THE "WHERE IS IT?" REFLEX: AUTOSHAPING THE ORIENTING RESPONSE

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The goal of this review is to compare two divergent lines of research on signal-centered behavior: the orienting reflex (OR) and autoshaping. A review of conditioning experiments in animals and humans suggests that the novelty hypothesis of the OR is no longer tenable. Only stimuli that represent biological "relevance" elicit ORs. A stimulus may be relevant a priori (i.e., unconditioned) or as a result of conditioning. Exposure to a conditioned stimulus (CS) that predicts a positive reinforcer causes the animal to orient to it throughout conditioning. Within the CS-US interval, the initial CS-directed orienting response is followed by US-directed tendencies. Experimental evidence is shown that the development and maintenance of the conditioned OR occur in a similar fashion both in response-independent (classical) and response-dependent (instrumental) paradigms. It is proposed that the conditioned OR and the signal-directed autoshaped response are identical. Signals predicting aversive events repel the subject from the source of the CS. It is suggested that the function of the CS is not only to signal the probability of US occurrence, but also to serve as a spatial cue to guide the animal in the environment.

Key words: orienting reflex, autoshaping, conditioning, learning theory

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The general theme of this review is the suggestion that the underlying mechanisms of the signal-directed autoshaped response (sign-tracking) and the orienting reflex are identical.

Although this may sound a trivial suggestion, to date theoretical accounts of autoshaping have not raised this possibility. To illustrate, neither the influential monograph of Hearst and Jenkins (1974), nor a recent book on autoshaping and conditioning theory (Locurto, Terrace, & Gibbon, 1981) contains a single paragraph on the orienting reflex. The converse seems also to be true. In two recently published books on the orienting reflex and goal-directed behavior (Kimmel, van Olst, & Orlebeke, 1979; Thompson, Hicks, & Shvyrkov, 1980), there is not a single reference to the autoshaping literature. I hope that the present review reflects part of the powerful trend in experimental psychology that promises to provide a unitary framework for analysis for a variety of psychological phenomena.

TRADITIONAL VIEW OF THE ORIENTING RESPONSE

The importance of the orienting reflex (OR) lies in its involvement in processes such as attention, perception, learning, and memory. However, the mechanism of how the OR contributes to these psychological processes has remained conjectural until now. The OR is usually defined in terms of a conjunction of

stimulus and response properties. Pavlov (1927) viewed it as follows:

> It is this reflex which brings about the immediate responses in man and animal to the slightest changes in the world around them, so that they immediately orientate their appropriate receptor organ in accordance with the perceptible equality in the agent bringing about the change, *making full investigation of it.* (p. 12, italics added)

According to Sokolov (1963), the OR possesses two important characteristics: it is evoked by novel, salient stimuli above the sensory threshold, and it decreases as a function of stimulus repetition (habituation). Sokolov's neuronal model theory described the OR as an inborn (unconditioned), automatic by-product of an encounter with unfamiliar stimuli. Mismatch between model and current stimulus input produces "impulses of discrepancy" (Sokolov, 1963, p. 289), which trigger an OR. Thus, what might be termed the traditional view of the OR is that it is a reflexive reaction to stimulus change, triggered by mismatch to a hypothetical neuronal model. However, it is difficult to define stimulus novelty in operational terms. Neutrality, salience, slightest change, novelty, and related terms are notoriously difficult to define. They are not controllable physical or physicochemical properties of the stimulus but always reflect a momentary relationship between the perceiving organism and the physical features of the test stimulus. Given a particular state of the organism, a stimulus change may evoke an OR. In a different state that same stimulus change would not, or would do so to a lesser degree (Maltzman, 1979; Ray & Brown, 1976). Consequently, the "threshold for novelty" (Sokolov, 1966, p. 352) will depend on stimulus antecedents and context within which the OR occurs. Since stimulus novelty is defined post hoc, as inferred from the reactivity of the organism, it cannot be determined whether the absence of the OR reflects familiarity with the stimulus or a state of reduced responsiveness with an increased "orienting threshold" (Sokolov, 1966, p. 352). Even if we accept that the OR is "a sign that the nervous system has detected a change in the stimulus" (Sokolov, 1963, p. 283), its absence does not guarantee that the stimulus

features have already been encoded in the neural model.

Another problem with the traditional definition is that the OR does not habituate to all stimuli. A trivial but revealing example is the OR that we give upon hearing our own name. The subject's own name is considered to be particularly effective in evoking an OR (Lynn, 1966; Siddle, O'Gorman, & Wood, 1979). Species-specific "calls" are also very resistant to habituation (Ploog, 1970). Thus, it appears that stimulus novelty is neither necessary nor sufficient for elicitation of the OR. It seems possible that there is a basic misunderstanding of the phenomenon under investigation. It is not clear whether the function of the OR is best characterized as enhancing the efficiency of the nervous system for processing of the novel stimulus or as preparing the organism for efficient processing of future environmental events. In addition, as Siddle and Spinks (1979) pointed out, the novelty hypothesis involves a logical problem in that the novelty of a stimulus can be determined only once the stimulus has been analyzed. When this has occurred, there is no requirement for enhanced processing because the stimulus has already been identified. Moreover, if stimulus novelty alone is sufficient to evoke an OR, the reflex may be maladaptive, in that the organism's ongoing behavior will frequently be disrupted by encounters with novel but nonimportant stimuli.

From the foregoing analysis it appears that the only acceptable definition of the OR remains its objective description in terms of skeletal movements toward the stimulus source and correlative changes in the autonomic nervous system. The "nature" of the evoking stimulus remains to be defined, however.

STIMULUS SIGNIFICANCE AND THE OR

Several investigators have concluded that the data did not require a model that included a matching process (Bernstein 1969; Germana, 1968; Grastyán, 1961; Kahneman, 1973; Maltzman, 1971). As early as 1968, Maltzman and Mandell (1968) argued: "Stimulus change per se is not the critical factor nor sufficient to induce an OR" (p. 99). Bernstein (1969) advanced the view that became known as the significance hypothesis of the orienting reflex

(Bernstein, 1973, 1979; Bernstein, Taylor, & Weinstein, 1975). This view amplified early Soviet opinions based on psychological investigations of the handicapped. Zemtsova (1969) observed that blind subjects showed an augmented OR to auditory stimuli that was highly resistant to habituation. She interpreted these results to mean that auditory stimuli have greater significance for the blind than for the sighted subject. A similar conclusion was reached by Tikh (1949) on a comparative psychological basis. She found that sound stimuli did not evoke an OR in the developing young of the ape. Children, on the contrary, were readily diverted by the sound. Tikh hypothesized that this difference could be traced back to the different kinds of communications used by the two species.

In Bernstein's original experiment the galvanic skin response (GSR; Voronin & Sokolov, 1960) was habituated to a visual stimulus. The stimulus was then altered on a test trial. All subjects were able to report on experimental inquiry that they had detected a change in the stimulus, but only 47% responded to the change with a GSR. Bernstein did not discard uncertainty or the mismatch process but suggested that an interaction between them and stimulus evaluation triggers the OR. O'Gorman (1979) criticized the significance detector hypothesis on several grounds. Most importantly, he pointed to the inadequacy in arguing for a revision of OR theory from a single set of data, in which only one component of the OR (GSR) was monitored (see also Barry, 1977). Second, he drew attention to the difficulties in coupling cognitive processes and physiological response classes. Third, Bernstein's conclusion was at variance with Vinogradova's findings (1965). She reported that a defensive reflex was successfully conditioned to a metronome paired with an electric shock in a subject who showed no OR during conditioning trials. "Postexperimental inquiry revealed that the subject did not see any connection between the stimulus; only with the help of leading questions could she remember that the metronome was used in the experiment; she said she 'did not pay attention' to it" (p. 52). Fourth, since there was no independent measure of significance, and judgments of "significant" were inferred solely on the basis of test trial responding, the hypothesis has remained tautological (O'Gorman, 1979; Siddle & Spinks, 1979).

However, there is a clear advantage of the significance hypothesis as opposed to the novelty notion: the significance of a stimulus can be explicitly introduced and varied experimentally. Although we can never be sure that a stimulus is truly nonsignificant (neutral), we can at least vary its significance by altering its correlation with an unconditioned stimulus (US).

CLASSICAL CONDITIONING AND THE OR

The term *classical conditioning* implies the experimental operations of CS-US pairing where the occurrence of CS and US is not contingent upon behavior of the organism. The orthodox view of conditioning implies that subjects automatically associate appropriately paired events. The general similarity of the form of the conditioned response (CR) and the unconditioned response (UR) observed in the salivation experiments led Pavlov to formulate his principle of stimulus substitution (1927). Stimulus substitution predicts that as a consequence of CS-US pairings, responses evoked by the CS will be determined by US qualities (Jenkins & Moore, 1973; Konorski, 1948, 1967; Pavlov, 1927). Several authors have suggested alternative characterizations of the function of the CS; for example, "a learned releaser" (Woodruff & Williams, 1976), "object substitute" (Hearst & Jenkins, 1974), or an "incentive stimulus" (Bindra, 1978).

An often cited anecdote from Pavlov's laboratory described a dog, which when let free after an experiment, ran to the metronome (CS) and began licking it (1934). If the established CS is within reach "the animal even tries to come in touch with it, namely; by means of its mouth. Thus, if the conditioned stimulus is the switching on of a lamp, the dog licks the lamp. . . In this way the conditioned stimulus actually stands for the animal in place of food" (p. 187). It is less known, however, that this incidental observation was later painstakingly elaborated by Pavlov's successor, P. S. Kupalov. I will describe his observations later. In the present context, it is enough to mention that this behavior was certainly not a consummatory response re-

leased by the US-surrogate (CS). On the first presentation of the signal (i.e., prior to CS-US pairing) "most often the dog turns his head toward the stimulus and looks at it; less frequently he approaches it . . . Some of the animals sniff at it, touch it with a paw, or lick it" (Kupalov, 1969, p. 741).

The discovery that the OR plays an important role in conditioning originates from Pavlov (1927). A previously habituated or a novel stimulus transformed into a CS evokes a large OR (Grastyán, 1961; Luria, 1973; Luria & Vinogradova, 1959; Maltzman & Raskin, 1965; Razran, 1961, 1971). Since the OR lawfully emerges during conditioning, it is regarded as a reliable predictor of learning (Grastyán & Vereczkei, 1974; Maltzman & Mandell, 1968; Sokolov, 1963). Once the learned connection is "firmly established, consolidated and automatized" (Sokolov, 1963, p. 292), the OR is claimed to disappear (Bykov, 1958; Grastyán, 1961; Lebedinskaya, 1965). The "orienting reflex has the property to become extinguished in the course of continuation of pairings" (Sokolov 1965, p. 150). During the formation of a CR, "an orienting response develops first and later undergoes into the *specific reaction corresponding to the nature of the reinforcement employed*" (Vinogradova, 1969, p. 714; italics in original). Does this imply that the OR is being gradually transformed into a UR-like consummatory response? There is a logical problem here: if the OR is directed to stimulus qualities of the CS (Holland, 1977; Prokasy & Ebel, 1967; Sokolov, 1963), how does it facilitate the formation of the CR, which is interpreted as being determined by US qualities through the process of stimulus substitution?

MEASUREMENT OF THE CONDITIONED RESPONSE

The question "what is a CR?" can be asked and answered in two general ways depending on expectations and the depth of the data analysis. First, in terms of operational definition: any change that differs significantly from appropriate controls (Rescorla, 1967) is essentially regarded as the CR. The second approach concentrates on its adaptive function and meaning for the organism. What is its survival value? How is it caused and controlled? How does it develop in the individual? And

how did it evolve in the species? (Simpson, 1962; Tinbergen, 1968). The first approach concentrates on the second of these questions. The problem with that approach stems from the difficulty in defining the "control" (Garcia, 1981). The subject may associate a variety of events in a conditioning experiment, and the change in behavior recorded by the experimenter is simply a convenient index of the formation of these associations. If stimulus substitution is the underlying mechanism of classical conditioning, then it is reasonable to look for the "true" CR late in the CS-US interval (Gormezano, 1966; Martin & Levey, 1978; Thompson, 1976). But what is the significance of other reactions that occur earlier in the CS-US interval? Furthermore, if the stimulus substitution principle proves to be an insufficient account of conditioning, several questions arise. By way of illustration, consider the following example:

1. Assume that the magnitude (or probability) of a response to a CS is a function of the ongoing behavioral state: when the CS is presented during Behavior A the response is twice as large as the response obtained during Behavior B.

2. The structure of inter-CS behavior changes across sessions in the following manner: In Session 1, presentation of CS coincides with Behavior A on half of the trials and with Behavior B on the other half; by Session 10 the intersignal activities change so that presentation of CS coincides with Behavior A on 90% of the trials and with Behavior B on 10% of the trials.

It follows from postulates (1) and (2) that in this hypothetical experiment there is an average of 27% increase of responsivity from Session 1 ($50 \cdot 2X + 50X = 150X$) to Session 10 ($90 \cdot 2X + 10X = 190X$) due to the change of intersignal activities. Is the increase due to CS-US pairing? What is conditioned? Experimental data are available to support both postulates. In a Pavlovian procedure with rats as subjects, the highest OR scores were obtained when sniffing was in progress at the moment of CS occurrence and lowest when the animals were engaged in grooming (Buzsáki et al., 1979a, Experiment 4). Similar observations were reported by Ray and Brown (1976). Changes in the intersignal structure of behavior are also well documented (Buzsáki et al.,

1979a, 1979b, 1981; Ray, 1977; Ray & Brown, 1976; Staddon, 1977). These intersignal effects might, at least partially, explain the trial-spacing effect of autoshaped key pecking (Gibbon, 1977, 1981; Jenkins, Barnes & Barrera, 1981). Changes of the inter-CS interval may considerably affect the inter-CS structure of behavior (Staddon, 1977), and consequently the magnitude of the CS-evoked response.

The issue is not whether any behavioral or autonomic changes occurring during the CS-US interval are the consequences of CS-US pairing, but whether any or all of them might be regarded as the "true" CR. In classical conditioning it is not only local reflexes, such as salivation, jaw and beak movements, licking, blinking, leg flexion, or nictitating membrane closure, that are modified by the conditioning procedure. These classes of behavior are representative of but one category of CRs, usually referred to as consummatory responses (Craig, 1918; Konorski, 1967), as opposed to a second category of responses, preparatory CRs, which are conditionable to CSs of longer duration (such as contextual and apparatus cues) and do not necessarily produce discrete reflex responses (Rescorla & Solomon, 1967). Since numerous components make up the CR, it is especially important to study the order in which the various reflex components of the OR appear in conditioning. Dykman, Mack, and Ackerman (1965) reported that in dogs the earliest reliable evidence of conditioning was reflected by somato-motor reactions such as eye-opening movements, perking of the ears, and head elevation. Autonomic measures (heart rate and blood pressure) showed alterations several sessions later. Further, somatic responses outlasted vegetative responses in extinction. Another problem with the exclusive use of autonomic measures, such as GSR, is that the CS- and US-related responses cannot be easily separated. It is essential for a CS that it must not initially elicit the same response as the US (Kling & Riggs, 1971). However, there is virtually no stimulus that will not elicit a GSR (Gormezano, 1966). Also, it is of utmost importance to ascertain what controls the different responses during the CS-US interval.

To overcome these difficulties a multiple behavior-oriented methodology is required which is capable of describing behavioral flow and relating the various succession of responses to eliciting events. Only in this way can one decide whether the orienting components of the CR represent an essential part of the conditioned response.

CONDITIONED OR

Biryukov (1965) exposed fox cubs to squeaks of mice. OR was either not observed or habituated rapidly upon repetition. However, when the cubs were allowed to chase and eat the mice, such experience conditioned the OR to the squeaks that proved almost unextinguishable. A similar way to produce prolonged ORs is to require the subject to respond to the stimulus. In this case the previously habituated OR is found to recover fully and to habituate very slowly (Gruzelier & Venables, 1973; Sokolov, 1963). The OR is unusually persistent in discrimination training, and is "as a rule, the stronger, the more difficult is the discrimination" (Sokolov, 1965). If novelty is the crucial dimension for eliciting an OR, it is hard to tell why the OR persists in a conditioning situation where the same physical signal recurs repeatedly. It is possible that the OR may reflect a more complex interaction than was considered in Sokolov's conception of an unconditioned "reflex receptor mechanism" (1960). A prerequisite for observing the signal-directed investigatory-orienting response is the use of freely moving subjects. Among the first investigators to use freely moving animals in a conditioning paradigm was Kupalov (1969, 1978; Kupalov & Yaroslavtseva, 1949). Kupalov's situation reflex paradigm requires a subject (always a dog) to go to a specific location in the experimental environment. The target location is marked by a carpet, usually a few meters from the food magazine. When the dog is situated correctly on the carpet, the conditioned signal, signifying the availability of food reward, is switched on by the experimenter. The goal is to teach the animal to sit or stand on the carpet correctly until the delivery of the CS, at which time the dog runs to receive food at the appropriate location. The location of the carpet and the CS (buzzer, metronome, or light) can be changed when required.

Kupalov and his associates repeatedly observed that during the course of training, an increasing tendency to orient toward the CS source developed. This consisted of head turn-

ing toward the CS and sporadically approaching it and licking it. Although similar responses were observed in some dogs prior to conditioning (see above), the incidence of such transactions was considerably higher during the course of conditioning. Yakovleva (cited in Kupalov, 1978, p. 91) described that some dogs were unable to move from the sounding metronome (CS), reached for it, and jumped on the barrier behind which the metronome was placed. Sometimes the dog stopped on its way to the food bowl, returned to the metronome and intently watched it for several seconds, and only then, with some effort, turned to the food bowl. Kupalov called this CS-directed response the "primary alimentary motor reaction" differentiating it from the "secondary food reaction," which was directed toward the food source (US). Kupalov's interpretation of these findings was that the start place and the CS acquired the features of the food stimulus and that the behavior of the animal could be best described as like that of a dog hunting or catching his prey.

Similar observations of the targeting reflex were frequently made in Konorski's laboratory using a modified version of the place reflex, but these were interpreted as pathologic magnet reactions (Stepien 1974; Stepien, Stepien, & Konorski, 1960) or a result of "parasitic" instrumental contingencies hidden in classical contingencies (Konorski, 1967; Konorski & Lawicka, 1959; Lawicka, 1979).

Dramatic signal-directed tendencies were reported by Grastyán and Vereczkei (1974) with cats as subjects. They used Kupalov's situation paradigm with the auditory CS placed behind the starting platform. It was found that approach to and contact with the CS-source (a loudspeaker) developed in the course of conditioning. In some animals this orienting tendency transiently suppressed the goal response, and the cats even refused food that was offered by the experimenter. The authors attributed this behavior to the conflict between CS-directed tendencies and the goal-directed instrumental response. Based on these observations Grastyán and Vereckei (1974) offered a complete reinterpretation of the role of the OR in conditioning. In essence, they proposed that under the effect of reinforcement the CS becomes a new goal, and that is why the animal approaches it instead of the old goal (the food magazine). Further, they suggested that

the occurrence and persistence of the "instrumentally conditioned orienting response" (p. 128), claimed to be a sufficient condition for learning, may also be the only necessary condition. Most important, they pointed to the adaptive function of the signal-directed OR: in nature, where signal and signaled usually coincide, approach to the signal results in food reward.

Since the Kupalov's place reflex is basically an instrumental paradigm in which the signal occurs as a result of subject-experimenter interaction (Ray, 1977), it was not possible to tell whether the signal-related activities were due to a Pavlovian CS-US relationship or a learned operant response-reinforcer relationship. This problem will be elaborated upon later.

Since the skeletal components of the OR are defined in terms of signal-centered behavior (e.g., directing the eyes and head toward the source of the stimulus), we asked whether similar responses emerge and persist during the course of classical conditioning.

Our experiments were conducted in a large experimental cage with cats as subjects. The source of the auditory CS (the loudspeaker) was placed on the wall opposite the food magazine. The purpose of the spatial separation between CS and US was to permit a clear separation between approach to the signal source and approach to the site of the reinforcer. The CS (2 sec long, 500-Hz tone) was automatically followed by the US (raw meat). A daily session consisted of 20 trials. Intertrial intervals ranged from 20 to 80 sec. In a subgroup of animals CS-US pairing was followed by extinction and discriminative reconditioning. In the discriminative phase, CS + and CS − (both tone signals) were delivered from the same loudspeaker. The CS-directed behavior of the cat was rated on a 4-point scale in the following manner: '1' was given for pricking of the ears or turning of the head less than 30° towards the source of the CS, '2' for turning 30 to 90°, '3' for greater than 90° of head turning and/or stepping towards the loudspeaker. Zero was given for a response other than towards the source of CS regardless of its magnitude (e.g., scratching, ambulation, grooming, jumping to feeder). OR scores were summed for a day resulting in a maximum daily score of 60 for an individual animal. This subjective description was complemented

by objective indexes, such as eye-movement recording, neck-muscle electromyogram, and head-movement recording (for further details see Buzsáki, Grastyán, Molnár, Tveritskaya, & Haubenreiser, 1979a; Buzsáki, Haubenreiser, Grastyán, Czopf, & Kellényi, 1981).

Figure 1 illustrates the development of the OR during CS-US pairings, extinction, and two-tone discrimination. In the course of 300 to 700 trials, the OR to the reinforced stimulus (CS+) did not decrease, whereas the OR to the nonreinforced stimulus (CS−) did decrease. Responses during the CS-US interval fell reliably into two classes: (INI) initial behavior early in the CS-US interval corresponding to OR toward the source of the CS; (TER) terminal behavior that consistently occurred just before food delivery and was directed toward the food magazine (Staddon & Simmelhag, 1971). TER included activities like turning of the head back to the food magazine, sniffing, pawing, and occasionally jumping to the feeder.

This "two-phase" responding was already evident in the first conditioning session. The time-course of INI and TER behavior within a single trial varied with training, showing a general decrease of the INI/TER ratio. It was a consistent observation that if the head of the animal was already directed toward the loudspeaker, presentation of CS evoked a quick head jerk toward the food magazine. The data of this experiment indicate that in a Pavlovian situation OR toward the CS persists throughout conditioning. This occurs even though it is always the TER, not the INI, that is contiguous in space and time with food reinforcement.

However, in the Pavlovian arrangement there is no independent measure of learning. Thus, we could not demonstrate how the development of OR correlated with learning per se. Also, in the classical conditioning situation the occurrence of US might not only reinforce CS-related behavior but interfere as well with the OR in progress. If, however, the occurrence of US is paced by the subject, this latter problem can be eliminated. The discriminated instrumental procedure fits this requirement.

In a second experiment we compared the development of the OR with the decrease of intertrial (CS-off period) responding. The latter was regarded as an index of learning. The apparatus was the same as that used in the classical conditioning experiment. The upper part of the protruding food magazine was converted into a pedal by placing a microswitch below the panel. In addition, a pneumatic pressure transducer was connected to the pedal. Each cat was put into the apparatus for half an hour daily for 5 to 7 consecutive days (adaptation). On the last day of the adaptation phase, the tone signal was presented 20 times with an intertrial interval of one minute (habituation). Next, the animals were handshaped to press the pedal in order to obtain a food reward. In the go, no-go discrimination phase only those presses that occurred in the presence of the tone CS were rewarded. The CS was switched on by the experimenter and terminated by the cat's lever press. Those presses that occurred in the absence of the CS were termed intertrial pedal presses (ITP). Besides CS-directed responses prestimulus behavior (PRE, during the 1.0 sec preceding CS), like ambulation, standing, sitting, lying, grooming, abortive pressing, etc., and the position of the head (relative to the source of CS) were also recorded. The principal findings are shown in Figures 2 and 3.

The most striking finding was the low level of responding to the tone signal during habituation and in the first conditioning sessions. In fact, some of the animals did not respond to the tone at all. This observation is contrary to the general belief that novel stimuli will invariably elicit an OR. Some earlier observations, however, corroborate this finding. Kar-
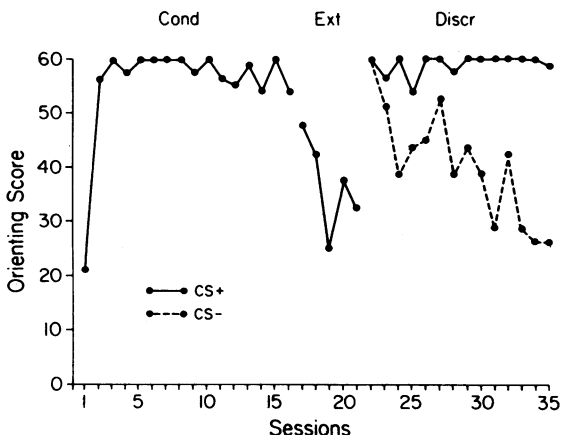

Fig. 1. A representative orienting response curve in a single cat during classical conditioning (Cond), extinction (Ext), and two-tone discrimination (Discr). Ordinate: total orienting score per session. Solid line: responses to CS+; dashed line: responses to CS−.
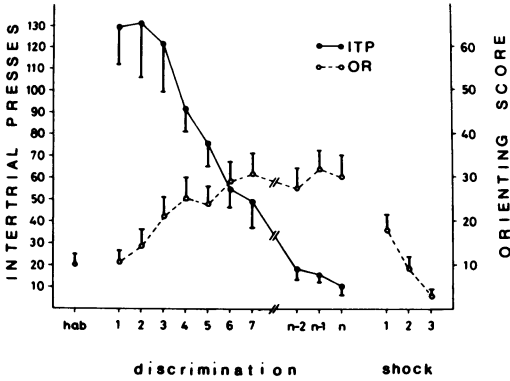
Fig. 2. The development of orienting response (OR) and intertrial lever presses (ITP) across sessions in a group of 13 cats. Vertical bars indicate standard error of the mean. hab, habituation session; shock, unavoidable shock sessions. Note the inverse relationship between the number of intertrial presses and orienting score.

mos, Grastyán, Losonczy, Vereczkei, and Grósz (1965) looked very carefully at the effects of an unfamiliar stimulus on the cat's behavior. When a novel stimulus was presented in its home cage, it did not elicit stimulus-directed orientation. Occasionally it induced behavior unrelated to the stimulus, such as eating, defecating, etc. Informal observations with human subjects also support the finding that novel stimuli do not necessarily evoke an OR. A sudden loud noise "does not do so when it comes from outside the laboratory, when it is clearly not some part of the experimental arrangement" (Maltzman 1979, p. 278). Bernstein (1979) argued that the elicitation of OR by a novel but nonsignificant stimulus is probably so infrequent as to constitute exceptional circumstances. Kupalov also reported that in the first conditioning session sometimes "the animal runs toward the food box upon the first delivery of the stimulus" (1969, p. 791), instead of exhibiting an OR. Similar observations were reported by Sheafor (1975). In a situation where rabbits were regularly supplied with water, he observed a jaw-movement response (the normal UR to water) to a novel tone never itself associated with the US. The presentation of CS similarly affected the behavior of our cats during early discriminative sessions. CS-induced effects were not source specific. Upon presentation of the CS, ongoing lever pressing came to a halt, the animal began to sniff at the pedal or the floor, raised
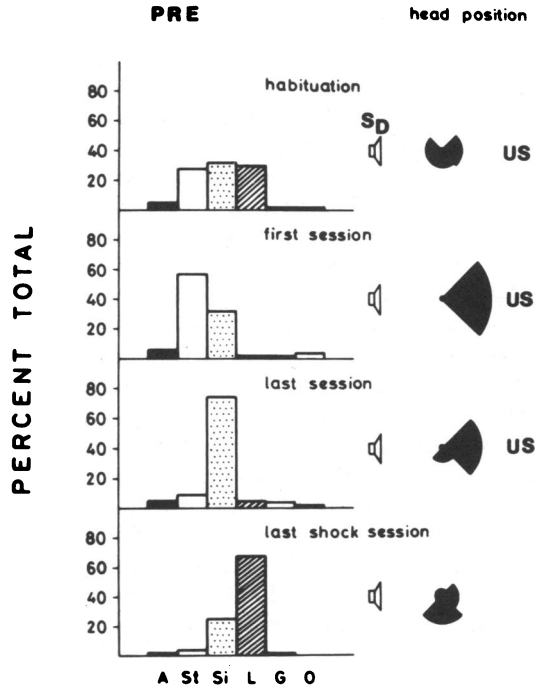

Fig. 3. Percent occurrence of presignal (PRE) classes of behavior in different sessions. A, ambulate; St, standing; Si, sitting; L, lying; G, grooming; O, other behavior. Right: position of the head in relation to the source of the signal (SD) and food magazine (US) during the last second of the intersignal interval (PRE). The radius of each quadrant is proportional to the number of occurrences.

its head, and only occasionally turned its head toward the loudspeaker. Parallel with the decreasing number of intertrial presses (errors), this turning of the head became progressively greater in amplitude during subsequent sessions. Measurements of lever-press force clearly indicated that CS-directed behavior began to compete with the goal response. On several occasions in early sessions, instead of making a definite press, the cat placed its preferred paw on the lever gently, withdrew it, and occasionally repeated this "ritual" 5 to 8 times before an actual press (switch closure) occurred. Analysis of eye-movement recordings revealed that this competition of CS- and US-directed tendencies (INI and TER behavior) was evident even after the task was mastered (Figure 4). These oscillations were analogous to behavior observed by Zener (1937) in restrained dogs with a Pavlovian arrangement. "Occasionally there may be six or more successive glances from bell to food pan and back

during the interval" (p. 391). Since in our experiment the occurrence of US was response-dependent, the explanation that these oscillations represented induced interim activity, due to the delay of US, can be excluded.

To summarize, the spatio-temporal separation of the CS and US allowed us to analyze INI and TER behavior separately. The inverse correlation between the number of errors and ORs left little doubt that the OR occurred as a result of conditioning. The identical topography of the CS-directed behavior and the ORs to the same physical signal prior to conditioning (habituation) suggested that the underlying mechanism might be the same. Since signal-directed activity built up as a consequence of conditioning, then by definition, it was a conditioned OR.

The persistent nature of the OR has also been reported in several experiments using human subjects. Although the OR is commonly described as a generalized, holistic response with both skeletal and autonomic components, measurement in humans is usually restricted to its autonomic components. The galvanic skin response (GSR) appears to be the index most frequently used (Badia & DeFran, 1970; Barry, 1977). The multiple GSR responses occurring in the CS-US interval are claimed to represent different processes (Prokasy & Ebel, 1967). Stewart, Stern, Winokur, and Fredman (1961) recommended a response latency criterion to separate the GSR component. The CS-response (the OR or first response) is claimed to be determined by stimulus qualities (Prokasy & Ebel, 1967). The pre-US response (late or "second" response) is related to expectancy and anticipation of the US (Grings, 1977; Lockhart, 1966; Öhman, 1971, Stewart et al., 1961). Prokasy and Ebel (1967) showed the CS and pre-US responses to be independent both in terms of conditional probabilities and in terms of susceptibility to changes of CS and US variables. If the above analysis is correct, then according to the classical notion of the OR, parallel with
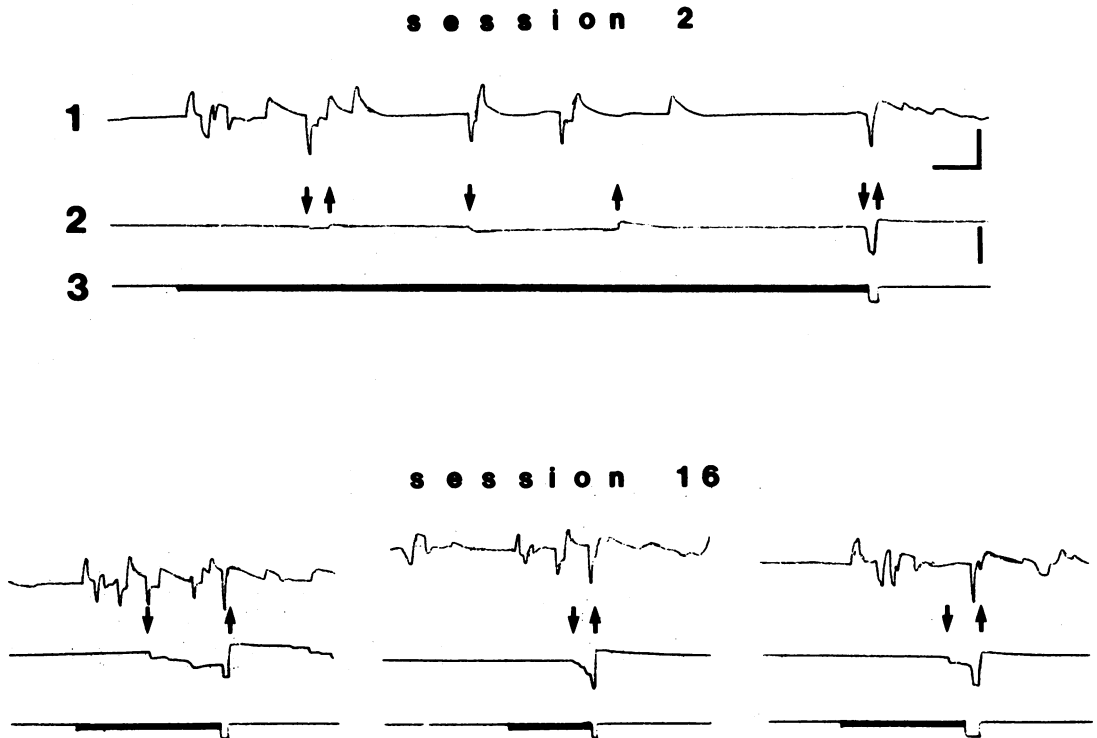
Fig. 4. Competition between signal-directed and goal-directed tendencies in an early and a late session. 1, electro-oculogram; upward deflections: saccadic eye-movements to the right (towards the source of the signal); downward deflections: eye-movements to the left (towards the food magazine). 2, force of lever pressing; arrows indicate presses and release of the lever. 3, heavy line: discriminative signal; downward deflection: switch closure. Note frequent gaze shifts between signal and food magazine, and the gradual increase of force of lever pressing on each trial. Calibrations: 1 sec, 1 mV; .5 N.

the development of the pre-US response, the CS-onset response should adapt. Gale and associates (Gale & Ax, 1968; Gale & Stern, 1967, 1968) and Öhman (1971, 1972) did not find this to be the case. Rather they found that the CS-onset component did not diminish after several hundreds of CS-US pairings. Both OR and pre-US anticipatory components reached maximum within the first few trials and remained throughout the conditioning series. Other response systems show similar characteristics to the GSR. This is particularly true of evoked brain potentials. The late component of the contingent negative variation (CNV) is commonly associated with anticipation, preparation, and expectancy of the US (TER). More recently, the early component of the CNV (INI) has been associated with orienting behavior and shown to be resistant to CS-US repetition (Callaway, 1975; Hillyard & Galambos, 1967).

These findings are difficult to reconcile with Sokolov's view that an OR is produced as a consequence of mismatch alone, independently of any other stimulus attributes (1960, 1963; Pribram & McGuinness, 1975). It seems clear from the above discussion that since Pavlov's (1927) original description of the "what is it?" reflex, the range of OR-eliciting conditions has steadily expanded. It has been demonstrated that an OR is never a consequence of stimulus change alone. On the other hand, pairing a stimulus with a positive reinforcer will invariably induce CS-directed responding. The support for the notion of the CS response (INI) as representing conditioned orienting behavior is very strong.

AUTOSHAPING

In their influential paper Brown and Jenkins (1968) reported that hungry pigeons began to approach and finally peck a lighted key (CS) if illumination of the key signaled that food (US) was forthcoming. In this classical conditioning paradigm, key pecking had no consequences, yet virtually each CS presentation reliably evoked it. Since this behavior required no hand shaping, the term autoshaping was adopted. A more descriptive term, *sign tracking*, was suggested later by Hearst and Jenkins (1974). Although pigeons have been by far the most popular subjects for this kind of research, a number of studies have demon-

strated its existence in a variety of species (Hearst & Jenkins, 1974). The consistent finding that pigeons do not peck the source of an auditory CS has led some investigators to suppose that for the pigeon "auditory cues by their nature are not readily localizable" (Bilbrey & Winokur, 1973; Burt & Westbrook, 1980, p. 305; Schwartz, 1973). This conclusion is probably inadequate in the light of the neurophysiological evidence that the "spatial mapping" system does not reside in specific sensory systems (Buzsáki, Grastyán, Mód, & Winiczai, 1980; O'Keefe & Nadel, 1978; Whittington, Hepp-Reymond, & Flood, 1981). A possible explanation for the lack of pecking to auditory targets is offered by experiments showing that visual cues in birds play a primary role in food selection (Wilcoxon, Dragon, & Kral, 1971).

Several excellent reviews of the autoshaping literature appeared recently (Davis & Hurwitz, 1977; Dickinson & Boakes, 1979; Honig & Staddon, 1977; Locurto et al., 1981).

The conclusion of the vast amount of autoshaping research can be summarized briefly: if you allow an animal to move freely, it will approach and contact localizable stimuli predicting positive reinforcement. The main goal of this review is to argue that this signal-directed behavior is a conditioned orienting response. If, in a response-independent paradigm, a tendency to approach a positive CS defines the autoshaped response, then the conditioned OR meets this criterion. From this viewpoint, autoshaping is not a new phenomenon, but rather, a new way of looking at an old paradigm (Buzsáki, Grastyán, Molnár, Tveritskaya, & Haubenreiser, 1979a).

Theoretical accounts of autoshaping (Hearst, & Jenkins, 1974; Jenkins, 1973, 1977; Mackintosh, 1974; Moore, 1973) do not share this view. First and most important, the learned OR is seen as a newly acquired *preparatory* behavior suppressing the consummatory act of eating, whereas the autoshaping response is generally interpreted as being a signal-triggered *consummatory* activity (Jenkins & Moore, 1973; Locurto, 1981; Moore, 1973; Peterson, Ackil, Frommer, & Hearst, 1972). Second, the autoshaped response is commonly explained by substitution, surrogation, and generalization principles (cf. Hearst & Jenkins, 1974) and as such determined mainly by the qualities of the US, whereas the topography of the condi-

tioned OR is determined primarily by the quality and spatial location of the CS (Holland, 1977; Prokasy & Ebel, 1967; Shettleworth, 1978; Wyrwicka, 1972). For example, Jenkins & Moore (1973) reported that exposure to CS-US pairings caused the pigeon to peck the CS light spot in a way that resembled the consummatory reaction evoked by the reinforcer (either grain or water). Also, rats showed different responses to the lever CS depending upon whether it signaled food or brain-stimulation US (Peterson et al., 1972). After a number of pairings of CS and food US, the rats approached and contacted the lever with the forepaws (touching and pressing) or with the mouth (gnawing and licking). Approach and contact of the lever also occurred with brain stimulation US, although less oral responding and more sniffing was observed. A note of caution is in order here: the descriptions of CS-directed tendencies with the two types of USs in the Peterson et al. study may reflect a difference more of the degree than of the kind. This might simply be attributed to the different magnitude of the reinforcing effects of food and brain stimulation USs.

Other autoshaping experiments question the stimulus substitution explanation (Boakes, 1977; Gamzu & Williams, 1971; Hogan & Roper, 1978; Shettleworth, 1978; Woodruff & Starr, 1978). For example, Wasserman (1973) reported using heat reinforcement to sustain key pecking in chicks. The appropriate UR to heat is wing-flapping, not pecking. Woodruff and Williams (1976) used a lighted key as CS and water-US injected directly into the mandibles of unrestrained pigeons, and observed that the CS-related response (approach, bowing, rooting) was dissimilar to the US-elicited response (swallowing). They, together with Timberlake and Grant (1975), conclude that a biologically preorganized behavior system is conditioned to the CS, and those responses in the behavior system that are "released" or "elicited and supported" by the CS constitute the autoshaped response. Further, in higher order autoshaping experiments (Burt & Westbrook, 1980; Holland, 1977; Leyland, 1977; Nairne & Rescorla, 1981; Rashotte, 1981; Rashotte, Griffin, & Sisk, 1977; Rescorla, 1980) the topography of the second-order CR does not depend on the response evoked by the first-order reinforcing CS.

Although this latter group of experiments lends support to the view that "preparatory" is an apt description of the autoshaped response, it is not clear why in other experiments the CS-directed response resembles the US-related response. I suggest that the degree of spatial discontiguity between CS and US might be responsible for the divergent results. In our experiments spatial separation of CS and US sites allowed a clear distinction between INI and TER behavior. TER (US-directed) activities definitely showed some resemblance to the UR (biting screws on the wall, nosing, pawing, and scratching the magazine wall). It is possible that the autoshaped responses that showed resemblance to the UR were actually TER responses. In the experiments of Wasserman (1973), Timberlake and Grant (1975), and Woodruff and Williams (1976) separation of INI and TER responses was relatively easy since the locations of CS and US were far apart. In a more typical autoshaping arrangement CS and US sites are closer and are usually placed on the same response panel (e.g., Jenkins & Moore, 1973). Consequently, distinction between INI and TER behavior may be more difficult. The spatial proximity of CS and US and the relative dominance of TER late in conditioning might explain why the topography of the autoshaped response is judged as resembling the UR. The topography of TER behavior depends on the type and strength of the reinforcer also in situations where time is the only variable that signals the imminence of reinforcement (Anderson & Shettleworth, 1977; Hurshman & Moore, 1976; Reberg, Mann, & Innis, 1977; Staddon, 1977). In second-order conditioning when both first-order and second-order stimuli were presented on the same key, the second-order CS showed sensitivity to the current value of the first-order CS. However, autoshaped responding to a second-order CS paired with an auditory first-order CS, delivered from another location, was relatively insensitive to changes in that first-order stimulus (Nairne & Rescorla, 1981). That some part of pecking behavior may correspond to TER activity is supported by Moore (1973). He noted that autoshaped pigeons occasionally abandon the CS key to peck down the wall to the US site.

Boakes (1977, 1979) distinguishes goal-tracking (TER) from sign-tracking (INI) behavior. When compared with goal tracking, sign tracking develops faster, is more strongly sustained

by partial reinforcement, and extinguishes more slowly. He argues that goal tracking may be regarded as a form of consummatory responding and sign tracking as a form of preparatory behavior (1979). "Two-phase" responses were also observed in monkeys when presented with discrimination problems in which the discrimination stimulus was spatially discontiguous with the site of the instrumental response (Polidora & Fletcher, 1964; Polidora & Thompson, 1965). The monkeys invariably looked at the site of the stimulus and touched it before executing the required instrumental response.

The distinction between INI and TER responses is further supported by experiments in which the magnitude of reinforcer was manipulated. A CS paired with a higher magnitude US evoked strong key pecking in the early portion but weak pecking in the later portion of the CS-US interval (Gibbon, Farrell, Locurto, Duncan, & Terrace, 1980; O'Connell & Rashotte, 1982). In agreement with the present analysis, these authors concluded that the relatively weak key pecking late in the CS period is due to the strong tendency to approach the US site (TER) when the US magnitude or probability are high.

The foregoing analysis lends support for the
· claim that the conditioned OR (INI) and the sign-tracking component of the autoshaped response are identical. The conditioned OR approach shares several features of the sign-tracking formulation but is couched in a different conceptual language.

A widely discussed problem of associative learning is the occasional lack of conditioning despite CS-US temporal contiguity. These related phenomena are termed "overshadowing" (Mackintosh, 1974; Pavlov, 1927) and "blocking" (Kamin, 1961). The compound signals used in these experiments are almost exclusively stimuli of different modalities (e.g., light and tone). None of the experiments in this research area has addressed the question of how the degree of spatial discontiguity (relative to US) and localizability of the stimuli affect "overshadowing" or "blocking." The observation of Schwartz (1973) is relevant here. During an initial phase of an autoshaping experiment, food was delivered in the presence of a tone CS. No pecking occurred in this phase. In a subsequent phase the occurrence of food was signaled by a compound CS consisting of the tone and a lighted response key.

This latter, easily localizable portion of the compound CS did sustain key pecking; that is, no blocking occurred (see also Gibbon, 1981; Tomie, 1976).

STIMULI SIGNALING AVERSIVE REINFORCERS

Protopopov (1909, cited in Skipin, Ivanova, Kozlovslaya, & Vinnik, 1969), working in Bechterev's laboratory, was probably the first investigator of conditioned defensive reflexes. The procedure is identical with the salivation experiment: the CS and the aversive US are presented independently of the subject's behavior. In this procedure, therefore, the behavior of the animal does not attain its chief purpose—avoidance of a noxious stimulus (Bolles, 1970; Skipin et al., 1969). In a modified version, the CS signals that the aversive event is imminent but the subject can avoid it by active responding (Bechterev, 1933). Several investigators argue that there is a critical difference between procedures with avoidable and unavoidable aversive stimuli (Bolles, 1970; Seligman, 1970). The unique feature of avoidance procedures is the fast rate of learning. Signals correlated with dangerous events may be avoided after a single pairing (Bolles, 1970; Garcia & Ervin, 1968; Seligman, 1970). Burstein (1977) argues that "any population which required 5, 10 or 20 trials or experiences to acquire a fear response to the sight or sound of a dinosaur would be destined for rapid extinction" (p. 122). By contrast, when an aversive stimulus is unavoidable, subjects may flee or engage in aggressive behavior and finally response tendencies become suppressed and the subject may fall asleep (Bolles, 1970; Pavlov, 1927).

As in appetitive situations, the importance of the CS location and CS-related activities received little attention in aversive conditioning procedures. The marked facilitation of avoidance learning by separation of stimulus and response, described by Biederman, D'Amato, and Keller (1964), remained unnoticed, perhaps because it arrived in a theoretical vacuum. The use of houselight flashes and placing the source of an auditory CS outside the experimental chamber have remained common practices.

Recently, we investigated the effect of an unavoidable aversive event on the OR (Buz-

sáki, Grastyán, Molnár, Tveritskaya, & Haubenreiser, 1979a; Buzsáki et al., 1981). Following appetitive conditioning, the CS previously paired with food was paired with an electric shock to the neck region of the cat. As a consequence, the previously established OR toward the CS source markedly diminished (Figure 2). When rewarded trials were interspersed among aversive trials, CS-directed tendencies varied systematically according to the opposite consequences of the same CS (Figure 5).

Recent experiments of Hearst and his colleagues (Hearst & Franklin, 1977; Karpicke, Christoph, Peterson, & Hearst, 1977) also emphasize the importance of CS localizability in aversive situations. In the Karpicke et al. study, rats performed an intermittently reinforced operant response and received periodic presentation of a visual CS for foot shock located either very near or far from the operant manipulandum (Experiments 4 and 5). Presentations of the near CS resulted in marked suppression of the operant response, whereas the far CS was without effect. Periodic observations revealed that the rats of both groups tended to restrict their activities to parts of the apparatus away from the CS source. Similar withdrawal from a localized CS was also obtained in pigeons when the CS predicted the absence of food (Hearst & Franklin, 1977; Jenkins & Boakes, 1973).

An alternative to avoidance of the aversive CS is elimination of its source from the subject's environment. Hudson (1950) observed that rats often sprayed bedding material toward and over (i.e., buried) stimulus objects associated with an aversive US. Localizability

of the CS source is prerequisite to this burying response (Pinel & Treit, 1978). Calhoun (1963) described numerous examples of burying behavior as a viable defensive response of rodents in the wild. More research is required to elucidate how animals cope with aversive CSs. The available evidence suggests that subjects do not approach or make contacts with the source of CS, but rather behavior is directed away from signals of aversive CSs.

These same studies provide support for the view that it is not the novelty, uncertainty, or mismatch of the CS that attracts or repels the subject. The acquired affective "charge" (i.e., rewarding or aversive) seems to be the relevant dimension.

STIMULUS-REINFORCER VERSUS RESPONSE-REINFORCER CONTINGENCIES

It is common practice to make a distinction between Pavlovian and instrumental procedures. The Pavlovian procedure, by definition, is a response-independent paradigm, whereas in the instrumental (or operant) procedure, occurrence of the reinforcer depends on the prior occurrence of a specified response (Hearst, 1975; Konorski, 1948, 1967; Rescorla & Solomon, 1967; Skinner, 1938). Both procedures involve temporal sequences of events: stimulus-response-reinforcer. Because the US used in a Pavlovian arrangement can usually serve also as an instrumental reinforcer, a response that occurs in the presence of the CS might be adventitiously reinforced and emerge as a consequence of instrumental rather than Pavlovian contingencies (Amsel, 1972; Herrnstein & Loveland, 1972; Jenkins, 1977; Kimble, 1961; Konorski, 1967; Schwartz & Williams, 1972; Skinner, 1948, 1969). The CS-directed behavior occurs on the first occasion for some unspecified reason, is accidentally contiguous in time with the occurrence of the US, is strengthened by an instrumental contingency, and is thus more likely to occur again. This results in repetitive, stereotyped "superstitious" (Skinner, 1969) or "parasitic" (Konorski, 1967) behavior. Indeed, preliminary training in an instrumental procedure might facilitate the acquisition of the autoshaped key peck (Davol, Steinhauer, & Lee, 1977; Jenkins, 1977; Schwartz, 1973). The adventitious reinforcement hypothesis arose from a tacit assumption
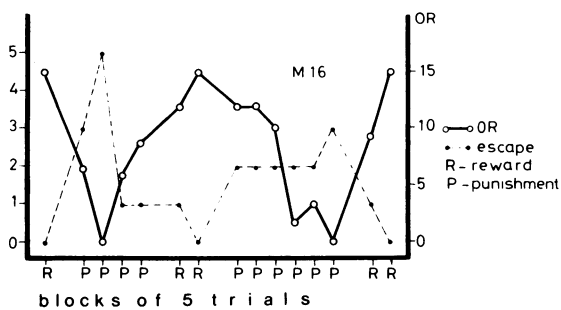

Fig. 5. Orienting scores (OR, right ordinate) and the number of escape attempts (left ordinate) during successive food-reinforced (R) and shock-reinforced (P) blocks of trials within a single session in cat M 16. Note the inverse relationship between OR and escape attempts.

that response-reinforcer contingencies are somehow more fundamental than stimulus-reinforcer contingencies (Staddon, 1977). If the "superstitious" instrumental reinforcement is responsible for the emergence and maintenance of the conditioned OR and autoshaped key pecking, then the theoretical value of the phenomenon is zero.

One way to distinguish between the Pavlovian and the adventitious-instrumental accounts of autoshaping is to make the occurrence of the key-pecking response physically impossible during training. Such an experiment was reported by Breland and Breland (1961). Chickens were trained in an operant box to pull a loop for food reinforcement. This response at the same time released a small ball (CS) in a miniature baseball field placed alongside the training box. When they removed the cage for photography,

> chickens that had been well conditioned in this behavior became wildly excited when the ball started to move. They would jump up on the playing field, chase the ball all over the field, even knock it off on the floor and chase it around, pecking it in every direction, although they never had access to the ball before. This behavior was so persistent and so disruptive, in spite of the fact that *it was never reinforced* [italics mine], that we had to reinstate the cage. (p. 683)

A more formal experiment of this kind was done by Kirby, Muir, and Moore (cited in Moore, 1973). After extended training with an inaccessible but visible CS key, the pigeons were given access to the key during unreinforced test trials. "When the key was first illuminated, eight of the nine animals approached it within seconds" (p. 164). Similar behavior was observed by Zentall and Hogan (1975), Wasserman, Hunter, Gutowski, & Bader (1975), and Pavlov (see above). A second procedure relevant to the evaluation of Pavlovian vs. instrumental contingencies is the omission-training procedure (Sheffield, 1965), in which reinforcement occurs only on those trials in which the CR did not occur. The omission procedure has resulted in rather mixed results. In all studies the omission contingency diminished CS approach tendencies. However, the magnitude of the effect varies greatly across studies. In the majority of the experiments, despite reduction of the auto-

shaped response, the omission procedure never eliminated completely approach to a CS for food (Atnip, 1977; Barrera, 1974; Bilbrey & Winokur, 1973; Davey, Oakley, & Cleland, 1981; Griffin & Rashotte, 1973; Jenkins et al., 1978; Locurto, Terrace, & Gibbon, 1976; Lucas, 1975; Patten & Rudy, 1967; Peden, Browne, & Hearst, 1977; Stiers & Silberberg, 1974; Wasserman, 1973; Williams & Williams, 1969; Woodward, Ballinger, & Bitterman, 1974). In other studies an omission contingency completely eliminated signal-centered responses (Boakes, 1977; Gamzu & Schwam, 1974; Powell & Kelly, 1976; Wessells, 1974; Woodruff & Williams, 1976).

In addition, Jenkins (1973) and Wessells (1974) criticized the validity of omission-training results. They argued that although key pecking per se results in loss of reinforcement, prepecking approach tendencies such as orientation might be adventitiously reinforced on each trial. Such a modified operant interpretation, they suggest, could handle the omission for pecking results. One potential problem with this kind of reasoning is that of infinite regress. If all overt behavior is punished by omission of food, movement antecedents (e.g., perception or subjective evaluation of the CS) might still be consistently reinforced (Peden, Browne, & Hearst, 1977). Both Dickinson and Mackintosh (1978) and Staddon (1977) argue that the finding that CS-directed movements can be modified by their consequences does not force the conclusion that acquisition of the response depended on accidentally present instrumental contingencies (see also Jenkins, 1977; Locurto, 1981).

We used a different rationale to examine the possibility of the adventitious operant account. Rats were trained under signal (SD) + reward (Rd) spatial-contiguity condition. Whether the animal learned to approach the same place in the apparatus (Rd) or the same single cue (SD) was determined by testing under SD-Rd spatial discontinuity conditions long after performance had been stabilized. In this test the animal could approach either SD or Rd but not both. Note that the initial condition mimics the alimentary conditions experienced by animals in their normal habitat. Because under natural circumstances the stimuli signaling food and the food itself are inseparable, an animal approaching the relevant stimulus ipso facto approaches food. In the
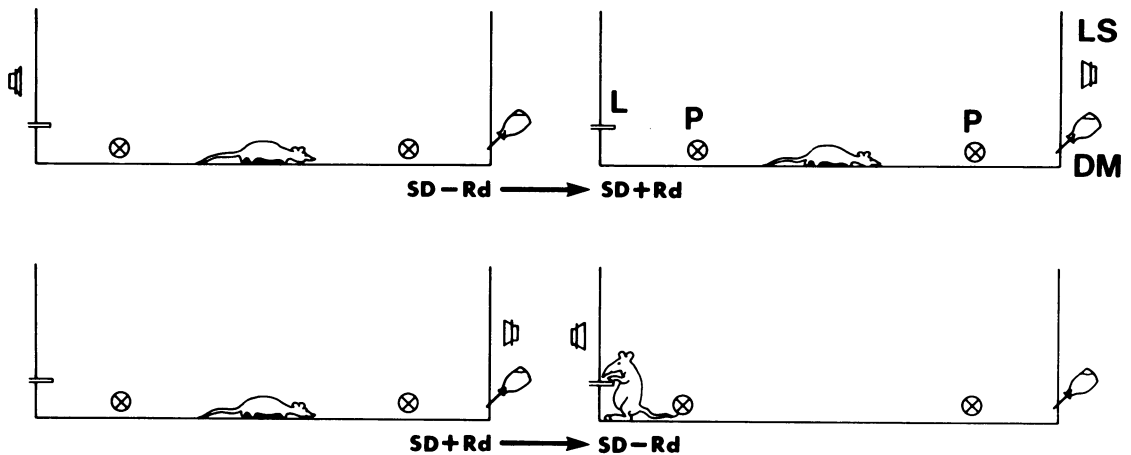
Fig. 6. Schematic of the experimental design. LS, loudspeaker delivering the discriminative signal (SD); DM, drinking magazine delivering water reward (Rd); L, lever; P, photocell.

laboratory, however, we can separate the cue from its significate.

The animals were trained in a straight alley to repeatedly press a lever placed at one end of the alley until a discriminative tone signal (SD) appeared and then to run for a water reward (Rd) available at the other end (Figure 6). The SD was automatically switched on after a random number of lever presses (2 to 6; VR4). The acoustic signal was delivered by one of the two miniature loudspeakers placed above the lever and drinking magazine, respectively. Light beams and phototransistors were located 30 cm from both the lever panel and the magazine panel. The following behavioral measures were recorded: lever-press duration, start time (latency from SD onset to the breaking of the lightbeam close to the lever), run time (time elapsed between breaking of the two successive photobeams), return time (time elapsed from the end of water availability to the next lever press), session time (duration of a session to complete 20 trials), approaches to the magazine in the absence of SD (intertrial runs), lever-press perseveration (additional lever presses after SD onset), the number of occurrences of grooming and rearing, the number of fecal boli, and lever-press topography.

In the initial phase of the experiment, for one group of rats the SD was presented from the loudspeaker above the drinking magazine (i.e., spatially contiguous with reward); another group was trained with SD delivered through the loudspeaker above the lever (spatially discontiguous condition). Both groups

were trained for ten consecutive days. In the next phase of the experiment, the sites of SD deliveries were reversed. The issue was whether changing the source of the acoustic conditioned signal has any effect on behavior.

The principal findings are shown in Figure 7. The spatial location of the signal had a differential effect on the two groups. The initially discontiguous group spent more time in the lever area after presentation of the signal and perseverated more. When SD was presented from above the water magazine, the latency to leave the lever area decreased in this group. The major question of interest was the behavioral change of the initially contiguous group in the second phase of the experiment. Positioning SD above the lever caused significant increases of lever-press duration, start time, perseveration, rearing, intertrial run, and defecation measures. After the presentation of SD, some animals ran down the alley and returned without drinking and resumed lever pressing. The explanation offered for the results was that the rats learned to approach the SD and maintained this behavior throughout conditioning. Spatial discontiguity of SD and reward merely helped to uncover this signal-directed tendency (Buzsáki et al., 1979b).

Since the direction and topography of motor behavior during testing under the SD-Rd discontiguity condition was markedly different from the behavior learned under the SD + Rd contiguity condition, adventitious instrumental contingencies could play no role in the determination of SD-controlled behavior. Several
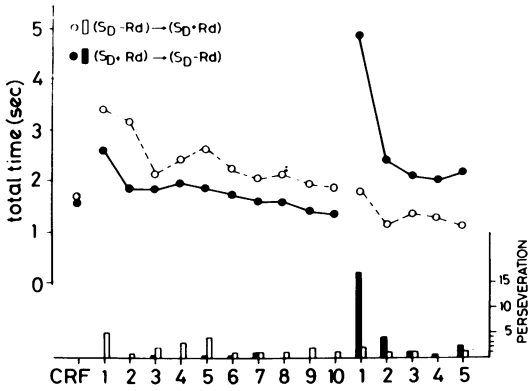
Fig. 7. Total time (start + run times) and lever-press perseveration measures during successive sessions for the discontiguous→contiguous (unfilled circles and columns) and contiguous→discontiguous (filled circles and columns) groups. CRF is last session of continuous reinforcement stage. Note that SD rearrangement differentially affects the two groups.

other observations argue against an adventitious reinforcement account in the present experiment. Many responses (e.g., sniffing, rearing), more prevalent than OR to SD in the first session, were eliminated by the end of training, although these classes of behavior were initially more proximal (both in space and time) to the reinforcer than SD-directed activities. On the basis of the "superstitious" account, one might expect that rats would have reared and sniffed with increasing probability close to the magazine. Likewise OR to SD would have dropped out since responding to SD had no direct associative linkage with water reinforcement. However, the opposite was found. We can conclude that some contingencies are effective in controlling some responses but not other responses, and that certain kinds of behavior (e.g., conditioned OR, sign tracking) occur with both response-independent and response-dependent procedures. These findings are important for at least one reason. They demonstrate that the artificial separation of cue and significate is not a requirement for the emergence and maintenance of the conditioned orienting response. Spatial separation is a tool but not a cause! Quite the contrary seems to be the case: pigeons approach the CS less often when the CS and US are far apart than when close together (Peden et al., 1977). Associations are more easily acquired between events that are spatially contiguous (Testa, 1975), but not impossible when they are separated (Grastyán

& Vereczkei, 1974). An instance of this unnatural situation was recently studied in human neonates (Alegria & Noirot, 1978). Head, eye, mouth, and crying responses were recorded in breast-fed and bottle-fed babies. A breast-fed baby, when in his mother's arm (whether it is the left or right), will find the nipple of the breast by orienting the upper lip towards the source of the mother's voice (CS + US spatial contiguity). For a bottle-fed baby the situation is quite different. A right-handed mother almost always takes the baby in her left arm, the bottle in the right hand, and gives it to the baby with the wrist slightly turned towards the body. As a consequence, the baby will find the "nipple" by mouthing to the left, that is in the direction opposite to the source of the mother's voice (CS-US spatial discontiguity). Breast-fed babies were found to orient both head and mouth in the same direction. Bottle-fed babies were likely to orient their heads towards the voice looking for a face, but oriented their mouths in the opposite direction. Thus, the experiment demonstrated that the mother's voice did not simply trigger sucking behavior (TER), but it was consistently preceded by orienting toward the voice (INI).

THE "WHERE IS IT?" REFLEX

The theory of how associations in Pavlovian conditioning are translated into performance is still inadequately developed (Boakes, 1977). Although it seems obviously adaptive to salivate or flex one's leg in anticipation of food or a painful stimulus to the foot, one might question the adaptive significance of the autoshaped OR in a response-independent laboratory situation. Instead of continuing the debate about the priority of Pavlovian or instrumental contingencies in signal directed behavior, it might be more fertile to examine the phenomenon under investigation from an evolutionary perspective.

Orientation implies directing the sensorium to improve conditions to perceive and evaluate the evoking signal. It is contended that the perceptual system is anatomically "wired" to the motor components of the OR, and possibly at certain phylogenetic levels the two may be indistinguishable. Orientating movements of lower phyla (taxis) offer such examples. The OR, I suggest, is elicited by a biologically relevant stimulus. By "relevant" is meant that

the animal is capable of reacting to it, approaching it, investigating its important features, or avoiding it. Implicit in this formulation is that both novel and learned stimuli are capable of eliciting an OR, provided they contain biologically relevant information. "Key" stimuli of the ethologists provide numerous examples of the former class of stimuli (Eibl-Eibesfeldt, 1951; Ewert, 1976; Kovach, 1971; Lorenz, 1969; Ploog, 1970; Tinbergen, 1951). The persistence of signal-centered behavior in learning situations, summarized in this review, illustrates the conditionability of the OR.

A primary goal of behavior is to avoid harmful situations and approach beneficial ones (Arnold, 1960; Glickman & Schniff, 1967; Grastyán, Szabó, Molnár, & Kolta, 1968; Martin & Levey, 1978; Troland, 1928; Young, 1961). In organisms where appropriate responding to stimuli involves position changes, a prerequisite of reaction is adequate localization of the stimulus. Translation of the perceived information into a spatially oriented motor reaction requires that the evoking signal (i.e., its source) must have been spatially located. "Passive" perception of an attractive conspecific, prey, or a predator in the environment would be of little benefit without the capability of the organism to localize and react upon the perceived item. The neuronal substrate for stimulus localization has developed very early in evolutionary history, if one judges it from its location at the subcortical level. It is phylogenetically older than the specific pattern-recognition systems (Ewert, 1976; Schneider, 1969). The separability of localization and recognition is illustrated by the finding that following ablation of the superior colliculus, the golden hamster is not capable of localizing patterns in space, although it can still distinguish them. In the reverse type of experiment following cortical lesions, pattern recognition is eliminated, but localization remains intact (Schneider, 1969).

In nature, activity is a prerequisite of any kind of food-procuring. I suggest that this concomitantly evolved action system, which gives meaningfulness to the perceptual system, constitutes the orienting response. The question "what is it?" (Pavlov, 1927) thus must be complemented by a simultaneous enquiry: "where is that thing?" Both questions imply that the animal is interpreting its environ-

ment, not by automatic associations but by actively responding.

From the above it follows that the function of the CS is not merely to signal the probability of US occurrence, but also to serve as a "sign post" in the environment to guide the animal. The spatial contingency of CS and US (i.e., their constant spatial relation) makes the CS a signal for US occurrence. Recognition of the guiding feature of the CS may finally discredit the validity of the distinction between classical and instrumental conditioning. According to Skinner (1935), respondents "require no external point of reference in their elicitation or description," in contrast to operants which "require points of reference for their elicitation" (p. 68). The vast literature on signal-directed behavior provides evidence that this differentiation is no longer tenable.

It is therefore not surprising that hungry animals engage in a variety of activities in situations predicting food (Falk, 1961; Staddon, 1977; Staddon & Simmelhag, 1971). Conditioning trials provide the opportunity for the subject to discover the predictors of the US. Any stimulus change or situation that has already been correlated with feeding will upon subsequent occurrence trigger food-searching mechanisms, provided the animal is hungry. We supposed elsewhere that under the effect of positive reinforcement the predictor (CS) becomes a new goal independent of the primary reinforcer (Buzsáki et al., 1980; Grastyán & Vereczkei, 1974; see also Rescorla, 1980). Within this conceptual frame the CS is no longer viewed as a substitute or surrogate of the US, but as a new goal with a capacity that goes beyond the specific goal (US) that had given rise to it. Detection of a significant feature (CS) in the environment induces stimulus-centered responses, and this behavior further increases the likelihood that previously unperceived features of the signal source and its environment will be detected. By approaching the CS source various new attributes (e.g., shadow, echo, smell, size, its distance, its relation to other objects), not experienced from a distal position, will be learned.

When all potentially important features of the predictor (CS) are discovered (i.e., the biologically relevant attributes of the signal source are learned), the autoshaped OR will be restricted to contextually important features of the CS. As a consequence, the "amplitude" of

the OR may decrease. Since the relevance of the predictor never disappears so long as the CS-US relationship remains unchanged, the OR will be sustained, even though overt behavioral components might no longer be detected. The fact that the OR may be relatively inaccessible to the observer late in conditioning raises problems of measurement but does not detract from the potential organizing force of the concept.

As discussed above, the present formulation of the autoshaped response differs from the stimulus or object substitution concepts of directed action (Hearst & Jenkins, 1974). It does not depend on speculations about whether the mechanism involved in the response is classical conditioning, stimulus generalization, or anything else. It was shown that conditioned signal-directed responses occur in an identical fashion in response-dependent and response-independent paradigms regardless of the absence of strict Pavlovian contingencies. The concept of conditioned OR is at variance also with the conditional release hypothesis of the autoshaped response (Woodruff & Williams, 1976). This hypothesis suggests that consummatory fixed-action patterns are released by signals for impending reinforcing stimuli. In contrast to the rigidity of fixed-action patterns (Hinde, 1970) the conditioned OR shows a rich variability in its form determined primarily by the type and location of the CS. The learned-release hypothesis cannot answer the question of why the CS, which is claimed to release the fixed-action pattern, becomes the target of that behavior (Jenkins, Barrera, Ireland, & Woodside, 1978).

Stimuli predicting danger, pain, or threat to life will repel the organism from the source of these stimuli. Some investigators suggest that avoidant behavior of this sort is mediated by special preprogrammed systems that operate independently of conventional learning processes (Bolles, 1970; Burstein, 1977; Garcia & Ervin, 1968). The available evidence suggests that, indeed, animals tend to withdraw from aversive CSs. This negative sign-tracking (Green, 1978; Leclerc & Reberg, 1980; Peden et al., 1977; Wesp, Lattal, & Poling, 1977; Boakes, Note 1) decreases the likelihood that the animal will learn its detailed features. More research is needed, however, to elucidate the nature of behavior evoked by stimuli predicting aversive USs.

Briefly, I suggest that the cat knows more about the mouse than vice versa.

FINAL COMMENT

The purpose of the present review was to point out that research on the function and causation of directed action began considerably earlier than it is usually dated with the discovery of autoshaping. Investigations of the OR began simultaneously with the discovery of the conditioned reflex. Although the theoretical emphasis in Eastern European literature has been on the perceptual, information-processing, and response-directing mechanisms that the OR is claimed to control, most of the Western literature has been concerned with the parametric description of a few (almost exclusively vegetative) parameters during the evocation, habituation, and reevocation of the OR (Siddle & Spinks, 1979). This might explain why research on autoshaping and the OR has progressed independently and have had virtually no impact on each other. Since both lines of research have accumulated a considerable amount of valuable data in connection with learning and conditioning, future research might profit greatly by combining the two approaches.

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