Learned helplessness in the rat: Effect of response topography in a within-subject design

Cristiano Valerio dos Santos [a,*], Tauane Gehm [b], Maria Helena Leite Hunziker [b]

[a] *Universidad de Guadalajara, Mexico*
[b] *Universidade de São Paulo, Brazil*

ABSTRACT

Three experiments investigated learned helplessness in rats manipulating response topography within-subject and different intervals between treatment and tests among groups. In Experiment 1, rats previously exposed to inescapable shocks were tested under an escape contingency where either jumping or nose poking was required to terminate shocks; tests were run either 1, 14 or 28 days after treatment. Most rats failed to jump, as expected, but learned to nose poke, regardless of the interval between treatment and tests and order of testing. The same results were observed in male and female rats from a different laboratory (Experiment 2) and despite increased exposure to the escape contingencies using a within-subject design (Experiment 3). Furthermore, no evidence of helplessness reversal was observed, since animals failed to jump even after having learned to nose-poke in a previous test session. These results are not consistent with a learned helplessness hypothesis, which claims that shock (un)controllability is the key variable responsible for the effect. They are nonetheless consistent with the view that inescapable shocks enhance control by irrelevant features of the relationship between the environment and behavior.

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1. Introduction

Exposure to inescapable shocks has been shown to impair subsequent performance on an escape contingency, whereas escapable shocks produce no such effect (Seligman and Maier, 1967). This behavioral effect, named learned helplessness, has been reported many times, by different laboratories, and with different species, which attests to the generality and robustness of the phenomenon (Peterson et al., 1993). However, despite being consistently reproduced, the precise process that gives rise to it is not yet clear.

A handful of hypotheses, with varying degrees of success, have been put forward to explain this effect. Some of them claimed that the inescapable shocks produce motor inactivity that interferes with escape learning (Glazer and Weiss, 1976). However, the most accepted explanation, also named the learned helplessness hypothesis, maintains that organisms exposed to inescapable shocks somehow learn that their responses bear no relationship to shock onset/offset. So, because this first experience is opposite to the second one, when a relationship does exist (under the escape contingency), an impairment of performance is produced (Maier and Seligman, 1976).

Despite the considerable amount of empirical support this hypothesis has received, many questions remain unanswered and need to be addressed before a general account of the phenomenon is offered. For example, impairment in the test is observed when nose poking is required to terminate shocks only if the animal is allowed to move freely inside the experimental chamber (Yano and Hunziker, 2000); when its movements are restricted (e.g., by confining subjects into a plastic tube and delivering shocks through the tail), previously inescapable shocks facilitate responding (Glazer and Weiss, 1976). Also, it is not yet clear whether organisms learn that there is no relationship between their responses and shocks or whether they learn that there is no relationship between their responses and environmental events in general. For instance, while some have found that inescapable shocks also impair learning maintained by positive reinforcement (Rosellini et al., 1982), others found no effect (Capelari and Hunziker, 2009; Mauk and Pavur, 1979).

Shock predictability seems to matter as well: if shocks are predictable, a learning impairment was observed in male, but not in female, rats; unpredictable shocks, on the other hand, produced impairment regardless of gender (Castelli, 2004; Kirk and Blampied, 1985).

Finally, the escape response used to evaluate the effect also may be important. Hunziker and Santos (2007) have shown that

* Corresponding author at: Centro de Estudios e Investigaciones en Comportamiento, Francisco de Quevedo 180, C.P. 44130 Arcos Vallarta, Guadalajara, Mexico. Tel.: +52 33 38 18 07 30x5804; fax: +52 33 38 18 07 30x4.

E-mail address: behaca@yahoo.com (C.V.d. Santos).

the learning impairment following inescapable shocks depended on the topography of the response required to escape. When running from one side of a shuttle box to the other was required, a difference between experimental and naïve groups was observed when rats had to go forth and back (replicating the results of Maier et al., 1973); however, in spite of this difference, a more detailed analysis of the pattern of responding in the test revealed that not even naïve subjects learned to escape (i.e., response latencies did not show a downward trend), which casts doubt on the adequacy of this response requirement to assess learning deficits. When a single response of jumping a barrier was required, naïve animals clearly learned to escape, but impairment was observed with inescapable animals. Moreover, this impairment was still present 28 days after exposure to inescapable shocks, which is contrary to previous findings that showed a transient effect after 72 h or more (Maier, 2001). In the following three experiments we further explore the importance of the topography of the escape response to the learned helplessness effect.

2. Experiment 1

The effect of inescapable shocks is reduced with the passage of time when the response of running (Maier, 2001), but jumping (Hunziker and Santos, 2007) is used in the test. Nose-poking has already been shown to be equally impaired by inescapable shocks (Yano and Hunziker, 2000), but no data has been obtained on how durable this effect is. This experiment evaluated this question by exposing male rats to inescapable shocks and later testing them under two conditions: jumping and nose-poking, which were conducted 1, 14 or 28 days after exposure to inescapable shocks.

2.1. Method

2.1.1. Subjects

Forty-two three-month-old naïve male albino Wistar rats served as subjects. They came from Butantan Institute in São Paulo and were housed individually, with water and food freely available. The experiment was carried out during the light phase of a 12-h light/12-h dark cycle.

2.1.2. Equipment

Three experimental chambers were used: two square chambers and one rectangular shuttle box. The square chambers, made of aluminum and plexiglass, were 21.5 cm long, 21.5 cm wide and 21 cm high. The right wall contained a round opening, 3 cm in diameter, through which the rat could insert any of its body parts (usually the nose). On the other side of the wall, a photoelectric cell was mounted. If the rat inserted any body part at least 1.5 cm deep into the opening, a light beam was interrupted and a nose-poking response was registered. The grid floor of each of the experimental chambers was constructed of stainless steel rods 0.3 cm in diameter and spaced 1.3 cm apart. These chambers were connected to two *Lehing Valey* 113-33 electric shock generators, which delivered scrambled shocks through the grid floor.

The shuttle box was 50 cm long, 15.5 cm wide and 20 cm high. It consisted of two compartments of equal size, separated by an acrylic wall. In this centre wall, there was a 7.5-cm-high and 6-cm-wide rectangular opening 8 cm above the grid floor. This opening allowed the rat to jump from one side to another. Each compartment had an independent grid floor, constructed of stainless steel rods 0.3 cm in diameter and spaced 1.3 cm apart, which was depressed by the animal's weight. When this happened, a microswitch was activated, registering the animal's presence in that compartment. Two cylinder metal rods (similar to those on

the floor) were located at the base of the opening that separated the compartments. A *BRS Foringer* 901 electric shock generator and a scrambler delivered shocks to the grid floor and the metal rods at the base of the opening.

The three experimental chambers were housed in light- and sound-attenuating boxes equipped with a fan for ventilation and masking noise. Sessions were run by a PC, with a piece of software especially developed for this experiment.

2.1.3. Procedure

The subjects were randomly divided into three experimental groups ($n = 14$). Each experimental group was initially exposed to one session of inescapable electric shocks (treatment). During this session, subjects received 60 electric shocks in the square chambers, each with a fixed duration of 10 s and with an intensity of 1.0 mA, delivered on a variable time schedule 60 s (range 10–110 s). The orifice on the right wall of these chambers was covered with a round metal plate, so that subjects were not allowed to emit the nose-poking response. In this session, the rat had no control over any aspect of the shocks.

These three groups were then exposed to two different escape test sessions, 24 h apart. In both tests the animals received 30 shocks with an intensity of 1.0 mA and maximum duration of 10 s, delivered through the grid floor on a variable time 60 s schedule (range 10–110 s). The tests differed on the escape contingency in effect. The nose-poking test was conducted in the same square chamber used in the first session, except that the orifice on the right wall was uncovered. In this test session, the shock was interrupted immediately if the rat emitted a nose-poking response. If the animal did not emit this response during the shock, it terminated automatically after 10 s. The jumping test was conducted in the shuttle box where shock was interrupted if the rat jumped from one compartment to the other. If the animal did not jump during the shock, it was terminated automatically after 10 s. In both tests, each shock started one trial, and the time between the shock onset and termination was recorded as the latency of that trial.

The first experimental group was exposed to these tests 1 and 2 days (24 and 48 h, respectively) after treatment; the second experimental group was exposed to these tests 14 and 15 days after treatment; the third experimental group was exposed to these tests 28 and 29 days after treatment. Half of the subjects were initially tested for nose-poking and then for jumping; the other half was tested in the reversed order.

2.1.4. Data analysis

A repeated-measures analysis of variance, with order of exposure and interval between treatment and tests as between-subject factors and trials as the within-subject factor, was conducted. The dependent variable (latency) was tested for normality (Shapiro-Wilk), homogeneity of variance (Levene), and sphericity (Mauchly) and all tests corroborated the adequacy of the analysis. After an effect of the independent variables was found, univariate tests, corrected for multiple comparison using the Bonferroni method, were conducted to find which conditions differed. To do so, the SPSS 13 software was used and a level of significance of 0.05 was adopted in all experiments.

2.2. Results and discussion

Because the manipulation of the interval between treatment and test produced no significant results, data from subjects with different intervals were grouped in the following analysis. Fig. 1 shows escape latencies on both tests. The left panel presents data from groups initially required to jump and then to nose-poke; the right panel presents data from groups initially required to
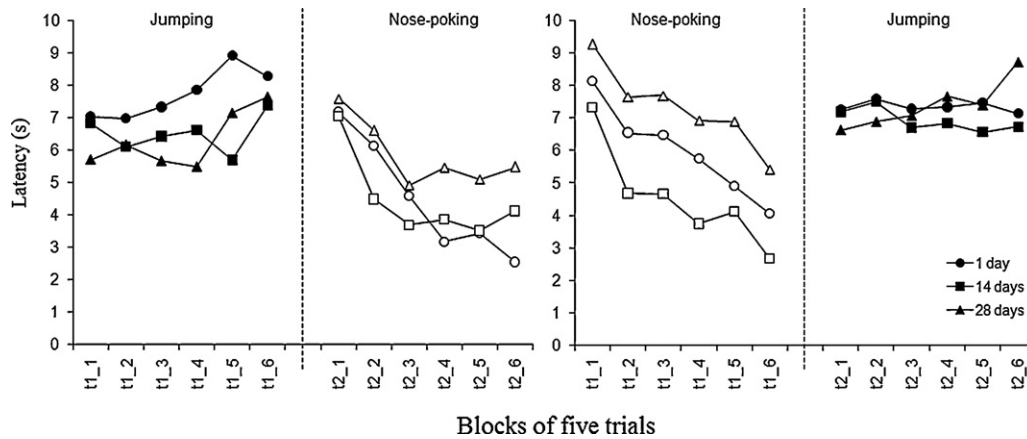
Fig. 1. Response latencies, grouped in blocks of five trials, for subjects previously exposed to inescapable shocks with different intervals between treatment and test (see legend). On the *x*-axis, the number before the underscore stands for the day of testing (on the first or second day) and the number after the underscore stands for trial block. The left panel shows data from groups initially tested under the jumping response criterion (filled symbols) and later under the nose-poking response criterion (unfilled symbols). The right panel shows data from groups initially tested under the nose-poking response criterion and later under the jumping response criterion. These tests were conducted 24 h apart, regardless of the order.

nose-poke and then to jump. When the required response was nose-poking, animals learned to escape shocks, showing higher latencies in the first block of trials and a gradual decrease as session progressed. Conversely, when the required response was jumping, animals did not learn to escape: response latencies were either stable or increased as session progressed. The analysis of variance for repeated measures showed no significant effect of trials [$F(5,128) = 2.46$, $p = 0.06$] or order of exposure to the tests [$F(1,40) = 1.58$, $p = 0.21$], but a significant interaction between trials and order of exposure [$F(5,144) = 9.85$, $p < 0.001$]. Bonferroni tests with the significance corrected for multiple comparisons revealed both within- and between-subjects differences: nose-poking latencies were lower than jumping latencies in most blocks of trials ($p < 0.05$).

As reported by Hunziker and Santos (2007), jumping latencies decrease as the escape session progresses for naïve subjects, but not for rats previously exposed to inescapable shocks, regardless of the interval between treatment and test. The present results replicate and extend these findings, which suggest that requiring a single response of jumping a barrier provides a sensitive measure to the manipulation of inescapable shocks. When nose-poking was required in the present experiment, however, response latencies also decreased. This result is at odds with previous findings that showed that nose-poking latencies remain high and relatively stable after exposure to inescapable shocks (Yano and Hunziker, 2000).

Before trying to explain these results in relation to any theoretical position, two additional experiments were conducted to ensure the reliability of these findings and to evaluate whether some subject variables may have been responsible for the failure to replicate. The first variable is gender: Yano and Hunziker's rats were female, while ours were male, and there is evidence that, in tests of learned helplessness with the jumping response, gender may interact with some variables (like drugs or shock unpredictability – Gouveia, 2001) in determining the learned helplessness effect. Second, their rats and ours originated from different laboratories. Even though both laboratories follow strict procedures for breeding animals, the unintended selection of a biological characteristic, such as different pain thresholds (or other), may have inadvertently occurred. To permit a more direct comparison of the results, the second experiment partially replicated the first, using male and female rats coming from the same laboratory as those used by Yano and Hunziker (2000).

3. Experiment 2

3.1. Method

3.1.1. Subjects
Eight male and eight female rats, similar to the ones used in Experiment 1, served as subjects. These rats came from Adolfo Lutz Institute and were housed in the same conditions as in Experiment 1.

3.1.2. Equipment
Same as Experiment 1.

3.1.3. Procedure
Subjects were exposed to one treatment session (inescapable shocks) and two test sessions (nose-poking and jumping, in this order), 24 h apart each. Sessions were conducted exactly as described in Experiment 1.

3.1.4. Data analysis
A repeated-measures analysis of variance, with sex as the between-subject factor and trials as the within-subject factor, was conducted. The dependent variable (latency) was tested for normality (Shapiro-Wilk), homogeneity of variance (Levene), and sphericity (Mauchly) and all tests corroborated the adequacy of the analysis. After an effect of the independent variables was found, univariate tests, corrected for multiple comparisons using the Bonferroni method, were conducted to find which conditions differed.

3.2. Results and discussion

Fig. 2 shows escape latencies, grouped in blocks of five trials, in both tests. As in Experiment 1, nose-poking latencies were higher in the first block of trials and gradually decreased as session progressed. Conversely, jumping latencies remained relatively stable. An analysis of variance for repeated measures showed a significant effect of trials [$F(5,46) = 8.438$, $p < 0.001$], which indicates a difference between the response topographies, but no significant effect of gender [$F(1,14) = 0.084$, $p = 0.77$] or interaction gender × trials [$F(5,46) = 2.282$, $p = 0.08$].

The data from Experiments 1 and 2, taken together, suggest that neither subject's gender not its origin was responsible for the differences between Yano and Hunziker's results and ours related to the reduction of nose-poking latencies, but not jumping laten-
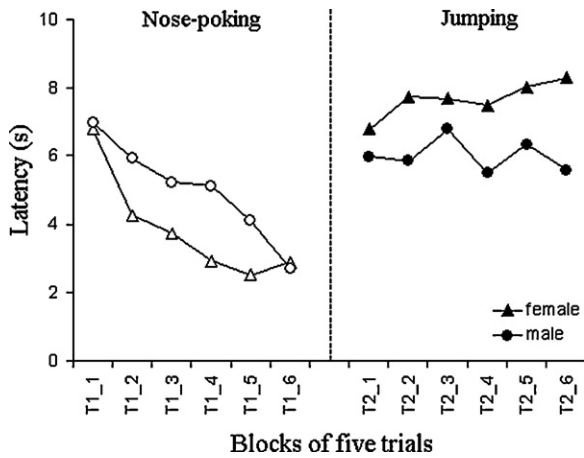
Fig. 2. Response latencies, grouped in blocks of five trials, for female (triangles) and male (circles) subjects previously exposed to inescapable shocks. Curves on the left (unfilled symbols) refer to the nose poking test and the curves on the right refer to the jumping test (filled symbols). On the x-axis, the number before the underscore stands for the day of testing (on the first or second day) and the number after the underscore stands for trial block.

cies, after exposure to inescapable shocks. The third experiment was designed to further explore the phenomenon using a reversal design with increased exposure to the response requirement in the shuttle box (jumping). Given more opportunity to respond, will jumping latencies eventually decrease? In case subjects fail to jump consistently, will the added experience with shocks that were not escaped impair the subsequent performance of the nose poking response? In case subjects learn to nose poke, will jumping be affected when re-exposed to the escape contingency in the shuttle box?

4. Experiment 3

4.1. Method

4.1.1. Subjects
Eight male rats, similar to those used in Experiment 2 and kept under the same housing conditions, served as subjects.

4.1.2. Equipment
Same as Experiment 1.

4.1.3. Procedure
Subjects were initially exposed to one treatment session (inescapable shocks), conducted exactly as in Experiment 1, and four tests sessions, conducted 1, 8, 9, and 10 days after treatment. The first, second and fourth test sessions were conducted in the shuttle box, where jumping was required to terminate shocks. The third session was conducted in the square chambers where nose-poking was required to terminate shocks. Test sessions were run exactly as in Experiment 1, except that 60 shocks were delivered in the first and second sessions, while 30 shocks were delivered in the third and fourth sessions.

4.1.4. Data analysis
A repeated-measures analysis of variance, with trials blocks as a within-subject factor, was conducted. The dependent variable (latency) was tested for normality (Shapiro-Wilk), homogeneity of variance (Levene), and sphericity (Mauchly) and all tests corroborated the adequacy of the analysis. After an effect of the independent variables was found, univariate tests, corrected for multiple comparison using the Bonferroni method, were conducted to find which conditions differed.

4.2. Results and discussion

Fig. 3 shows escape latencies, grouped in blocks of five trials, in both types of test. In the first jumping test, subjects presented an erratic response pattern, without any evidence of a systematic reduction in response latencies. In the second jumping test, conducted seven days after the first one, the same erratic response pattern was observed. In the nose-poking test session, subjects emitted the required response consistently, with latency reduction throughout the session. When jumping was once again required for shock termination in the last test session, latencies remained at high levels comparable to the second jumping test with the same erratic pattern of responding. These results were corroborated by an analysis of variance for repeated measures, which showed a main effect of trials [$F(35,245) = 8.826$, $p = 0.001$]. Multiple comparisons among blocks of trials revealed that nose-poking latencies were significantly lower than jumping latencies ($p < 0.05$).

The third experiment was an attempt to answer three questions, namely: (1) would the subjects previously exposed to inescapable shocks learn to jump eventually when given more trials than in previous experiments?; (2) would the added shocks received in case of failure to jump affect nose poking?; and (3) would jump-
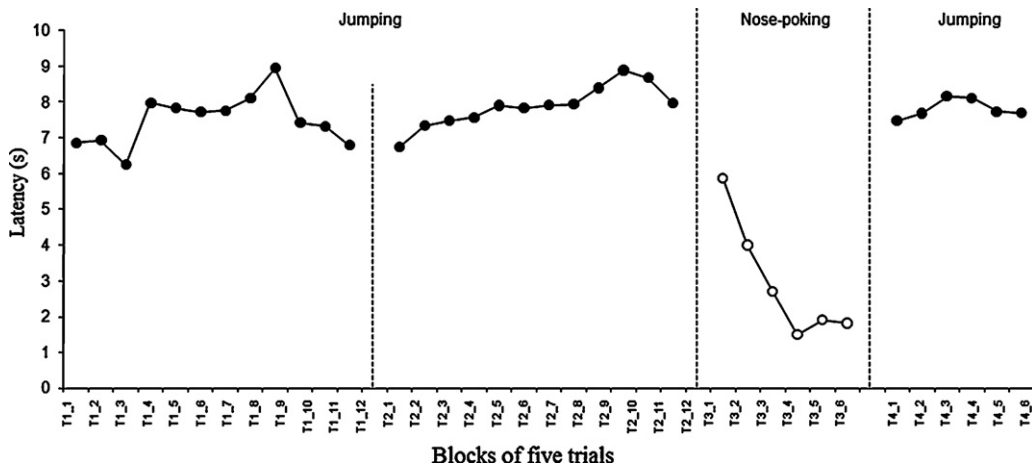

Fig. 3. Response latencies, grouped in blocks of five trials, for subjects previously exposed to inescapable shocks. The first, second, and fourth graphs refer to the jumping test and the third graph (unfilled circles) refers to the nose poking test.

ing be affected when re-exposed to the shuttle box in case subjects learned to nose-poke (as in the previous two experiments)? The answer to all three question seems to be no. Arranging 60 trials in two days had no effect on jumping acquisition for all subjects except one. It is possible that arranging even more trials would facilitate responding, but this seems unlikely given each shock that an animal fails to escape is a new "inescapable" shock that might add to the inescapable shocks it had received previously. Nose poking, on the other hand, was not affected by the added exposure to shocks and learning to nose poke did not affect subsequent performance in the shuttle box either, which suggests that these response topographies might differ in some critical feature that makes them particularly sensitive or insensitive to the effects of inescapable shocks. Four possible candidates are discussed below.

5. General discussion

Jumping and nose poking (and their respective experimental preparations) differ in some features that might be – together or in isolation – responsible for these results. The first one could be response difficulty. It could be argued that jumping might be more difficult than nose poking (i.e., involving a longer chain of responses), and inescapable shocks might affect only difficult responses. In previous studies, a learning impairment was observed only when the response required after exposure to inescapable shocks was made more difficult, such as when rats were required to run back and forth in a shuttle box (Maier et al., 1973) or press a lever three times while receiving shocks (Seligman and Beagley, 1975). However, we have no evidence that jumping was actually more difficult than nose poking. When naïve subjects are exposed to the jumping contingency, their response pattern is virtually identical to naïve subjects exposed to the nose-poking contingency: higher latencies in the first trials and a gradual decrease throughout the session (Yano and Hunziker, 2000). Thus, it seems unlikely that response difficulty played a role.

The second feature is context similarity. Nose poking tests were conducted in the same experimental chambers used to deliver inescapable shocks, except that the opening in the wall was covered by a metal plate, making nose poking impossible, whereas jumping tests were conducted in a different chamber (shuttle box). It might be argued that context similarity facilitated responding in some way. However, there is evidence that context similarity, rather than mitigating the effect of inescapable shocks, *maximizes* it. For example, in an experiment conducted by Maier et al. (1995), rats were exposed to inescapable shocks and later tested for escape responding in an environment that could be either the same as or different from where they had received inescapable shocks. When tests occurred in the same environment, learned helplessness was observed seven days after exposure to inescapable shocks; when the test environment was different, helplessness was not observed after two days. Thus, it also seems unlikely that being tested in the same chamber where inescapable shocks were delivered should facilitate subsequent responding that results in shock termination.

A third possible feature is the amount of motor activity required to emit both responses. If the exposure to inescapable shocks reduces motor activity, as has been suggested by some (Glazer and Weiss, 1976), escape learning should be facilitated when nose poking is used in the test – because nose poking entails lower activity – and impaired when jumping is used, since a high level of activity is needed to emit this response. However, systematic observations (not presented) of the behavior of the rats during electric shocks suggested a high level of motor activity in both tests, which should have caused the opposite of what was observed.

Nevertheless, a careful and precise measurement of the level of motor activity during shocks is needed to rule out this possibility altogether.

Finally, in Yano and Hunziker's study, electromechanical equipment was used to control events in the session, while the events in our sessions were controlled by a computer. We hypothesize that the use of electromechanical equipment may have introduced a short delay between response emission and shock offset and this short delay may have made the detection of the contingency more difficult. Supportive evidence for this hypothesis was provided by Minor et al. (1984), who exposed rats to inescapable shocks and later to an escape task where shocks could be terminated by choosing one arm of a Y-shaped maze; choosing the other arm had no effect over shocks. When there was a short delay (350 ms) between response emission and shock offset, performance on the task was poorer compared to a no-delay group. This effect was greatly magnified when, in addition to the delay, there was an experimenter in the room. The authors concluded that inescapable shocks might render animals more sensitive to irrelevant features of the environment (for example, the small delay between response and shock offset) and less sensitive to proprioceptive cues that might lead to the correct response. So, if inescapable shocks make the subject more sensitive to different characteristics of the contingency, the delay between response emission and shock offset inherent to Yano and Hunziker's procedure may have been sufficient to prevent animals previously exposed to inescapable shocks from detecting a new contingency between what they did and what happened as a result. This view that inescapable shocks cause some, but not all, of the characteristics of the contingency to gain disproportionate control over the animal's behavior is also supported by Lee and Maier's (1988) work, in which, compared with naïve rats, rats previously exposed to inescapable shocks were *more* likely than naïve rats to find the correct arm of a water maze during an escape test when it was signaled by an accurate cue, which suggests more control by a particular feature of the external environment.

Interestingly, the hypothesis that inescapable shocks cause some characteristics of the contingency to gain *more* rather than less control over the animal's behavior also may help explain why learning to jump was impaired even when subjects had learnt to escape shocks by nose-poking the day before. This datum is inconsistent with a learned helplessness hypothesis if we consider that experiencing an actual contingency between behavior and shock offset should have counteracted the previous experience where such a contingency was absent. However, a difference in the delays between responses and shock offset also may help account for these results. When nose poking was required, subjects only had to insert the nose (or any body part) within the orifice in the wall and this caused an immediate termination of the shock. Jumping, on the other hand, required the subject to position itself facing the opening in wall that separated the compartments and propel its body through it, receiving electric shocks in the meantime. We suggest that this small difference in delay between response initiation and shock termination may have made the detection of a contingency more or less difficult and this small delay may be very important for rats previously exposed to inescapable shocks but not naïve subjects.

Moreover, another procedural detail might have made the detection of a contingency with nose-poking easier: when the animal emitted the correct response, the electric shock that was being administered through the floor of the same chamber terminated. When an animal jumped from one compartment to the other in the shuttle box, the relationship between response and consequence is less clear: to escape shocks, the animal removes itself from the situation where shocks are happening and it does not have experience with shock elimination per se in the same compartment (i.e., shocks could have ended on the other side long after the animal

jumped the barrier). So, it seems that the control over shock termination was made much less explicit when jumping was used in the test.

The explanation that inescapable shocks cause some characteristics of the contingency to gain *more* control over the animal's behavior seems particularly promising for two reasons. First, it provides a more molecular account of the phenomenon, instead of relying on more molar variables, such as learning that there is no relationship between what one does and what happens in the environment. It is not yet clear how an organism might come to detect this lack of relationship and until this question is answered, an explanation based on such a process might not be as parsimonious as one wishes. Second, this explanation may be easily put to test. For example, if it is correct, then one would expect that animals exposed to inescapable shocks should not learn to nose poke if a delay is imposed between the response and shock offset. These empirical tests might tell us which explanation better suits the results.

It is important to note that our data do not refute the learned helplessness hypothesis, given that control groups not exposed to inescapable shocks were not run in the present study. Control subjects, however, do learn to jump barriers to escape shocks, as reported elsewhere (Hunziker and Santos, 2007; Sanavio and Savardi, 1980). The reduction in response latencies when nose-poking was required that we observed here also is evidence of learning, and this response pattern is in clear contrast to the pattern observed with jumping. Therefore, our data might be in a way comparable to previous work that observed impairment in performance after exposure to inescapable shocks. However, given that the hypothesis of learned helplessness emphasizes the lack of control over shocks as the critical variable to produce to effect, it is difficult to see how it might explain why an experience of control over shocks does not override the effects of inescapable shocks.

Acknowledgements

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