

Effects of Poisoning on Predatory and Ingestive Behavior Toward Artificial Prey in Rats (*Rattus norvegicus*)

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Ingestion of novel prey by vertebrate predators that is followed by illness typically decreases the predators' eating the prey more readily than their pursuing or killing it. We used artificial prey-food items (rolling ball bearings that predicted food pellets) to model and extend this finding in laboratory rats. During daily experimental sessions presentations of a novel bearing-food combination were intermixed with presentations of a familiar bearing-food combination. The poisoned animals received lithium chloride injections after each session. Experiment 1a showed that: (a) Poisoning markedly decreased ingestion of the novel food without decreasing the frequency of contact (nose, seize, carry, or chew) with the novel bearing predicting that food. (b) However, poisoning did significantly decrease the average duration of contact with the novel bearing. (c) Poisoning did not decrease behavior toward the familiar food and bearing. Experiment 1b showed that after moderate exposure to pairings of the novel food and bearing, poisoning decreased behavior toward both novel and familiar food and bearings. The results indicate that important aspects of predation can be simulated and examined in the laboratory by using artificial prey-food items. These results also support the conclusions that predatory behavior and ingestion reflect separable modes of behavior and that the presence of novel prey interferes with the generalization of poisoning effects to familiar prey.

The study of predatory behavior and its modification through learning is of considerable scientific and practical importance. Predatory behavior relates directly to issues of survival and the natural selection of stimulus-control mechanisms, motor programs, and motivational structure (e.g., Curio, 1976; Kenward, 1978; Leyhausen, 1956/1979). At a practical level predatory behavior often has considerable economic impact. Despite its importance the study of predatory behavior has been questioned because of ethical concerns with the fate of the prey. Huntingford (1984) has suggested a number of techniques to minimize potential objections to studies of predation, including field studies of natural encounters, a reduction in the number of subjects, and the use of model predators. The present experiments provide an example of another technique for the study of predatory behavior by using an artificial prey-food item (a moving ball bearing predicting food) to study the control of predatory behavior in rats.

Rats reliably come to direct complex predatory behaviors to rolling ball bearings that predict the delivery of laboratory pellets (Timberlake, 1983; Timberlake, Wahl, & King, 1982). After 7-10 days of pairings of ball bearings with food, rats frequently dig the bearing out of the entrance hole, seize it with their forepaws, stuff it into their mouths, carry it about the chamber, turn it in their paws and gnaw it, hold it to the floor under one paw, and retrieve it if it rolls away. Rats show

similar behaviors in the capture of live prey (Karli, 1956; W. Timberlake, personal observation, May-June, 1977). Seven other rodent species also have shown close relations between natural predatory behavior and their responses to a moving ball bearing (Timberlake & Washburne, 1987).

The present research further explored the use of artificial prey-food items to study predatory behavior by questioning whether rats will show the poison-induced dissociation between attack and feeding previously reported for natural prey items. Poisoning has been shown to suppress eating more readily than predation in a variety of carnivorous and omnivorous mammalian species, including coyotes (Gustavson, Garcia, Hankins, & Rusiniak, 1974), coyotes and wolves (Gustavson, Kelly, Sweeney, & Garcia, 1976), ferrets (Rusiniak, Gustavson, Hankins, & Garcia, 1976), laboratory rats (Berg & Baenninger, 1974; Krames, Milgram, & Christie, 1973; Milgram, Caudarella, & Krames, 1977; Rusiniak et al., 1976), laboratory mice (Lowe & O'Boyle, 1976), ringtail cats (Etscom, 1978), hamsters (Langley & Knapp, 1984), and grasshopper mice (Langley, 1981). Similar results were reported for wild hawk attacks on live prey (Brett, Hankins, & Garcia, 1976). The present research also questioned whether poisoning effects in rats will generalize from novel to familiar prey. Several studies with natural prey items have shown minimum generalization (e.g., Brett et al., 1976; Nicolaus, Cassel, Carlson, & Gustavson, 1983).

If similar results are obtained by using ball bearings that predict food as model prey items, it would support the possibility of using artificial stimuli to explore the control of predatory behaviors. Experiment 1a established whether poisoning produced a differential reduction in eating a novel food compared to attacking a novel bearing and whether any reduction in ingestion or predation generalized to familiar stimuli. Experiment 1b tested the possibility that generaliza-

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tion to familiar prey-food items could be enhanced by increased familiarity with the novel prey-food item prior to poisoning.

Experiment 1a

Rats conditioned to a high level of interaction with a ball bearing predicting food were presented on a random half of their daily trials with a novel ball bearing (differing in sound of movement, texture, taste, odor, and visual pattern) paired with a novel, saccharin-coated food. On the other trials the familiar ball bearing continued to predict the familiar food. This procedure was intended to mimic aspects of the sudden emergence of novel, alternative prey in natural settings. The use of ball bearings as Pavlovian predictors of food allowed us to separate predatory from ingestive behaviors both in terms of the controlling stimuli and by not requiring predatory behavior before ingestive behavior could occur. The presence of both novel and familiar ball bearings and food allowed us to determine the extent to which avoidance of either predation or ingestion generalized to more familiar prey. If behavior in this simulation resembles previous results with natural prey, the rats should avoid ingesting the novel food after poisoning but continue to attack the novel ball bearing (though perhaps with reduced intensity; see Langley, 1981). In addition, the effects of poisoning should not generalize to the familiar bearing and food (e.g., Nicolaus et al., 1983).

Method

Subjects. The subjects were 18 naive, male, albino Wistar rats, approximately 120 days of age at the beginning of the experiment. The animals were housed individually under a 12:12 hr light/dark cycle and were maintained at 85% of their ad lib body weights by daily postsession feedings.

Apparatus. The apparatus was described completely in Timberlake et al. (1982, Experiments 1 and 2). Briefly, it consisted of a sheet metal box (30 × 61 × 30 cm) with a Plexiglas roof and front. The entire box was slanted 5° to the left, and the floor of the box slanted in from the front and back to a brass trough that ran the length of the apparatus. Ball bearings entered the trough at the right end through a small hole and rolled the length of the apparatus in 3.1 s (if undisturbed), exiting through a small hole just to the left of two adjacent food receptacles. If the ball bearing was displaced from the trough by the rat, the pitch of the floor returned it to the trough when it was released. Noyes pellets (45 mg) were delivered singly to the food receptacles by Waltke Scientific Feeders.

The commercial-grade, steel ball bearings were 1.6 cm in diameter. They had been placed in organic acid detergent, so their color was dark grey. The novel ball bearings were created by painting alternating one-quarter sections of the bearing using white lacquer. The novel bearings felt, smelled, and tasted different to humans and had a more variable sound and a flashing appearance as they rolled. If the rats chewed the lacquer off, the bearing was repainted.

Procedure. Previous to the experiment all animals received 16 days of 10 Pavlovian pairings a day of ball bearings and food (standard 45-mg Noyes pellets). As expected from Timberlake (1983) and Timberlake et al. (1982), the average median percentage of trials with a contact increased from 30% in an initial baseline to 76% during the last three days of training. The animals were then divided into two groups: poison and control. Each group received 4 days of 16 ball bearings per session on a variable-time 50-s schedule. A random

half of the bearing presentations per session were novel (striped); the remaining bearings were familiar. Following the exit of each novel ball bearing, the novel food was delivered (saccharin-coated, 45-mg Noyes pigeon pellets). After each of the first three sessions, the poison group received an ip injection of lithium chloride (.15 M at 2% of body weight) an average of 20 min posttrial. The control group was injected with a comparable volume of physiological saline. Measures of behavior during the first session served as an estimate of the unpoisoned reactions of the animals (baseline). All subsequent trials for the experimental animals followed poisoning on the previous day.

Results and Discussion

Figure 1 shows the average number of pellets eaten during the baseline session and the three sessions following lithium chloride injections. It can be seen that animals in the control group ate all of both the novel and familiar pellets. Animals in the poison group ate all the familiar pellets but markedly decreased their consumption of the unfamiliar pellets following the poisonings. This phenomenon was confirmed in a one-between, two-within analysis of variance that revealed significant effects of poison, novelty, sessions, and all interactions, all $p < .01$. Figure 1 also shows that the mean percentage of trials with a bearing contact was not significantly affected by poisoning. Neither poisoning, novelty, nor sessions produced a significant effect, all $p > .10$. However, the figure also shows that the average duration of contact with the novel bearing decreased following poisoning, $t(8) = 8.32$, $p < .01$, whereas the average duration of contact for the control group did not, $t(8) < 1$, $p > .10$.

Thus, poisoned rats continued to exhibit predatory responses to the novel ball bearing, though they markedly reduced their ingestion of the novel food. However, there was a decline in the average duration of interaction with the novel bearing, supporting Langley's (1981) finding that poisoned grasshopper mice decreased the length of prey engagement though not frequency of contact. It may be that a decline in duration of contact following poisoning is mediated by the taste of the prey rather than by its appearance or movement. Our results also indicated that the effect of poisoning was specific to the novel food and bearing. The decline in average duration of interaction with the novel bearing without a similar decline for the familiar bearing shows that the rats discriminated between the two types of bearing and that the decline in duration was not a nonspecific outcome of poisoning.

Experiment 1b

Although their duration of predatory behavior to a novel ball bearing predicting food was reduced by repeated poisoning, animals in Experiment 1 continued to contact the bearing reliably. Further, there was no indication of any decremental effect of three poisonings on behavior to the familiar food or bearing. The latter result suggests that poisoning effects with natural prey may be limited to interaction with novel prey. In support of this contention, free-ranging crows with access to poisoned green eggs and safe white eggs significantly reduced their intake of green eggs without changing their ingestion of the familiar white eggs (Nicolaus et al., 1983). Yet

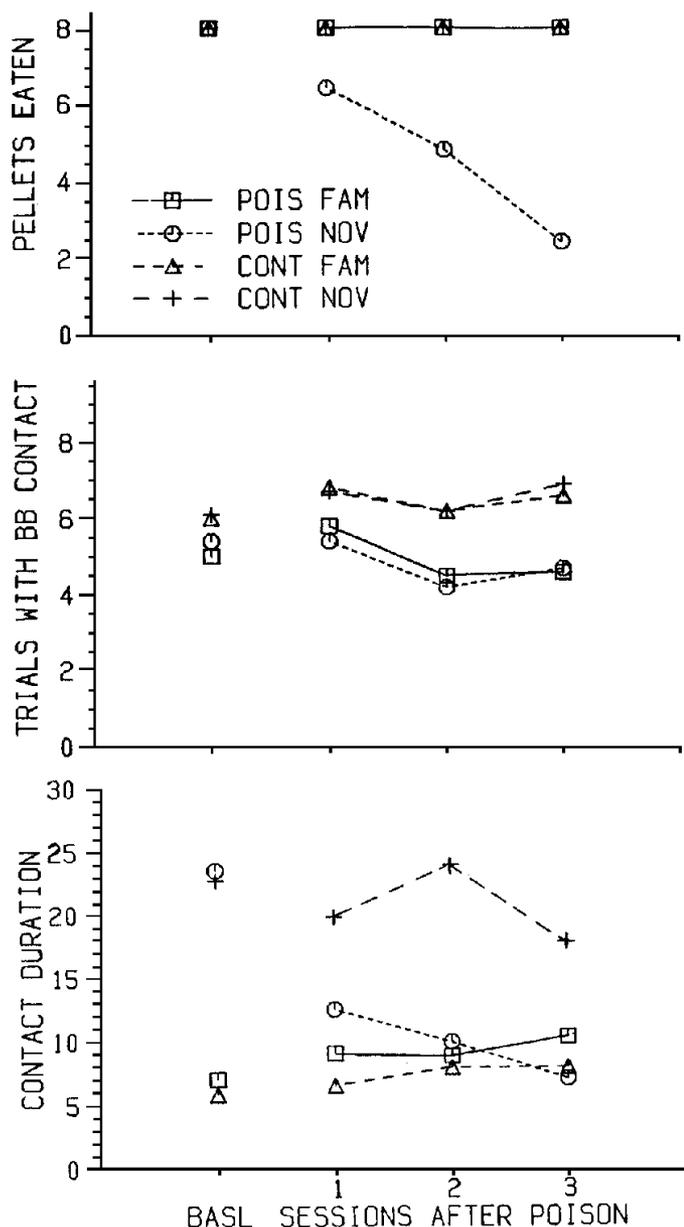


Figure 1. Averages for the number of pellets eaten, the number of trials with contact with a ball bearing that predicted food, and the duration of contact with ball bearings (in seconds) by the poisoned and control groups in the session prior to any poisoning (baseline) and in the three sessions after daily poisonings. (During each session eight novel and eight familiar ball bearings were presented, each followed by a corresponding novel or familiar food pellet. Average duration of bearing contact was based only on trials with a contact. All data are from Experiment 1a.)

there is some evidence of generalization of poisoning effects to familiar prey with both hawks and coyotes (Brett et al., 1976; Gustavson et al., 1974; Gustavson et al., 1976).

Experiment 1b tested whether reduced novelty of a new prey-food item might facilitate generalization of avoidance to familiar prey. Our basic premise was that the unique salience of novel prey-food as a conditioned or discriminative stimulus

for poisoning effects interferes with generalization of the effects of poisoning to familiar prey-food items. Experiment 1b tested this premise by poisoning the control group from Experiment 1a. During Experiment 1a these animals had received 32 pairings of novel ball bearings and food (four days) intermixed with an equal number of pairings of familiar bearings and food. In the present experiment these animals received five more days of the same pairings but with daily postsession injections of lithium chloride.

Method

Subjects and apparatus. The subjects were 9 animals from the control group in Experiment 1a. The housing, maintenance conditions, and apparatus were the same as in Experiment 1a.

Procedure. The animals received the same procedures as the poisoned group in Experiment 1a. Each of four daily sessions was followed by poisoning, and behavior to the bearings and food was recorded on the next day. This meant a total of one baseline session and four successive test sessions, all but the last test session followed by poisoning.

Results and Discussion

Figure 2 shows that repeated poisonings decreased intake of the relatively novel food nearly to zero and also decreased intake of the familiar food, $F(3, 24) = 44.02, p < .001$. In a test of simple main effects of sessions on the intake of (relatively) novel and familiar foods, both reductions were significant, $F_s(3, 24) = 38.5$ and 3.24 , both $p_s < .05$. Figure 2 also shows a decline in contact with both relatively novel and familiar bearings as a function of poisoning days, $F(3, 24) = 10.70, p < .001$, but no difference in reaction to the two bearings, $F(1, 8) = .04, p > .10$. Finally, Figure 2 shows a significant decrease in average contact duration as a function of poisoning trials, $F(3, 24) = 4.76, p < .01$. However, in tests of simple main effects, only the decline in average duration of contact with the relatively novel bearing was significant, $F_s(3, 24) = 5.52$ and $1.59, p < .01$ and $> .10$, respectively, for the relatively novel and familiar bearings.

In short, with continued poisoning days animals exposed to familiar and relatively novel food significantly decreased intake of both foods. Poisoning also decreased the frequency of contact with the familiar and relatively novel prey stimuli (bearings), though the average duration of contact was reduced significantly only for the more novel bearing. Because there was no control group in the present study, it may be argued that the observed changes were due to the passage of time or experience rather than poisoning. However, the five days of exposure to the combination of novel and familiar bearings prior to poisoning showed stable responding for these animals on all measures. In addition, there was no indication in previous work that animals stop eating pellets or interacting with predictive bearings as a function of sessions (Timberlake, 1983; Timberlake et al., 1982).

General Discussion

It appears that a procedure in which a moving ball bearing serves as a Pavlovian conditioned stimulus for the delivery of

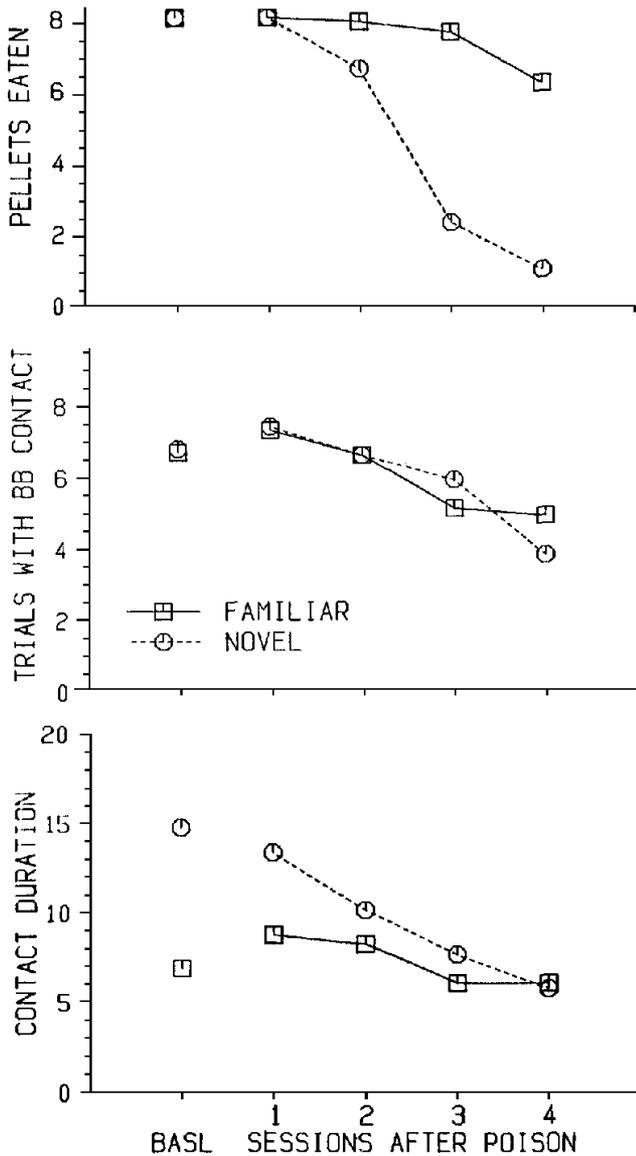


Figure 2. Averages for the number of pellets eaten, the number of trials with contact with a ball bearing that predicted food, and the duration of contact with ball bearings (in seconds) in the session prior to any poisoning (baseline) and in the four sessions after daily poisonings. (During each session eight novel and eight familiar ball bearings were presented, each followed by a corresponding novel and familiar food pellet. Average duration of bearing contact was based only on trials with a contact. All data are from Experiment 1b.)

food to hungry rats models important aspects of predation on natural prey items and thus provides an opportunity to study determinants of predatory behavior in a laboratory simulation not involving killing. The validity of our simulation of predation is supported by two observations. First, the rats treated the bearing as they would live prey by digging it out of the entrance hole, seizing it in their mouths, running about the cage with it, sitting and gnawing it, restraining it, and retrieving it. This is not to say that all of these responses are

exclusively linked to predation but that the sequence and topography of behavior highly resembles instances observed with live prey. Second, as in field research the rats showed rapid suppression of ingestion of a novel food following poisoning but no suppression of frequency of attack on the bearing predicting it.

This dissociation of the determinants of ingestion and attack has been obtained frequently with natural prey (e.g., Baxter, 1979; Brett et al., 1976; Krames et al., 1973; Langley, 1981; Langley & Knapp, 1984; Rusiniak et al., 1976), and it is not surprising given that poisoning appears more readily associated with gustatory than with exteroceptive stimuli (e.g., Garcia, Hankins, & Rusiniak, 1974). Ingestion is controlled largely by gustatory cues, whereas attack is typically controlled by exteroceptive cues. A potential basis for dissociation is also present in the relatively independent control of killing and eating that appears in development (e.g., Fox, 1969) and in reports that a predator will seek out the opportunity to exhibit predatory behavior without accompanying ingestion (e.g., Baxter, 1979). Consider that moving cues, especially for more carnivorous animals, may trigger continued predation even in the face of conditioned avoidance (Langley, 1981). For example, a ferret poisoned following ingestion of rats continued to kill them by trampling them with its forefeet even though apparently unable to bring itself to bite them (Rusiniak et al., 1976).

It is worth noting that this pattern of persistence of interaction with the bearing but decreased ingestion of food would not be expected on the basis of the relative delay to the aversive consequence. Though the poisoning was closer in time to the ingestion of food than to interaction with the bearing, the difference was only a few seconds compared with a delay period of 20 min to the injection and longer to its effects. Neither is this pattern of results (persistence of a conditioned response following devaluation of a reinforcer) a predominant finding in the general Pavlovian literature (Rescorla & Holland, 1982).

However, this pattern of results has been obtained in laboratory research. For example, Holland and Straub (1979) found that associating poison with unconditioned stimulus of food in rats failed to reduce activity, head jerk, or startle responses during a tone conditioned stimulus, though it did reduce the responses of head in the magazine and ingestion. When combined with the evidence for persistence of operant behaviors after devaluation of reward (e.g., Adams & Dickinson, 1981; Morgan, 1974) and the results summarized above distinguishing attack and ingestion, these results suggest the following generalization for the feeding system. More food-distant search behaviors (such as predation related search and attack, instrumental approach, or extensive required manipulation) will be less affected by devaluation of a reinforcer than behaviors more closely related to consumption (such as gnawing the bearing, sniffing a predictive bar [Cleland & Davey, 1982], or entering the food tray). Food-distant and food-proximate responses have been hypothesized to reflect separable modes of behavior (Timberlake & Lucas, in press).

Learning related to poisoning appears complex and multiply determined (Domjan, 1980). There appear to be specialized mechanisms by which a novel taste coupled with subse-

quent poisoning is immediately avoided, and other mechanisms by which taste potentiates avoidance of environmental cues (e.g., Galef & Osborne, 1978). There also appear to be less specialized processes mediating poisoning effects, such as second-order conditioning of context cues based on pairings with a conditioned noxious taste (e.g., P. J. Best, Best, & Ahlers, 1971; Melcer & Timberlake, 1985), primary conditioning based on direct pairings of exteroceptive stimuli or responses with illness (e.g., Mitchell, Kirschbaum, & Perry, 1975), and overshadowing of taste cues by a novel environment or taste (e.g., M. R. Best & Meachum, 1986; Revusky & Bedarf, 1967).

The generalization of poisoning effects in Experiment 1b may reflect some of these less specialized processes. Recall that with completely novel prey-food items in Experiment 1a poisoning rapidly decreased ingestion of the novel food but not frequency of contact with the bearing. In contrast, poisoning after 32 exposures to the novel bearing and food produced a slower decrease in ingestion of the novel food but was accompanied by significant decreases in ingestion of the familiar food and frequency of interaction with both bearings. These results appear to combine and extend two lines of previous laboratory research, one showing that initial avoidance of ingestion declines with decreased novelty of a taste cue (e.g., Siegel, 1974), and the other showing that the presence of a novel taste cue attenuates aversions to both exteroceptive stimuli and other taste cues (e.g., Revusky & Garcia, 1970; Revusky & Parker, 1976).

It seems that the mechanisms related to taste-aversion learning combine to produce maximum speed of effect and minimum generalization when a completely novel prey item is present. In the absence of such novel prey, poisoning may produce less rapid learning that is more readily generalized to other gustatory and exteroceptive stimuli. Some support for this conclusion is provided in the work of Brett et al. (1976), Gustavson et al. (1976), and Nicolaus, Hoffman, and Gustavson (1982). In the first study predation-experienced hawks that were poisoned following ingestion of a black mouse suppressed killing and eating of all mice, whereas addition of a novel bitter taste to a mouse followed by poisoning produced cue specific suppression. In the last study free-ranging raccoons received poison in chicken carcasses after moderate experience in killing and eating tethered chickens. They subsequently failed to kill any offered chicken, regardless of its resemblance to the poisoned prey.

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APA Buys *Clinician's Research Digest*

APA has acquired the *Clinician's Research Digest* and will take over formal publication of the digest as of July 1, 1988. Presently published by the California-based Relational Dynamics Institute, *CRD* offers practitioners brief summaries of clinically relevant research findings and other clinical information.

Clinton W. McLemore, PhD, president of Relational Dynamics, founded *CRD* in 1983. McLemore will continue to serve as *CRD* editor through June 30, 1988. A new editor, to be selected, will take over as of July 1, 1988.

The *CRD* acquisition was proposed by the ad hoc Committee on Practitioner Publications (PPC), chaired by Charles D. Spielberger. From 1984 to 1987, the PPC, established by the P&C Board at the behest of the BOD's Subcommittee on the Future of Professional Education in Psychology, made several recommendations for practice-oriented publications tailored for health service providers, school/educational psychologists, and I/O psychologists—including the development of monograph series for each group.

A continuing education program, which has also been acquired by APA, is offered in conjunction with the *CRD*. RDI will continue to operate the program under license from APA.

For the present, information on subscriptions to *CRD* and the *CRD* CE Program can be obtained from Clinical Information Services, P.O. Box 61025, Pasadena, California 91106-9990. *CRD* will be issued monthly beginning in January 1988. 1988 subscription rates: individuals, \$48; institutions, \$62.
