental response provides a desirable sensory change (due to obtaining of the desired US in approach behavior and the postponement of the undesired US together with the discontinuation of CS in avoidance behavior). In both cases the response gradually extinguishes when its performance no longer provides the sensory "better-being".

Avoidance conditioning is one of most popular tools in studying behavioral problems related to sciences such as functional anatomy of the brain, neuroendocrinology, neuropharmacology or developmental neurobiology. In spite of the popularity of the avoidance method, the nature of avoidance conditioning is not yet fully understood. The problem of resistance to extinction and the problem of motivation in avoidance behavior are still the topic of much discussion and controversy. This article represents a further attempt to help solve these problems.

THE PROBLEM OF RESISTANCE TO EXTINCTION IN AVOIDANCE BEHAVIOR

It is generally known that in order to establish a firm avoidance behavior it is necessary to start with pairing a conditioned stimulus (CS; e.g., a tone) with a strong unconditioned stimulus (US; e.g., a strong shock). The instrumental avoidance response (AvR; e.g., pressing a lever) trained afterwards to avoid the US, is very stable and highly resistant to extinction (1, 2, 5, 9, 14–18, 25, 26, 29, 33–37). This situation is contrary to that observed in classical conditioning or in instrumental conditioning related to food. As is well known, in classical conditioning, the withholding of electric shock to the animal's leg leads to the extinction of the defensive flexion of that leg in a few sessions (10, 19); similarly, the withholding of food results in extinction of salivary conditioned reaction in several trials (28). Also, the withholding of food in instrumental conditioning inevitably leads to extinction of the motor response (15–18).

The phenomenon of resistance of avoidance behavior to extinction had been studied by a number of investigators. It was found that the degree of resistance to extinction depends on such factors as the intensity of the US used in the initial phase of the training and the length of the interval between the CS and the US. The stronger the US (an electric shock) and the shorter the CS–US interval, the higher the resistance to extinction (12, 13, 33). In the cases where the shock was weak and the CS–US interval long, the extinction of the AvR occurred after several repetitions of the CS without the US (12, 13, 32, 33). On the other hand, when the shock was strong and given a few seconds after the CS was switched on, the AvR was always stable and observed for months of experimentation (5, 36, 37).

Mowrer and Lamoreaux (27) found that the establishment of avoidance behavior was facilitated when the response not only prevented the occurrence of the shock but also terminated the conditioned stimulus. The importance of the cessation of the CS immediately after the performance of the AvR for the establishment of the avoidance behavior and its resistance to extinction, was also pointed out by Bregadze (2), Fonberg (5), Sołtysik (36) and others.

According to Konorski's interpretation (16, p. 416–417), the performance of the AvR becomes a "barrier" preventing the formation of associations between the CS and the state of relief resulting from the postponement of the US. That way, the CS continues to be a "fear CS" as originally trained and, consequently, the extinction of the AvR is not possible.

Solomon and Wynne (35), on the other hand, based their explanation on the theory of "two-process learning" as proposed by Mowrer (25). According to that theory, pairing the CS and the US leads to the establishment of fear in the first stage of the training; the performance of the AvR enables the animal to escape from the feared stimulus in the second stage of the training. Solomon and Wynne (35) pointed out, however, that a quick performance of the avoidance response to the CS prevents not only the occurrence of the US, but also the development of fear; as a result, fear is "conserved" and, that way, protected from extinction. In addition, these authors assumed that classical conditioning is partially irreversible; this assumption was based on observations reported by Gantt (7, 8) that the classical cardiac reaction to CS was present in dogs for months and even years in spite that the US (which was responsible for the establishment of that reaction) was not used any more. The principles of "anxiety conservation" and the "partial irreversibility" therefore, are the factors responsible for the resistance of avoidance behavior to extinction.

It turned out, however, that the extinction of the avoidance response was actually possible in some conditions (besides those mentioned above). One of such conditions was making the AvR impossible to perform. In experiments of Solomon and his colleagues (34) a glass barrier was used to prevent the animal from jumping into the safety area; this procedure resulted in the extinction of the AvR in the situation with the barrier, but not in the situation without the barrier. In a study of Baum (1) the animal was forced to remain on the grid floor (where shock had previously been given) for a few minutes during which no shock was applied. This led to a rapid extinction of the AvR. More recently Prado-Alcala (29) found, however, that this method was not always effective unless combined with a "counterconditioning" through an intracranial stimulation which produced a behavior antagonistic to the avoidance response.

The most effective method of achieving the extinction of the AvR appeared to be the continuation of the CS after the performance of the AvR. This was obtained by Bregadze (2) and, independently, by Fonberg (5) in dogs. In Fonberg's study, the CS was continued after the repetitive performance of the AvR until the response did not appear for 10 s since its last performance. With the use of this procedure, a full extinction of the avoidance response occurred after only four sessions (46 trials altogether). This procedure was also successfully applied by Sołtysik (36) in his studies on differentiation and extinction of avoidance behavior. According to Sołtysik (36) the extinction of the AvR occurs in two stages. In the first stage, the CS, by being continued after the performance of the AvR, becomes a secondary reinforcement substituting for the US; this leads to the suppression of the AvR. In the second stage, after the removal of the protective (from extinction) role of the AvR, extinction takes place according to the rules governing the classical conditioning. Another explanation of this problem will be discussed below.

THE PROBLEM OF MOTIVATION IN AVOIDANCE BEHAVIOR

The fact that a simple change in the procedure such as extension of the CS beyond the AvR, disrupts avoidance behavior, suggests that the principles of "anxiety conservation" and "partial irreversibility" (35) are not sufficient to explain avoidance behavior and that still another factor may play a critical role in the behavior. What is that factor? According to Mowrer (25, 26) the action of the CS initially related to the US (e.g., a shock) produces a state of anxiety (fear); fear is removed after the performance of the AvR and discontinuation of the CS; therefore, the reduction of fear is the factor motivating the AvR. Miller (23) claimed that fear produced by the CS is a drive and feardrive reduction is the critical factor in sustaining avoidance behavior. According to these authors, the fear reduction in the Mowrer's concept, and the feardrive reduction in Miller's concept, is the reinforcement in the avoidance behavior.

Before proceeding with the present discussion, let us briefly consider the term "reinforcement". As is well known, the word "reinforcement" was first used by Pavlov (28) to describe the power of the US (food or acid solution placed in the dog's mouth following the action of the CS) to strengthen the connections between the CS and the US. In studies on instrumental behavior this term has been widely used in its empirical meaning and, frequently, as a substitute for the US (e.g., food in appetitive behavior or shock in aversive behavior). In appetitive behavior the term "reinforcement" refers to the obtaining of the US for the performance of the instrumental act. In avoidance behavior, however, the US is not used and, therefore, it cannot be called "reinforcement". In fact, the theoretical approach to the term "reinforcement" varies from author to author (14, 20, 23, 26, 30, 31, 38). Some authors expressed their doubts as to usefullness of the traditional concept of reinforcement in explaining behavior, especially avoidance behavior (30, 31). In view of this multiplicity of approaches the term "reinforcement" will not be used further in this article.

Let us now examine the meaning of the "anxiety reduction" (26) and of "fear-drive reduction" (23). Both these expressions refer to a change in the sensory state of the organism: due to the performance of the AvR a particular sensory state (anxiety, fear) disappears. If we assume that the state of fear is undesirable for the organism (as the animal acts to remove it by performing the AvR), we can say that the reduction of fear is a positive change in the sensory state (see 26, p. 129). This positive change obtained due to a performance of the AvR can also be considered an "improvement in the sensory state" or an achievement of sensory "better-being", according to the terminology previously used by this writer elsewhere (39, 40). Such an approach deals with an *induction,* i.e., a process leading to satisfying sensory state, rather than with a reduction, i. e., a process leading away from dissatisfying sensory state. Let us try to explain avoidance behavior from this point of view.

THE ORGANIZATION OF AVOIDANCE BEHAVIOR

It is generally assumed that the phenomenon of conditioning is a result of the associations formed between the neural representations of stimuli. There is an evidence that such associations can be formed and stored at the neuronal level (9, 11, 24). For example, in experiments of Morrell (24), the unitary activity of the polysensory parastriate neurons was recorded in conscious cats during the pairing of a visual stimulus (L) with an electric shock (S). Before the pairing, each of these stimuli evoked a different pattern of discharges. A combined application of L + S evoked a combined pattern of discharges, L.S. After a number of combined applications of L + S, L alone evoked the combined pattern L.S. This combined pattern, as a response to L, was observed throughout the approximately 60 min testing period after the withholding of the shock.

Morrell's experiments reveals the basis of classical conditioning, which may be used to explain the events occurring in the first stage of avoidance training. At that phase, the CS (e.g., a tone) and the US (e.g., a shock) are paired many times; as a result, a combined pattern of sensory traces of the CS and the US may be formed and stored in the polysensory neurons. Since then, the previous traces of neuronal activation related to the CS have become "contaminated" with the traces related to the US; as a result, the CS can now evoke *only* the combined pattern, as if the US was still present with the CS.

In the first stage of the avoidance learning procedure, classical conditioning takes place, i.e., the neuronal pattern CS. US is formed. In the second stage, when the AvR is introduced to prevent the shock, a new pattern of combined sensory traces is formed against the background of the old CS.US pattern. The new pattern consists of sensory changes related to the CS, AvR and noUS. The "noUS" denotes the sensory changes related to the absence of the US. The supposition that the US is not represented in the new pattern, is supported by the results of the experiments of Fonberg (6) in which this author examined the relationship between the CS and the US in avoidance behavior. After the establishment of the AvR in dogs, a test was performed in which the US, an electric shock, was given alone. A question was asked as to whether the AvR would occur during the shock or not. It turned out that the shock itseld did not evoke the AvR.

Nevertheless, there is an evidence that after the establishment of the AvR the old sensory pattern CS.US still remain active. When studying the neuronal changes during defensive conditioning in cats, Halas and Beardsley (9) observed that repeated applications of the CS alone continued to evoke the neuronal response in spite of the fact that the behavioral avoidance response was already extinguished. Sołtysik and Kowalska (37), in their study on changes in heart beat during classical and instrumental conditioning, demonstrated that new, neutral acoustic stimuli did not evoke any significant cardiac reaction, but an acoustic stimulus which had previously been paired with a shock produced an accelaration in the heart beat. This cardiac reaction disappeared as soon as the AvR was performed and the CS was discontinued, to appear again to the next application of the CS. This perseverance of the classical cardiac reaction, earlier described by Gantt (7, 8), seems to be a result of the "partial irreversibility" of classical conditioning, as proposed by Solomon and Wynne (35). The appearance of the neuronal changes and the cardiac reaction to the CS suggests that the sensory state of the organism might rapidly become undesirable. The return of the heart beat to normal after the performance of the AvR and discontinuation of the CS suggests that the sensory state improved.

The performance of the AvR, therefore, leading to the discontinuation of the CS, leads at the same time to the inactivation of the "old" memory pattern, CS.US, and consequently, to the disappearance of the undesirable sensory state, i.e., to an "improvement in the sensory state" and achievement of "better-being" (see 39, 40). This is the sensory reward which the animal receives each time it performs the avoidance response. Consequently, each application of the CS alone producing the AvR, strengthens the avoidance response instead of making it weaker. This is why avoidance behavior is so resistant to extinction.

As described above, the extinction of the AvR is possible when the CS is continued after the performance of the AvR. In that case, the memory pattern CS.US evoked by the CS remains active as long as the CS continues, sustaining the undesirable sensory state. With the

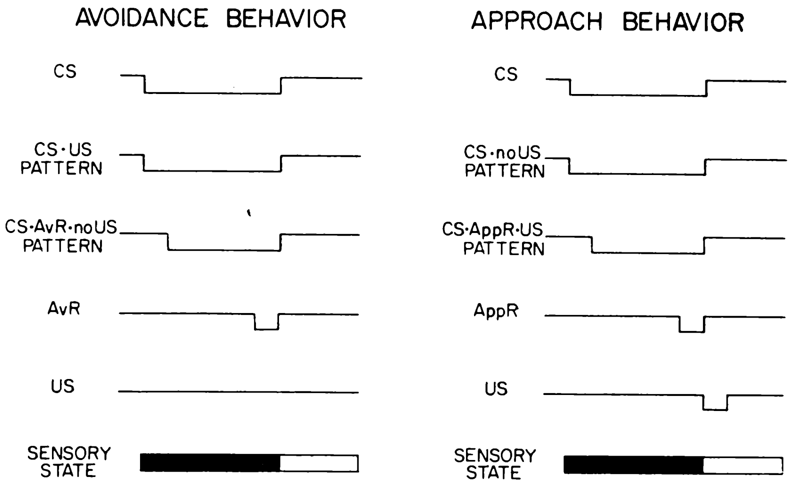

Fig. 1. A scheme showing a sequence of events occurring during and after the action of the conditioned stimulus in avoidance behavior and in approach (appetitive) behavior. CS, conditioned stimulus; US, unconditioned stimulus; AvR, avoidance response; AppR, approach (instrumental) response; CS.US, memory pattern of associations related to the presence of the undesired US during the action of CS in avoidance behavior; CS.noUS, memory pattern of associations related to the absence of the desired US during the action of CS alone in approach behavior; CS.AvR.noUS, memory pattern of associations related to CS, the performance of AvR and the postponement of the undesired US in avoidance behavior; CS.AppR.US, memory pattern of associations related to CS, the performance of AppR and the presence of the desired US; darkened field, undesirable sensory state of the organism; white field, sensory "better-being". Periods of action of CS and US, performance of AvR and AppR, and activation of memory patterns are shown by a drop in the corresponding lines. The scheme shows that in spite of the procedural differences between avoidance behavior (postponement of US after the performance of AvR) and approach (appetitive) behavior (occurrence of US after the performance of AppR), the final effect is, in general, the same: an achievement of sensory "better-being".

repetition of such procedure, the AvR loses its ability to improve the sensory state; in other words, the AvR is no longer rewarded by procuring sensory "better-being". Consequently, an extinction of the AvR takes place, similarly as it happens in approach (appetitive) instrumental behavior.

The view presented above makes it possible to extend the rules governing approach instrumental responses to avoidance behavior. Despite the procedural differences between these two behaviors, the performance of the instrumental response in either approach behavior or avoidance behavior leads to the same general result: an improvement in the sensory state (Fig. 1).

It is obvious that the terms used above such as "undesirable sensory state", "improvement in the sensory state" or "better-being" describe hypothetic, subjective feelings which cannot be strictly and objectively measured. However, these sensory states can be indirectly measured through recording the changes in autonomic responses, electrical activity of the brain, etc., accompanying the avoidance response. For example, changes in cardiac responses as recorded by Gantt (8) during classical defensive conditioning or by Sołtysik and Kowalska (37) during avoidance behavior, may serve as an indicator of the sensory state of the animal. The EEG recording may also prove useful in this respect. Some EEG correlates of reward in alimentary instrumental behavior were reported by several authors (3, 4, 21, 22). It is not excluded that an objective evidence of changes in the subjective sensory state during avoidance behavior will be found.

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