

TIME DEPENDENT CHANGES IN CONDITIONED SUPPRESSION

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ABSTRACT

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by

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The Kamin effect was investigated using a conditioned suppression procedure in a within-subjects design. Four groups of pigeons received Pavlovian conditioning "off the baseline" immediately followed by operant conditioning. During the Pavlovian phase, two groups received a forward pairing of a tone with shock, one group received a backward pairing and one group received a truly random pairing. One of the forward pairing groups also received a delay between the Pavlovian and operant phases. For all groups, keypecking was reinforced on a variable interval schedule during the operant phase. Testing sessions were identical to training sessions with the exception that the tone used during Pavlovian conditioning was presented either 0 min, 15 min, 30 min, 45 min, or 60 min following the onset of the operant phase. Testing sessions in which the Pavlovian phase was omitted were also included. The results showed U-shaped functions for 11 of the 12 pigeons in the forward pairing groups and for 3 of the 5 pigeons in the truly random group. The functions were flat rather than U-shaped for pigeons in the backward pairing group.

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By

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INTRODUCTION

In most studies of learning, retention is a monotonically declining function of the amount of time since original learning. An exception to this rule is the U-shaped function, known as the "Kamin effect," obtained following aversive conditioning with infra-human organisms. Kamin (1957), in a between subjects design, incompletely trained rats to avoid shock in a shuttlebox apparatus using a tone as the CS. Following this training, the subjects were divided into groups. One group was immediately given additional training on the shuttlebox task while the other groups received delays between initial and subsequent conditioning that ranged from 30 min to 17 days. The mean number of avoidance responses during retraining was used as the measure of performance. The results showed a decline in successful avoidance responses up to the one hour delay period. Groups with delay intervals greater than one hour showed progressively higher successful avoidance responses. For the 24 hour delay group, the number of avoidance responses did not differ significantly from the group retrained immediately. When performance was plotted as a function of the delay interval, a U-shaped function was obtained with the greatest deficit in performance occurring at the one hour delay interval.

The "Kamin effect" is always measured as a change in performance obtained after various retention intervals following the occurrence of aversive conditioning (Anisman, 1975; Brush, 1971; Klien & Spear, 1970). The function reflects changes in the ability of an organism to learn or perform an avoidance response. It is reasonable to assume, however, that if an organism's response to a CS used in Pavlovian aversive conditioning was measured over time, a U-shaped function would also be obtained.

To determine if time dependent changes in an organism's reaction to a CS occurs, it is necessary to use a procedure that does not require a specific avoidance response. Conditioned suppression, a decrease in the rate of an operant response during the presentation of an aversive CS, fulfills this requirement. Hunt and Brady (1951) developed a variation of the conditioned suppression procedure, known as "off the baseline" conditioned suppression, in which aversive Pavlovian conditioning occurs prior to testing the CS on an operant baseline. This method permits the manipulation of the retention interval between classical conditioning and testing of the CS on an operant baseline.

An "off the baseline" procedure has been used by McMichael (1966) and Tarpy (1966) to measure time dependent changes in the level of conditioned suppression. In both experiments, rats received avoidance training in a shuttlebox, followed after various retention intervals by testing in an operant chamber. Testing consisted of the presentation

of the tone used in training while lever pressing was reinforced with food. Their results showed a monotonic increase in conditioned suppression as a function of the retention interval. The failure of these studies to obtain a U-shaped function led Brush (1971) to tentatively conclude that a U-shaped function is not obtained when a conditioned suppression procedure is employed.

In an unpublished study from this lab, rats were given avoidance training in a shuttlebox. Following training, the rats were immediately placed in an operant chamber. A suppression measure for bar pressing was then taken at various retention intervals. Results showed a U-shaped function with rats at intermediate retention intervals showing maximum levels of suppression. The purpose of the present study was to determine if a U-shaped function is obtained following aversive Pavlovian training when the tone used in training is superimposed upon a baseline of operant behavior. The present study employed Pavlovian conditioning to avoid any problems resulting from the acquisition of an avoidance response during the training phase. To avoid any problems resulting from conducting training in a different chamber from the one used in testing, pigeons received both training and testing in the same chamber. Pigeons were selected as the experimental organisms because of the paucity of data on the "Kamin effect" with this species.

In contrast with most previous studies on the "Kamin effect," the present study used a within-subjects design.

The use of a within-subjects design permitted an evaluation of time dependent changes in conditioned suppression for individual pigeons. Klein and Spear (1973) also used a within-subjects design to investigate the "Kamin effect" but reported only group averages.

The present design consisted of an experimental group and three control groups. The experimental group received a tone followed immediately by shock during Pavlovian conditioning. To ensure that subsequent suppression of operant responding during the tone was the result of the pairing of the tone with shock, control groups were necessary. The traditional control group in Pavlovian conditioning has been a backward pairing of the CS with the US. However, Rescorla (1969) has argued that a CS which follows a US may become inhibitory because it predicts the absence of the US for a period of time. He suggested a "truly random" correlation of the CS with the US as the appropriate control condition. In a "truly random" control procedure, the probability of the US in the presence of the CS is equal to the probability of the US in the absence of the CS. Initially, Rescorla (1969) predicted that conditioning to the CS does not occur using a "truly random" procedure. However, Benedict and Ayres (1972), Kremer and Kamin (1971), and Quinsey (1971) demonstrated conditioning to the CS using "truly random" procedures. Rescorla (1972) later predicted that excitatory conditioning could occur using the "truly random" procedure but that with extended training,

conditioning would dissipate. Given this lack of consensus about the appropriate control group, both the traditional backward pairing control group and the "truly random" control group were used in the present study. The appropriate control group should fail to demonstrate time dependent changes in conditioned suppression thereby producing a flat function.

A third control group received forward pairings of tone with shock during the Pavlovian phase of daily training identical to the experimental group. However, while in the experimental group an operant phase immediately followed the end of Pavlovian conditioning, the control group received a delay period of varying lengths between the end of Pavlovian conditioning and the beginning of operant conditioning. This group was included to determine if responding on an operant baseline during the retention interval, the period of time between the end of Pavlovian conditioning and the suppression test, had any effect on the U-shaped function. If only the length of time between Pavlovian conditioning and testing is the important determinant of the U-shaped function, then the gradients in both the experimental group and the third control group should be similar.

METHOD

Subjects

Twenty-four white Carneaux pigeons were maintained at 80 percent of their free-feeding weight. Each pigeon was implanted with a stainless steel wire through each side of its pubic arch. The wires were attached to a phono plug mounted on the pigeon's back.

Apparatus

Two standard 3 key, Lehigh Valley Electronics experimental chambers were used. The center key of each chamber was illuminated with a black vertical line on a white background or a green (555 nm) wavelength. The stimuli were projected onto the key using an Industrial Electronics Engineers inline projector (model #10-0W78-1820-L). A houselight, consisting of a GE #1820 lamp, remained on during sessions. A GE #1820 lamp illuminated the food hopper during reinforcement. The onset of reinforcement was controlled by a Lehigh Valley Electronics Photosensor (model #221-10). A speaker, mounted on the front panel of the operant chamber was used to present the auditory stimulus. A B & K sound pressure meter was used to set the auditory stimulus at 65 db. above the ambient noise level. The chamber was modified for shock delivery as described by Klein and Rilling (1974). A high internal resistence

AC milliampere power supply, insensitive to external resistence changes up to 5000 ohms, was used as the shock source. A fan, providing masking noise and ventilation, remained on during sessions. The chambers were maintained in separate rooms separated by a central room in which programming and recording equipment was maintained.

Procedure

Pretraining

The pigeons were initially magazine trained and autoshaped to peck the center key. An autoshaping trial consisted of the illumination of the key with the 555 nm stimulus for 8 sec followed by access to a grain filled hopper for 3.5 sec. The autoshaping trials were controlled by a variable time (VT) 60 sec schedule in which the 555 nm stimulus followed by the access to grain was presented at variable times with a mean of 2 min independent of any response by the pigeon. Each session of autoshaping was 60 min in duration and was terminated when a pigeon emitted 100 or more responses to a 555 nm stimulus during the session for two consecutive sessions.

After autoshaping, the pigeons received one 60 min session on a variable interval (VI) 30 sec schedule followed by two 60 min sessions on a VI 60 sec schedule. Next, the pigeons received two, 60 min sessions of exposure to a 1000 HZ tone. A session consisted of 2 min presentations of the tone while a VI 60 sec schedule was in effect. The tones

were presented randomly throughout the session according to a VT 2 min schedule. During all of the sessions in which a pigeon pecked for reinforcement, the key was illuminated with the 555 nm stimulus.

Training

Following pretraining, the pigeons were divided into four groups: (a) a forward pairing (F) group, (b) a forward pairing with operant delay (FD) group, (c) a backward pairing (B) group, and (d) a truly random (R) group. Each group consisted of six pigeons.

A training session consisted of two phases, a Pavlovian conditioning phase and an operant conditioning phase. In the Pavlovian phase, the pigeons received presentations of a 1000 HZ tone and a 2 ma shock. In the operant phase, the pecking response was reinforced on a VI 60 sec schedule. Grain was never available during the Pavlovian phase and shocks never occurred during the operant phase.

The onset of the Pavlovian phase was signalled by the illumination of the houselight. The duration of the 1000 HZ tone was 2 min and the duration of the 2 MA shock was 1.5 sec. For the forward pairing (F) group and the forward pairing with operant delay (FD) group, the presentation of the tone was immediately followed by shock. The intertrial interval (ITI) was varied following a VT 2 min schedule. For the backward pairing (B) group, a trial consisted of the presentation of shock followed, after a 10 sec delay, by

the tone. The tone was followed by a 30 sec safe period before the next ITI began. A VT 2 min schedule determined the ITI. For the truly random (R) group, tone and shock presentations were programmed on independent VT 2 min schedules. For all groups, the Pavlovian phase ended when a pigeon had received 15 presentations of the tone and 15 presentations of the shock.

At the end of the Pavlovian phase, the center key was illuminated with the 555 nm stimulus for all groups except the forward pairing with operant delay (FD) group. During the operant phase, responding was reinforced on a VI 60 sec schedule. No tones or shocks occurred during this phase prior to testing. For the forward pairing with operant delay (FD) group, a delay between the Pavlovian and operant phases was imposed. This delay was indicated by the illumination of the center key with a vertical line stimulus. The delay period was either 0 min, 15 min, 30 min, 45 min, or 60 min in duration. The delay intervals were randomized across sessions with each subject receiving two sessions at each delay interval. During the delay period, no shocks or tones were presented, nor was reinforcement for responding available. At the end of the delay interval, the key was illuminated with the 555 nm stimulus and responding was reinforced on the VI 60 sec schedule.

For all groups, the operant phase was 60 min. Each session consisted of a Pavlovian phase followed by an operant

phase. There were 10 training sessions.

Testing

Testing sessions were identical to training sessions with one exception. During the operant phase the 1000 HZ tone was presented without shock for 2 min either 4 min, 15 min, 30 min, 45 min, or 60 min from the beginning of the phase. The Pavlovian phase preceded the operant phase as in training. The tone was presented only once per session for testing during the operant phase. The schedule of reinforcement remained in effect during the presentation of the tone. At least 24 hr intervened between testing sessions. For the forward pairing with operant delay (FD) group, the delay separating the Pavlovian and operant phases was terminated 4 min prior to the scheduled tone presentation. For the 4 min testing interval, no delay occurred.

All groups also received sessions in which the Pavlovian phase was omitted. These sessions were always 24 hours following a normal testing session. During these testing sessions, the tone was presented at one of the testing intervals and all testing intervals were sampled across pigeons.

The order of testing was randomized within and between pigeons with all testing intervals sampled across pigeons per day. The randomized schedule of testing was replicated three times giving each pigeon four tests at each interval. Each pigeon received a total of 24 testing sessions.

Suppression ratios were calculated using Kamin's (1961) formula. The formula is:

$$\frac{T}{\text{pre }T + T}$$
(1)

Where T is the number of responses emitted during the tone presentation and pre T is the number of responses emitted in the two minute period preceding the tone presentation.

RESULTS

The results for the forward pairing (F) group are shown in Figure 1. U-shaped functions, indicating maximum suppression at intermediate intervals, were obtained for 5 of the 6 pigeons in this group. The point of maximum suppression varied for individual pigeons with the maximum for P6517 and P10535 occurring at 15 min, for P6449 and P5701 at 30 min, and for P5767 at 45 min. For P4435, which did not produce a U-shaped function, maximum suppression occurred at the 4 min interval and suppression monotonically decreased as a function of the retention interval. The 1440 min interval on the graph represents the suppression obtained during the session in which the Pavlovian phase was omitted. For this interval, no systematic changes were observed in suppression as a function of the placement of the tone within the session.

The results for the forward pairing with operant delay (FD) group are shown in Figure 2. U-shaped functions were obtained for each of the six pigeons with maximum suppression occurring for P500 and P373 at 15 min, for P438 and P431 at 30 min, and for P922 and P4879 at 45 min.

A two-factor, mixed design, analysis of variance was performed on the data from the two forward pairing groups. The test was conducted to determine if the level of

Figure 1. The level of response suppression as a function of the testing interval for individual pigeons in the forward pairing (F) group.



Figure 2. The level of response suppression as a function of the testing interval for individual pigeons in the forward pairing with operant delay (FD) group.



suppression varied significantly as a function of the retention interval. The results showed a significant effect of the retention interval on the level of suppression ($F_{5,50} =$ 2.81, p < .025). The two groups were also found to differ significantly in the total amount of suppression over all testing intervals ($F_{1,10} = 23.8$, p < .001). A comparison of the two groups showed suppression levels in the forward pairing (F) group to be significantly higher than suppression levels in the forward pairing with operant delay (FD) group (see Figures 1 and 2). The analysis of variance showed no significant interaction between the group tested and time dependent changes in suppression ($F_{5,50} = .55$, p > .10).

A trend analysis was performed on the data to determine what type of function best fit the changes obtained in suppression as a function of the retention interval. The results showed that a quadradic, U-shaped, function provided the best fit ($F_{1,50} = 6.35$, p < .025). This test indicates that the functions obtained in the forward pairing groups were significant U-shaped functions.

Table 1 shows the average response rates during the pre-tone period and during the tone for all groups. The table was derived from averaging within and across pigeons and suppression ratios cannot be obtained from the data. A two factor, mixed design, analysis of variance was performed on the response rates during the pre-tone period for the two forward pairing groups. The test was performed to determine if any systematic changes in response rate occurred as a function of time. No significant effect of the retention interval on pre tone responding was obtained ($F_{5,50} =$.18, p > .10). A significant effect, however, was obtained between groups ($F_{1,10} = 6.57$, p < .05). The group effect resulted from the higher level of responding in the forward pairing with operant delay (FD) group as compared to the forward pairing (F) group.

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Group		Retention Intervals (Min)							
	4	15	30	45	60	1440			
F									
Pre-Tone	72 ^a	76	74	72	72	73			
Tone	36	28	24	31	28	30			
FD									
Pre-Tone	111	115	113	110	113	109			
Tone	103	95	88	92	108	99			
В									
Pre-Tone	54	51	51	46	53	48			
Tone	53	47	50	47	49	48			
D									
R Pro-Tone	ЛЛ	57	51	50	50	49			
Tone	34	35	30	29	32	45			

Average Response Rate During the Tone and Pre-Tone Periods

^aResponse rate is in responses per minute.

The results for the backward pairing (B) group are shown in Figure 3. Suppression was minimal in this group and the rate of responding during the tone was roughly constant across retention intervals. All pigeons within this group show relatively flat functions. The results from the truly random (R) group are shown in Figure 4. One pigeon in this group was dropped for failure to respond during the operant phase. Two of the remaining five pigeons, P4706 and P1110, show no suppression and flat functions. Three pigeons, P217, P2478, and P1062, show both suppression to the tone and U-shaped functions. The interval of maximum suppression for these pigeons varied from 15 min to 45 min. Thus, when suppression was obtained in the truly random (R) group, the resulting functions were similar to those obtained for the forward pairing groups while when no suppression was obtained, the functions were similar to those obtained with the backward pairing (B) group.

A comparison of group averages is presented in Figure 5. Due to the varied results obtained with the truly random (R) group, its group average is not included in the figure. For both the forward pairing (F) and the forward pairing with operant delay (FD) groups, the average point of maximum suppression occurred at the 30 min retention interval. The suppression level for the 1440 min retention interval approximately equaled the amount of suppression at the 60 min retention interval. A t test between the 60 min interval and the 1440 min interval was found to be nonsignificant for both the forward pairing (F) group ($T_5 = .69$, p > .10) and the forward pairing with operant delay (FD) group ($T_5 = 1.67$, p > .10).

Figure 3. The level of response suppression as a function of the testing interval for individual pigeons in the backward pairing (B) group.



Figure 4. The level of response suppression as a function of the testing interval for individual pigeons in the truly random pairing (R) group.



Figure 5. Group averages showing the level of response suppression as a function of the testing interval for the forward pairing (F), forward pairing with operant delay (FD), and backward pairing (B) groups.



DISCUSSION

The U-shaped functions obtained in this study demonstrate that time dependent changes occur in conditioned suppression. The phenomenon was reliably produced in eleven of the twelve pigeons which received a forward pairing of tone with shock. Although both forward pairing groups produced U-shaped functions, the forward pairing with operant delay (FD) group showed significantly less overall suppres-The reason for this difference is not clear. sion. This group also showed a significantly higher rate of responding during the pre-tone period. The higher rate of responding in this group may represent a "contrast effect" resulting from the imposition of a delay period between the Pavlovian and operant phases. The high rate of responding may in turn, have led to an attenuation of response suppression during the tone.

The use of a within-subjects design permitted an evaluation of time dependent changes in conditioned suppression within individual pigeons. The results showed that the point of maximum suppression varied from 15 min to 45 min across pigeons. Typically, "Kamin effect" studies have not used within-subjects designs and have not, therefore, detected this variance in the U-shaped function.

The minimum of the U-shaped function in the group averages of the two forward pairing groups occurred at the 30 min retention interval. In "Kamin effect" studies using rats, the minimum of the U-shaped function has typically occurred at the one hour retention interval. The difference in the minimum of the function between the present study and previous studies may have resulted from a species variable. The minimum of the U-shaped function in "Kamin effect" studies has been found to vary extensively as a function of the species used (reviewed by Squire, 1975). The experimental design may also have effected the minimum of the U-shaped function. The present study differed from previous "Kamin effect" studies by utilizing a within-subjects design, by using conditioned suppression as the dependent measure, and by not removing the pigeon from the experimental chamber during the retention interval. The minimum of the U-shaped function may be effected by such design variations.

A comparison of the control groups for Pavlovian conditioning shows an absence of conditioning in the backward pairing (B) group but the presence of conditioning and U-shaped functions in the truly random pairing (R) group. Although Rescorla (1972) has predicted that conditioning may initially occur with the "truly random" control, conditioning should dissipate with continued training. The pigeons, in the truly random pairing (R) group which showed conditioning, suppressed responding to the tone after over 30 days of Pavlovian conditioning. Therefore, it seems

unlikely that the conditioning demonstrated in these pigeons was a transitory effect resulting from the "truly random" procedure as suggested by Rescorla (1972). The presence of suppression in some pigeons and the absence of suppression in other pigeons in this group may have resulted from differences in the total number of forward pairings received. Some pigeons may have received a greater number of chance pairings. It seems unlikely however, that there would have been more then a negligible difference in the total number of forward pairings between pigeons after over 30 sessions on the "truly random" schedule. Benedict and Ayres (1972) have shown that random schedules with forward pairings occurring at the beginning of training are more likely to result in conditioning. In their study (Experiment 2) rats received either initial pairings or initial nonpairings of a tone with shock under computer generated "truly random" schedules. The rats were then placed on an operant schedule for food and the tone presented during barpressing. The results showed that the rats which received pairings of the tone with shock during the first 10 percent of training showed subsequent suppression of barpressing during the tone while groups which received an equal number of tone-shock pairings at other times during training showed no subsequent suppression of barpressing to the tone. In another study, Ayres, Benedict and Witcher (1975) selectively eliminated pairings of a tone with shock in "truly random" schedules.

They found that the total number of chance pairings did contribute to the presence or absence of conditioning to the tone. They also found that the absence of conditioning to the tone was significantly related to the number of shock presentations prior to the initial chance pairings of the tone with shock. It seems likely that the difference in conditioning between pigeons in the truly random pairing (R) group was the result of both the number of chance pairings which occurred during the early sessions of training and the number of shock presentations which occurred prior to the first chance pairing.

The results of the present study indicate that excitatory conditioning to the tone is essential for the occurrence of a U-shaped function. Furthermore, for the present study, the backward pairing (B) group, which received explicitly unpaired presentations of the tone with shock, provided the most appropriate control procedure for Pavlovian conditioning. In this group, all pigeons showed an absence of suppression and flat functions. The "truly random" control procedure as suggested by Rescorla (1967) was found to result in suppression and U-shaped functions in three of the five pigeons tested.

In the present study, U-shaped functions were obtained while in the McMichael (1966) and Tarpy (1966) studies a monotonic increase in suppression was observed. The numerous differences in the present design as compared with these previous studies makes a specific analysis of the differences

in results difficult. One factor which may influence whether a U-shaped function is obtained or not is the use of different chambers for training and testing, characteristic of previous studies, as opposed to the use of a single chamber for both training and testing, as in the present study. Brush (1970) has suggested that the use of two chambers in the McMichael (1966) and Tarpy (1966) studies may have led to problems with stimulus generalization during testing.

Anisman (1975) has attributed the "Kamin effect" to a decrease in the organism's ability to initiate voluntary responses at intermediate retention intervals. This "response inhibition" is said to result from changes in the levels of various neuro-transmitters produced by the organism's direct exposure to an aversive US. Under such a model, it is primarily the response which is inhibited at intermediate retention intervals with the CS-US association playing only a minor role. In the present study, the operant response should have varied systematically with the retention interval in the absence of the tone. The fact that it did not, and the lack of a U-shaped function in the backward pairing (B) group, indicates that conditioning to the tone was necessary for the production of a U-shaped function.

Klein and Spear (1970) have attributed the "Kamin effect" to a memory retrieval failure at intermediate

retention intervals. They have suggested that a type of "state dependent learning-dissociation" effect may be the mechanism responsible for retrieval failure. The organism learns the avoidance response under particular internal cues which are produced by the stress of shock. At intermediate retention intervals, the internal stimulus conditions which were present during original learning are no longer present or they cannot be re-established quickly. Organism's can acquire a conflicting task at intermediate retention intervals at a rate roughly equivalent to niave animals because the memory of the original learning task cannot be retrieved and therefore cannot interfere with the acquisition of a new task. Under this model, the level of performance is a function of the amount of transfer between training and testing. A memory retrieval interpretation of the "Kamin effect" would predict that, at intermediate retention intervals, an organism would have difficulty retrieving CS-US associations (Bryan & Spear, 1976). To be consistent, the model would also predict that if time dependent changes occurred in conditioned suppression, a decrease in the level of suppression would be observed at intermediate retention intervals. If the pigeons in the present study could not retrieve the association of the tone with shock, they should have shown less suppression at the 30 min interval. The results, however, show the greatest level of suppression at the intermediate retention intervals.

Denny (1958) proposed that the "Kamin effect" resulted from an incubation of fear over time. Under this model, fear reactions to the CS increase as a function of the retention interval to an asymptotic level. Fear then begins to dissipate to a base level approximately equal to the level of fear during initial training. If retraining of the avoidance response occurs when fear is at a maximum level, the animal reacts to the CS and the situational cues with fear reactions, such as freezing (Stein, Hoffman, & Stitt, 1971), which are incompatible with the appropriate avoidance response. The idea that freezing may be one of the behaviors which interferes with the active avoidance response has also been suggested by Anisman (1975). In the present study, maximum suppression occurred at intermediate retention intervals. Numerous theorist (Estes, 1969; Konorski, 1967; Mowrer, 1960; Rescorla & Solomon, 1967) have proposed that conditioned suppression reflects the conditioning of central motivational states. Under this position, and by labeling the central motivational state resulting from aversive conditioning as "fear," the present results can be considered to represent an "incubation of fear" effect. Regardless of whether or not one accepts conditioned suppression as a measure of "fear," the present results show changes in a pigeon's reaction to a tone paired with shock which are consistent with the Denny (1958) interpretation of the "Kamin effect."

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