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Individual differences in novelty-seeking are associated with different patterns of preference in a risk-sensitivity procedure in rats

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The preferences of organisms faced with changing conditions in food delivery situations have been studied under the rubric of risk-sensitivity. Optimal Foraging Theory often applies the energy budget model to explain the preferences shown by organisms, but in this paper we suggest a different approach, one based on the study of individual differences. A sample of rats was classified as high and low novelty-seeking. Afterwards, they were maintained at 75% or 90% of their body weight and exposed to a risk-sensitivity procedure. The results show that the novelty-seeking model is associated with different patterns of preference under a risk-sensitivity procedure, but that these patterns do not correlate with the level of food deprivation employed. Furthermore, we found that the spontaneous alternation between options in a choice situation correlates with the organism's preference during a risk procedure. Considering recent findings in the area of animal and human decision-making, our results are explained in terms of altered behavioral processes.

Risk-sensitivity is a key element of Optimal Foraging Theory (Stephen & Krebs, 1986), which attempts to explain under what conditions animals show a preference for variable outcomes, and why. In the basic procedure, animals are exposed to two options in successive trials using the same means of reinforcement, but different degrees of variability, such that one option has a fixed result and the other a variable outcome. Animals are classified as risk-prone if they prefer the variable option, and as risk-averse if they prefer the fixed option. In the third case, marked by no clear preference, it is said that the animal shows risk indifference.

The first demonstration of risk sensitivity was made by Caraco, Martindale and Whittam (1980), who proved that birds (yellow-eyed juncos, *Junco phaeonotus*) changed their preference from a fixed option to a variable option under the condition of increased food deprivation. Thus, Stephens (1981) proposed food deprivation as a useful predictor of preference in risk-sensitivity procedures, considering that the preference for the variable option is understood as a way to avoid or minimize the probability of suffering starvation. Therefore, this model predicts that increasing the level of food deprivation will provoke a higher preference for the variable option, even though preference for variability in delay is almost absent in some species (e.g., rats). In at least one experiment in our laboratory (García-Leal, Saldivar & Lemus, 2008), we found an effect of the level of deprivation (75% vs 90%) on preference for a delayed alternative in a risk-sensitivity procedure.

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Since that time, many experiments have demonstrated that the expected effect associated with food deprivation is often absent, or dependent on other variables, such as species or the type of reinforcer used (see Kacelnik & Bateson, 1996 for a review), so that the explanation of risk-sensitivity in terms of minimizing the probability of starvation remains incomplete. Nevertheless, the preference for variability (with respect to amount or delay) is still a salient topic of study.

More recent approaches have sought to explain variability preference by assuming that modification of certain behavioral processes will affect an animal's preferences in certain procedures. This approach is widely used in experiments on human decision-making. These behavioral processes can affect behavior not only in risk-sensitivity procedures but also in a wide variety of choice procedures. In this approach, a behavioral process is considered to entail a mechanism, such as a chemical or neurological change, that affects the organism's normal behavior. That is why we prefer to qualify the process or mechanism as *behavioral*, and not to use a more generalized term as could be *underlying process*.

A behavioral process can be altered in at least three ways: (a) by administration of a certain drug (e.g. alcohol or marihuana); (b) application of a procedure that affects the organism's state (e.g., causing stress); or, (c) regarding the organism's particular traits associated with relatively permanent behavioral modification (e.g. anxiety or impulsivity).

An example of the first case is the work of Kaminski and Ator (2001), who showed that administering D-amphetamine to rats increases the preference for the variable option in a risk-sensitivity procedure. The second case can be illustrated with the study conducted by Graham, Yoon and Kim (2010), in which administration of a stress procedure (shocks delivered intermittently) decreased optimal choice in rats. In this case, optimal choice was the preference for 0.12 ml with a probability of 0.8 instead of 0.04 ml with a probability of 0.8. Finally, the work of Rivalan, Ahmed and Dellu-Hagedon (2009) can be mentioned as an example of the third case, as their study found that rats initially prone to making disadvantageous decisions (classified as *bad decision-makers*) on an IOWA gambling task (version for rats), maintain the same pattern despite extended exposure, whereas rats prone to making advantageous decisions (*good decision-makers*) maintain their behavior throughout the procedure. In the IOWA gambling task, advantageous decisions are those that increase the rate of long-term gain (even when they are small in the short term), while disadvantageous decisions are those that decrease the rate of long-term gains (even when they are large in the short term). In the study by Rivalan et al. (2009), bad decision-makers were the subjects that had a very low mean percentage of advantageous decisions (around 20%) at the end of the procedure, while the good decision-makers were those that reached a very high mean percentage of advantageous decision (around 80%). Additionally, they found that these two groups of rats differed in terms of the behavioral processes assessed after the choice procedure. Specifically, the bad decision-makers showed greater sensitivity to the reward in a progressive ratio schedule and ran faster in a runway paradigm. These findings showed the effect of altered behavioral processes.

In the context of these findings and their implications for the study of risk-sensitivity and decision-making, the present study focused on the third case. Therefore, we used a model of individual differences in novelty-seeking in order to determine whether it may be associated with different preference patterns in a risk-sensitivity procedure. We used this model for two main reasons: (1) the novelty-seeking model has been associated with altered behavioral processes that affect decision-making and may influence the preference for variability (e.g. anxiety, impulsivity and stress; Flagel et al., 2010; Stead et al., 2006); and, (2) the possible association between novelty-seeking and the preference for variability has not yet been studied in rats. Under this consideration, the study should be regarded as a preliminary approach to the relationship between novelty seeking and risk-sensitive, due to 1) the sample size (8 rats, selected from a sample of twenty-five rats), and 2) because we only consider subjects with the most extreme scores in a novelty-seeking task (four rats per group), excluding subjects with medium scores. We will come back over these two issues at the discussion section.

Also, we explored the implications of the phenomenon called spontaneous alternation in a risk-sensitivity procedure. Spontaneous alternation, understood here as a change in the preferred option trial-by-trial, may be an important variable because it has been held to represent a form of exploration (Gaffan & Davies, 1982) that, in turns, is a measure of preference for novelty. In addition, spontaneous alternation can affect preference in choice procedures by changing the proportion of choices to a specific option, which could be a manifestation of novelty preference or a trend to reduce uncertainty. Hence, the main goal of our research was to explore the correlation among individual differences, particularly novelty-seeking in a risk-sensitivity procedure, taking spontaneous alternation as a behavioral variable. Finally, in light of the limitations of correlational studies, we propose some possible explanations that may account for the correlations found.

Method

Participants

Twenty-five Wistar male rats *(Rattus norvegicus*) aged 13 weeks at the beginning of the experiment were used. After the phenotypic classification (see the novelty test), eight of those rats were chosen for a risk-sensitivity procedure. All the rats were confined in their cages under laboratory conditions, controlled temperature, and a 12-hr dark-light cycle.

The rats were fed amaranth seeds (*Amaranthus caudatus*) throughout the experimental procedure, since they have been shown to be an effective reinforcer for this animal (Cabrera, Robayo-Castro & Covarrubias, 2010).

Procedure

Novelty test. A modified version of the so-called free-choice procedure previously used by Wooters, Dwoskin and Bardo (2006) was employed for the novelty test, though in our procedure, instead of two cages, we employed four operant transparent chambers (model MED EVN-007, each one 25.4 cm wide × 21 cm high × 31.8 cm long) linked by wooden bridges (60 cm long × 9 cm wide × 16.5 cm high). As Figure 1 shows (also Figure 2), each bridge was surrounded by transparent acrylic walls. All operant chambers were free of discriminative stimuli and levers.

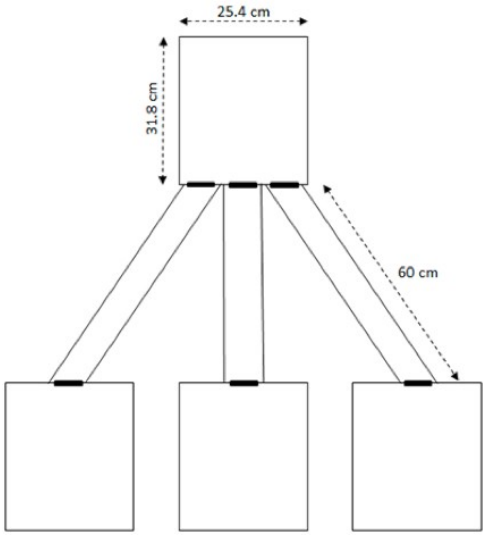

Figure 1. Scheme of the novelty test preparation.

Each one of the initial 25 rats was exposed individually to the experimental preparation for three consecutive days in a procedure that consisted in three sessions, one per day. During the first two sessions, each rat's activity was restricted to the initial chamber (the one at the top of Figure 1) for a period of 30 minutes. In the third session, the three doors of the initial cage were opened for 15 minutes to allow the rats' free access to the other three chambers, such that they could choose to stay in the initial cage or explore one or more of the other three cages. The time spent in each chamber (except the initial one) and on each bridge was regarded as exploration time, and this was the variable used for the phenotypic classification, considering the time spent outside the initial cage as a measure of novelty preference.

Figure 2. Chambers configuration used in the novelty test.

The variable exploration time was used to create two groups, each one made up of the four rats with the most extreme –low or high– scores. Following the criteria and nomenclature of Wooters, Dwoskin and Bardo (2006), the first group (LR, by low rate of exploration time) included the rats with the lowest exploration times (the lowest scores of the first quartile). It was considered as *less prone to novelty-seeking*. The second group (HR, by high rate of exploration time) was made up of the rats with the highest scores on the novelty-seeking test (the highest scores of the fourth quartile). We chose only the four rats for each group that had the most extreme scores (low or high) since there are no specific

established criteria or procedure for determining such classifications (see Hughes, 2007). After this phenotypic classification procedure both groups were exposed to a risk-sensitivity procedure. The other 17 rats were not included in the second phase of the experiment. We decided to choose the more extreme rats in order to get the clearest view. But at last it could be a limitation of this experiment, because it eliminates the possibility to observe rats with medium scores in novelty-seeking trait in our risk-sensitivity procedure.

Magazine Training Procedure. After the novelty test, both groups were exposed to a magazine training procedure in order to obtain basal levels for the lever-pressing response. In this procedure rats, under 85% of food deprivation, were exposed to a concurrent schedule of reinforcement with two components: FT30'' FR1. The procedure finished for each rat when it scored 100 responses during two consecutive sessions.

The risk-sensitivity procedure. For this procedure, operant chambers of the same model described above for the novelty test were employed, but the setting was modified. Each cage now had three levers (center, left, right), each one associated with a light. These lights (all of them white, but with variable intensity) signaled each one of the options presented. In this way, the rats were exposed to no-choice trials (center lever only), and free-choice trials (left and right levers simultaneously), according to the procedure described in the following paragraphs. The lights that signaled each alternative were not counterbalanced between rats, so that the most intense white light was used for the option that delivered a constant outcome, and the less intense white light signaled the option that delivered a variable outcome. The position of the alternatives was counterbalanced between blocks of sessions. See later for a more extensive explanation to this concern.

After that, the rats were exposed to a choice procedure that offered a constant delay and a variable delay. In our study, the values considered for the delay of each alternative were adopted from the work of Zabludoff et al. (1988). For the variable alternative we used the following values: 5, 10, 25 and 50 seconds; while for the constant option, a delay of 22.5 seconds was used. The procedure consisted in two phases with 24 sessions each one. The position of the options was counterbalanced in the phases so that 12 sessions began with the constant option on the left side and the variable option on the right side, and the other 12 had these positions reversed. During the first phase, the rats were maintained at 75% of their body weight. In the second phase, they were maintained at 90% of their body weight. This weight were controlled adding food after each experimental session (approximately 8gr. of amaranth per day). Adding more than 8gr. gradually increased body weight, and using less than 8gr. decreased it. So, the level of privation was higher for the first phase than for the second phase. A period of 15 days was allowed between phases, during which all rats had free access to amaranth until reach the expected weigh. We decided not to counterbalanced the order of privation level because, as later will be described, we didn't find an effect of the privation level over the preference for the variable or risky alternative.

Ten blocks of trials were conducted in each session; each block consisted of two no-choice trials and four free-choice trials. The constant option (C) was associated with a high-intensity white light located over the lever. Intensity was fixed using a 4-level fader control (control model MED EVN-226A, activating input #1). This alternative delivered the reinforcer, which was a fixed amount of 0.05 g of amaranth after a constant delay of 22.5 seconds. The variable option (V) was associated with a low-intensity white light located over the other lever. The intensity was fixed using the same fader control but activating input #3. That option delivered the reinforcer, also 0.05 g of amaranth, but only after one of the following delay intervals: 5, 10, 25 or 50 seconds. The values were presented randomly with equal probability (using a random sample with replacement), such that both options delivered the same mean reinforcement, but with different variability in delay.

During the no-choice trials, both alternatives were presented individually in a random order but with the same probability (0.5 for both options, fixed and variable), always in the center of the panel. During the four free-choice trials, the constant and variable alternatives were presented simultaneously. The position of the options during the free-choice trials was counterbalanced as follows: C-V (first 12 sessions), and V-C (final 12 sessions). This order was used in both phases. Only one response was required to select each alternative (no time out was applied in the absence of any response). An interval of 10 s was interposed between trials. During that interval all lights were turned off and the levers were retracted.

Measure of spontaneous alternation. Regarding the setting of choice and no-choice trials during the risk-sensitivity procedure, only changes of preference (from C to V or V to C) after the first choice trial were taken as cases of spontaneous alternation. Each change from the variable option to the constant option, and vice versa, was assumed as a case of spontaneous alternation. Hence, the maximum number of alternations per block was three. For example, a choice pattern like C-V-C-V would count as three alternations, while C-V-V-V would only count as one.

Results

Novelty Test

Figure 3 plot the individual exploration time considering the twenty-five rats evaluated in the novelty test. The exploration times distributed according to a Gaussian distribution (z of Kolmogorov-Smirnov = 0.59, $p > 0.05$). For the risk-sensitivity procedure, the four rats with the lowest and highest scores, respectively, were taken to form the LR and the HR groups (Figure 4).

Risk-sensitivity Procedure

In order to analyze preference, only the effective choices for the variable option in the first and last three-sessions of each phase are reported (Figure 5). Based on the number of participants on each group, and that we only consider the effective choices for the variable option, the main assumptions of parametric statistics could not be reasonable verified. Thus, we ran from the beginning non-parametric pairwise comparisons, without a prior multifactorial ANOVA including the block-session type (initial vs final), phenotypical classification (LR vs HR) and deprivation level (low vs high), with corresponding later post-hoc comparisons.

Nevertheless, we found significant differences using non-parametric tests, that are more restricted on their criteria than corresponding parametric alternatives, so it seems that the effects reported are very consistent even the minor number of participants.

During the first phase of the procedure, LR showed a difference between initial (65.52%) and final preferences (96.04%) for the variable option (Wilcoxon $Z = -3.1$ $p < 0.01$). The same result occurred in HR, whose initial and final preferences were 41.32% and 78.29%, respectively (Wilcoxon $Z = -2.9$, $p < 0.01$). The second phase also revealed a statistically significant difference between initial and final preferences for both LR (initial: 71.26%; final: 98.74%; Wilcoxon $Z = -2.9$, $p < 0.01$), and HR (initial: 33.59%; final: 87.18%; Wilcoxon $Z = -3.1$, $p < 0.01$).

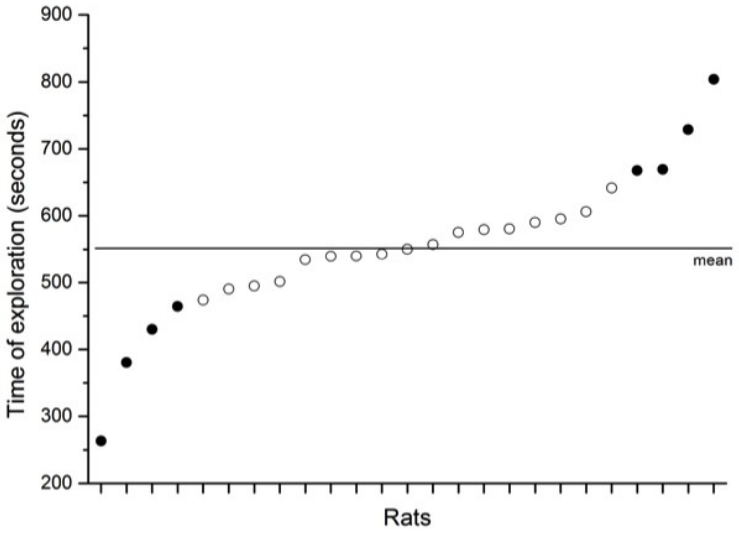

Figure 3. Individual time of exploration in the novelty test, ordering them from least to most. Black-dots signal the rats selected to the risk-sensitivity procedure.

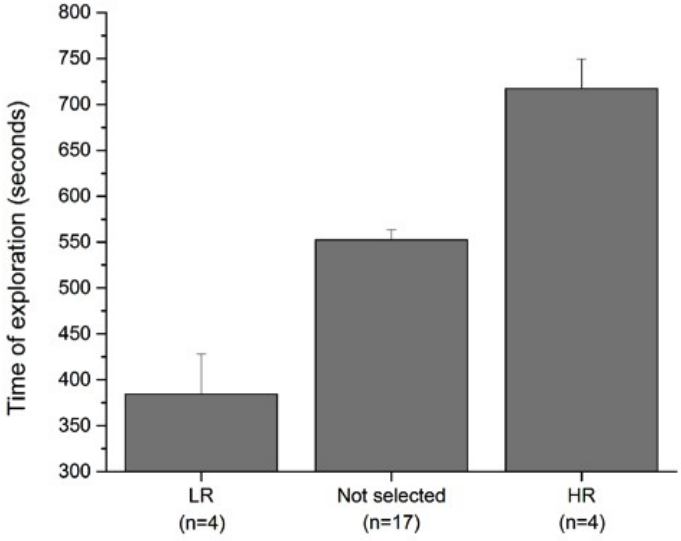

Figure 4. Mean exploration time (mean±SE) for both groups considered, and the total number of subjects assessed in the novelty test.

There were no statistically significant differences between initial and final preferences in the same group when analyzed according to phase. Although the initial preference of the LR rats in the first phase (65.52%) was lower than in the second (71.26%), this difference did not reach statistical significance (Wilcoxon Z = -0.7, p > 0.05). Regarding the final preferences across phases (96.04% in the first, 98.74% in the second), the LR rats showed no statistically significant differences (Wilcoxon Z = -0.9, p = 0.34). A similar trend was found in the case of the HR rats, as there was only a small decrease in their initial preferences for the variable option from phase 1 (41.32%) to phase 2 (33.59%), but this difference did not reach statistical significance (Wilcoxon Z = -1.3, p = 0.2). Similarly, regarding their final preferences in phase 1

(78.29%) and phase 2 (87.81%), there were no statistically significant differences (Wilcoxon Z = -1.6, p = 0.1). Comparing final preferences between groups in each phase, there was a significant difference: LR rats had greater final preference for the variable option (96.04%) than HR rats (78.29%) in phase 1 (Mann-Whitney U = 14, p < 0.01). In phase 2, the difference remains with 98.74% in LR rats and 87.18% in HR rats (Mann-Whitney U = 9, p < 0.01).

These data suggest: a) LR preferred the variable option more than HR at the initial and final parts of both phases; b) neither the preferences for the variable option among the LR rats nor those of the HR rats were affected by the level of food deprivation (Figure 5).

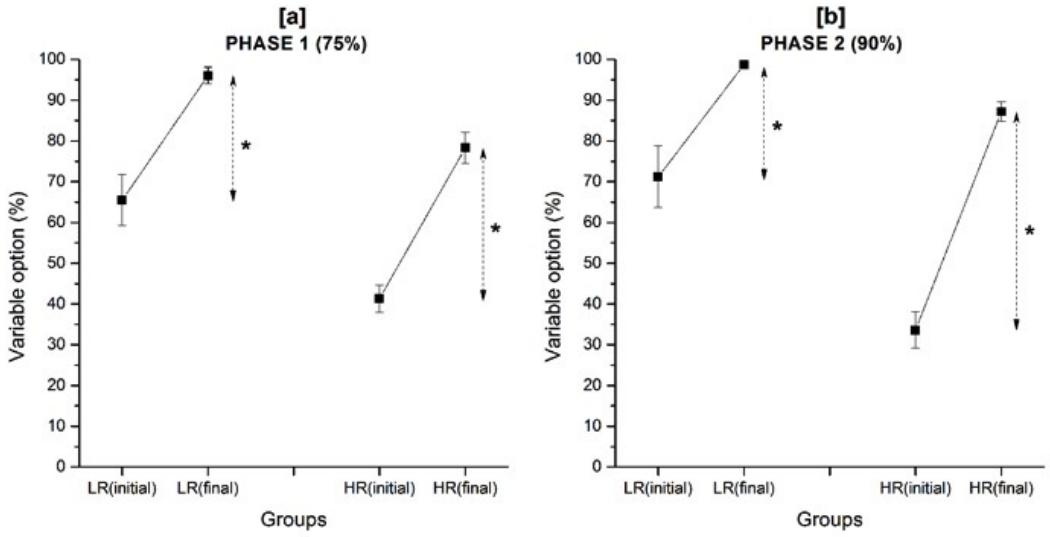

Figure 5. Mean percentage (mean±SE) of initial and final preference by groups. (a) Phase 1: deprivation level 75%; (b) Phase 2: deprivation level 90%. * indicates differences above chance, p<0.01)

A grain-fine analysis was done considering the preference for the variable alternative, session by session. As the sessions proceeded, the LR group developed a higher preference for the variable option compared to the HR group. This preference became more noticeable across sessions and continued in both phases. Thus, although both groups developed a preference for the variable option, that of the LR rats was always greater than in HR. This pattern is plotted in Figure 6.

After changing the position of variable option between phases, a decrease in percentage of choice for that alternative is observed. The differences on the recovery of preference for variable alternative are interesting. As can be seen in Figure 6 the LR rats has greater preference for the variable option than HR rats since phase 1, and recovers immediately that preference in phase 2 faster than HR rats. Comparing initial preferences between groups in each phase confirm this trend. LR rats has a greater preference for the variable option (65.52%) than HR (41.32%) during the first phase (Mann-Whitney U = 24, p = 0.01). During the second phase, when a change in preference is expected due to the counterbalancing of the levers, the trend remains, so, the initial preference of LR rats (71.26%) is greater than the HR rats (33.59%) (Mann-Whitney U = 14, p < 0.01). LR group recovered a level of preference for the

variable option, above 85% during phase 1 and close to 100% during phase 2, in only two sessions. In contrast, the HR group needed more sessions to recover the same level of preference observed during the first block of sessions on each phase (see Figure 6).

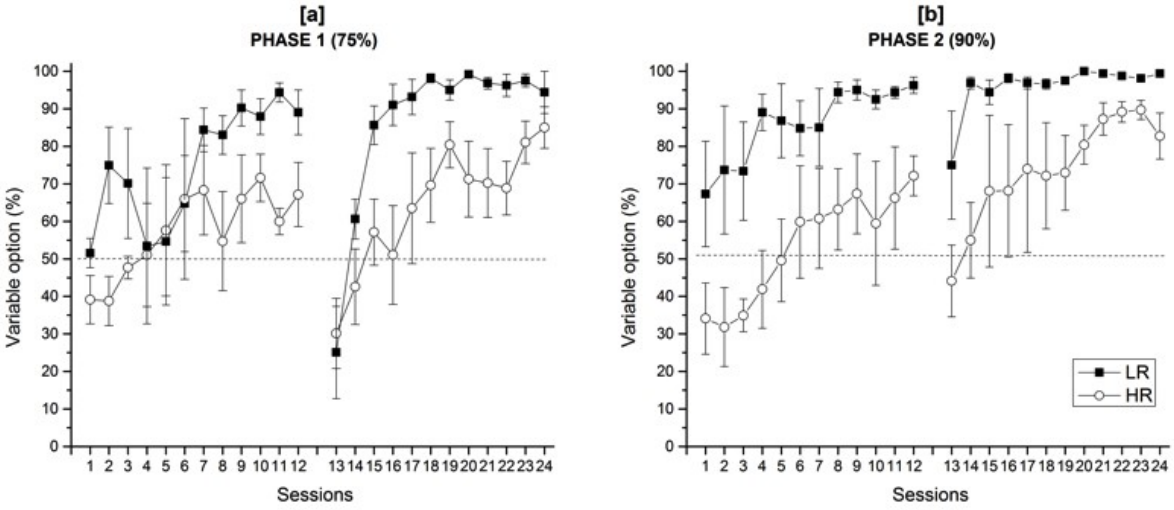

Figure 6. Mean percentage (mean±SE) of preference for variable option by session. (a) Phase 1: deprivation level 75%, groups LR and HR. (b) Phase 2: deprivation level 90%, groups LR and HR.

Finally, we conducted a spontaneous alternation analysis. Figure 7 plots the spontaneous alternation between alternatives. In this case, we averaged the total percentage of spontaneous alternation (the mean percentage considering all sessions) between groups for each phase. In addition, and in order to plot the general pattern across the procedure, we averaged the percentage of spontaneous alternation session-by-session for each group and phase.

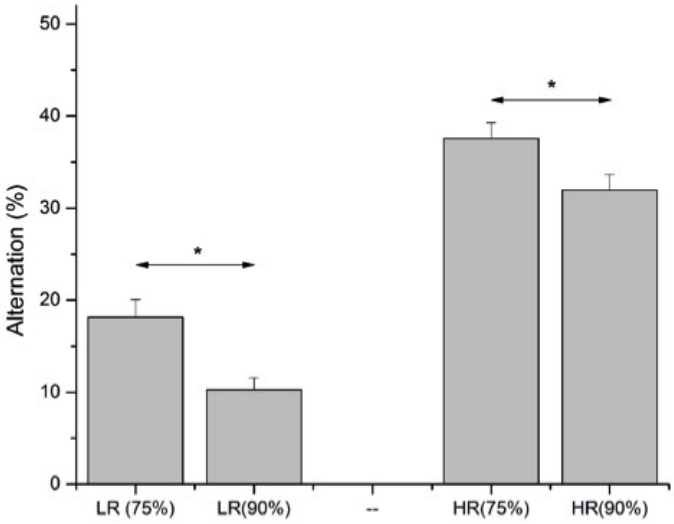

Figure 7. Total mean percentage (mean±SE) of spontaneous alternation by group and phase.

Our results show a noticeable difference in the mean percentage of alternation between groups in each phase, such that in phase 1 the mean percentage of spontaneous alternation in LR was 18.15%, whereas in HR it was 37.56%. This difference is statistically significant (Mann-Whitney $U = 1902$, $p < 0.01$). In phase 2, LR had a mean percentage of 10.27%, while HR had a mean percentage of 31.99%, this difference also reaches statistical significance (Mann-Whitney $U = 1280.5$, $p < 0.01$).

Upon comparing the mean percentage of spontaneous alternation across phases, considering all sessions, we found a significant decrease from phase 1 to phase 2 in both groups. In LR rats the decrement is from 18.15% in phase 1 to 10.27% in phase 2 (Wilcoxon $Z = -4.4$, $p < 0.01$). In HR rats the decrement is from 37.56% in phase 1 to 31.99% in phase 2 (Wilcoxon $Z = -2.4$, $p = 0.016$).

Finally, Figure 8 shows the mean percentage of spontaneous alternation session-by-session for both groups and phases. HR apparently showed higher percentages of alternation than LR in almost all sessions.

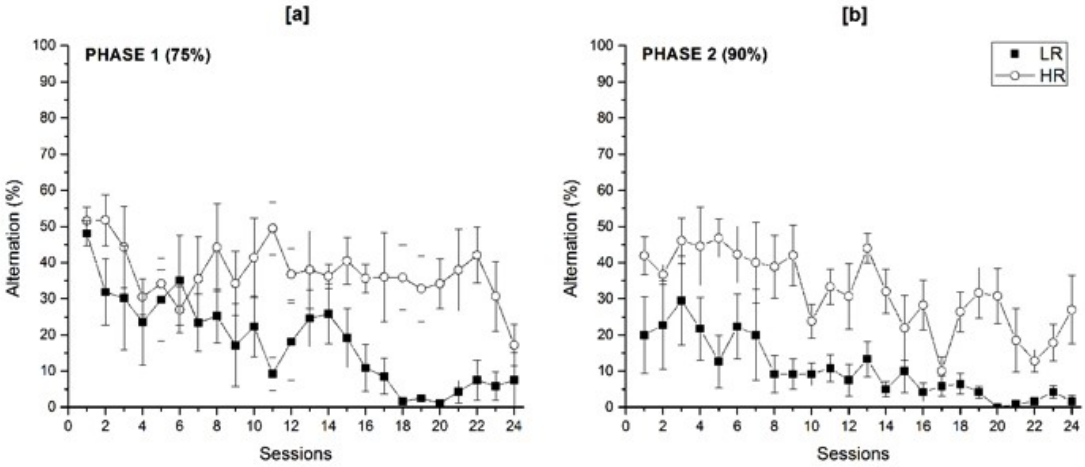

Figure 8. Mean percentage of spontaneous alternation (mean±SE) by group and session. (a) Phase 1: deprivation level 75%. (b) Phase 2: deprivation level 90.

Discussion

The main goal of this experiment was to explore whether individual differences in novelty-seeking behavior could affect preference in a risk-sensitivity procedure. Additionally, we evaluated the behavioral phenomenon of spontaneous alternation as a possible correlated variable.

In order to measure individual differences in novelty-seeking, an adaptation of the free-choice test proposed by Wooters et al. (2006) was used. At this point, considering the phenotypic classification done from the exploration time recorded in this task, two main reasons contribute to propose this paper as a preliminary approach to the study of the relationship between novelty-seeking and risk-sensitive:

1) the number of subjects that conformed each group, and mainly, 2) the final decision to compare only the choice behavior of the rats with the most extreme scores from the original sample assessed in the novelty-seeking task.

It could be argued that the lack of a third group composed by central values turns out to be a clear limitation of the present experiment, and we believe it is, because assessing a group conformed by subjects with medium scores, in fact, could contribute to a better understanding of the relationship between a phenotypic classification and the behavior of the subjects. Therefore, including subjects from the central part of the distribution can be a way to explore if the studied trait has *dichotomic effects* on preference or if its *effects* are graded. This possibility has empirical support in the study of Rivalan et al. (2009) where their subjects showed during the phenotypic classification values clearly allocated low, middle and high in the distribution. However, they only took to assessment low and high values of the distribution. Accordingly, future studies exploring the relationship between novelty-seeking and any behavioral measure should take into consideration subjects with values allocated in the central part of the distribution. The question about the criterion to use in the process of a phenotypic classification remains unsolved, and it should be considered in future research as a keystone for a more reliable research topic.

Even regarding the previously mentioned, we decided not to include in our experiment subjects from the central part of the distribution in order to take the more extreme punctuations (explorations times), and then getting a better phenotypic classification. We proceeded in this way following previous research in which only subjects with the extreme punctuations are taken to assessment. As it has been mentioned in the introduction section, there is not complete consistence in the strategy employed to make a phenotypic classification for novelty seeking (for a review about novelty seeking assessment see, Hughes, 2007). For example, Gancarz et al. (2012) only took subjects with extreme values (leaving out central values) and found a significant correlation. Nevertheless, other studies have taken values below and above the median (including central values) to correlate them with a particular behavior (Wooters et al., 2006), finding again significant correlations. Other novelty-seeking studies also employed an exclusion criterion to get the subjects with the extreme punctuations. For example, Zhu, Bardo, Bruntz, Stairs and Dwoskin (2007) excluded subjects that had values ± 5% of the median and still reported a significant correlation. There are even other studies in which they do not describe what happened with the subjects in the central part of the distribution (Cain, Smith & Bardo, 2004).

Without forgetting that including a third group conformed by subjects with medium scores could be a significant improvement of this experiment, and for sure contributes to better supported statements, we can conclude about several issues.

The results from the novelty test showed that the rats had different exploration times, and this allowed us to classify them into LR and HR groups. With respect to the risk-sensitivity procedure, the first main finding was that the classification employed was associated with a change in preference for the variable option regardless of the level of food deprivation. The second significant result was that the classification correlated with different patterns of preference across sessions, where the LR rats

preferred the variable option consistently when compared to the HR rats. Finally, as Figure 8 shows, the analysis of spontaneous alternation revealed that the HR rats alternated more than the LR rats upon averaging all sessions and plotting across sessions.

Our findings suggest that risk sensitivity, at least in this experiment, could be explained in terms of altered behavioral processes rather than in terms of a single rule about the minimization of probabilities of starvation. This idea has been previously suggested in economy (Loewenstein, 1996), and assessed with humans using the IOWA Gabling Task (Roussos et al., 2009), but has not been studied in risk sensitive procedures. Although the idea of minimization of probabilities of starvation can be useful explaining some findings, it also has been widely criticized under several regards, due to debatable assumptions about rationality and maximization (Kacelnik, 2006; Pyke, 1984). The debate about these assumptions go beyond the scope of this paper. Nevertheless, the found effects here presented support the idea of altered behavioral processes as an alternative explanation (against the first explanations of risk sensitivity) and open up the possibility of exploring risk sensitivity in a different way. This could allow analyze other relevant variables not yet studied, in this case, novelty seeking and spontaneous alternation, as suggests this paper. Nevertheless, the precise relationship between novelty seeking, spontaneous alternation and risk sensitivity requires further exploration at conceptual and empirical level. For example, it is possible to assume that novelty seeking is a *behavioral trait* (or behavioral process) which affects indirectly risk sensitivity through a mechanism that we could name as spontaneous alternation, or may be novelty seeking directly causes patterns of preference in risk sensitivity procedures with correlated effects on spontaneous alternation. This kind of concerns cannot be solved with the present findings.

By the other hand, regarding the findings as empirical facts, the next considerations can be stated. The association between novelty-seeking and risk aversion has not been reported in earlier research, at least not in regard to risk-sensitivity procedures using animals as subjects; thus, there are no antecedents in other animal-based experiments that could lead to find the precise correlation between the variables studied. Given that the novelty-seeking model provides a way to conceptualize the sensation-seeking trait in humans, experiments with humans offer the closest sources of comparison. Hence, considering that in humans the preference for novelty has been associated with risk preference using a decision-making task, that is distinct from a risk-sensitivity procedure (Roussos, Giakoumaki & Bitsios, 2009), our results would appear to be contradictory. However, the novelty-seeking model is also correlated with different behavioral processes in humans and animals (see Blanchard, Mendelsohn & Stamp, 2009 for a review). For example, LR subjects have been associated with high levels of anxiety (Pawlak, Ho & Schwarting, 2008) that may have contradictory effects on preference. In humans, anxiety has been associated with risk-proneness (de Visser, et al., 2010), but also risk-aversion (Mueller et al., 2010). Therefore, such comparisons have a very limited scope due to procedural differences and the distinct results manifested by humans and animals.

Another way to account for our data involves findings on altered behavioral processes in rats. In this regard, Flagel et al. (2010) used a novelty test procedure based on locomotor activity, and then bred LR rats with LR rats, and HR rats with HR

rats, in a selective breeding procedure. Later, they exposed each generation to a series of different procedures in order to assess altered behavioral processes. On the basis of this procedure they reported that the LR rats had higher levels of impulsivity than the HR rats in a delay-discounting procedure. Taking into account the fact that impulsivity has been suggested as an important variable in preference for variable delays in humans and animals (Mazur, 2004), these mechanisms can be considered a possible explanation. However, in the same study, HR rats showed higher levels of impulsivity than LR rats on other measures (specifically, a differential reinforcement of low rate of responding or DRL procedure). So, in light of these inconsistences, in order to prove the effect of impulsivity in our experiment a delay-discounting procedure would be necessary.

The fact that the level of food deprivation did not affect preference has been reported previously. For example, Zabludoff et al. (1988) found no correlation between the level of food deprivation and preference for the variable option in their risk-sensitivity procedure. Our findings add more evidence that questions the initial explanations of risk-sensitivity based on the assumption of minimizing the probability of starvation (Stephens, 1981). On the other hand, the results of the present study are consistent with those of Rivalan et al. (2009), who found that initial classification was associated with the rat's preferences, regardless of the levels of food deprivation employed (95, 90 and 80%), and regardless of extended exposure to the procedure. This means that despite of prior training with exposure to the options, their bad decision-makers still developed a preference for the disadvantageous options, though more slowly than in absence of prior training. The pattern reported by these authors is similar to the preference pattern found in our study. In their procedure, the bad decision-makers never attained the same preference as the good decision-makers and, as in our procedure, the HR group never reached the same preference as LR. However, there are procedural differences, since they employed a rat version of the IOWA Test and we used neither extended exposure to the procedure nor prior training. The aforementioned pattern from extended exposure opens up the possibility that the HR rats have a *slower rate* of learning in relation to the value of the options. Of course, this possibility requires further research.

The higher levels of spontaneous alternation found in the HR rats and their effect on preference appears to be a new finding. Past experiments on risk-sensitivity, using the novelty-seeking model, did not analyzed it. Intuitively, if we regard spontaneous alternation as a means of exploration (here, exploration of the other alternative), then it could be predicted that HR rats would be more prone to novelty than LR rats, and more prone to alternate. In this sense, one could argue that given the preference pattern of LR rats (similar to a ceiling effect) it is impossible to expect high or moderate percentages of spontaneous alternation; whereas in the HR rats this phenomenon could be expected because of their less extreme preference. However, this is not necessarily true because even with mean preference percentages of around 70% or 80%, the percentage of spontaneous alternation could be low because this index is calculated by analyzing the specific, trial-by-trial patterns, so less extreme preferences in and of themselves do not imply higher percentages of spontaneous alternation. To assess that levels of spontaneous alternation can account for the differences in preference found would require a procedure that makes it possible to assess differences in spontaneous alternation without manipulating the variability in reinforcer delay. It is important to point out that there is no evidence of

differences in spontaneous alternation in LR vs. HR rats in operant paradigms. Nevertheless, neurobiological differences related to dopamine receptors and subcortical structures (e.g., accumbens nuclei, basal ganglia, vestibular nuclei) have been reported (Blanchard et al., 2009). This evidence could give account of the found differences in spontaneous alternation, given the fact that dopamine is one of the neurotransmitters that affect spontaneous alternation (Einat & Szechtman, 1995).

In a review of spontaneous alternation, Richman, Kim and Dember (1986), reported that increasing the level of food deprivation can cause *perseverative behavior* and, consequently, a decrease in spontaneous alternation. Obviously, this would be contrary to our first finding (an increment with high food deprivation). But they also observed that individual differences in *emotionality* affected spontaneous alternation. If we take into account that food deprivation and individual differences can affect spontaneous alternation, then it is unclear which one might have caused the effect found in our experiment; indeed, there might even be an interaction effect between food deprivation and individual differences in novelty-seeking.

In sum, some hypothesis could be proposed to account for data reported. Additional experimentation would be necessary to prove any one of these possible explanations.

1. The preference for the variable option in LR rats could have been caused by increased delay-discounting that augmented the value of this option (since two of the delays were shorter than the constant option). This hypothesis would be consistent with the findings of Flagel et al. (2010). Subsequent experiments should explore the relationship between novelty seeking and possible differences in delay-discounting procedures.

2. The higher levels of spontaneous alternation in the HR rats generated a preference pattern that was less extreme than that of the LR rats. This occurred because the HR rats are more prone to novelty, and so more prone to alternating. This alternation trend between options has been reported on risky choice experiments in humans, referred as *erratic choice patterns* (Yechiam, Busemeyer, Stout & Bechara, 2005). Like a sub-product of that behavioral trend, the HR rats seem less risk prone than LR rats. Actually, it doesn't necessarily mean that the LR rats be more risky than HR rats. In this case the answer appears less obvious, because spontaneous alternation can be cause and consequence of less extreme preferences.

3. The HR rats have a *slow rate* of learning with regards to the value of the alternatives that, in turn, causes a less extreme preference than that of the LR rats. This would explain why HR rats never reached the level of preference of LR rats, and needed more sessions to recover previous percentage of choice when the position of the variable option was changed on each phase of the experimental procedure. Deficits on learning in risky choices have been reported in animals (Rivalan et al., 2009) and humans (Brogan, Hevey, O'Callaghan, Yoder & O'Shea, 2011). So, it is possible that this deficit on learning affects HR rats. An assessment of this possibility would require an extended exposure of sessions.

4. A fourth hypothesis could be that LR rats had been *hypoactive* during the risk procedure, so they moved less than HR rats and, obviously, alternated less. This possibility addresses the problem of separate locomotor activity from novelty seeking. Gancarz, Robble, Kausch, Lloyd and Richards (2012), using a choice procedure between an option without programmed consequences and another associated with visual stimulus (lights), found a relation between locomotor activity in a novelty seeking procedure and response rate to visual stimulus (regarded as novelty stimulus). HR and LR rats did not differ in the preference for the option that produce visual stimulus, even when HR rats showed greater response rate to the alternative associated with visual stimulus. Thus, novelty seeking can be related with high general activity, but high novelty seeking does not necessarily mean high locomotion (e. g. preference for novelty places or changing patterns of stimulus; see, Berlyne, 1960). To address this question a separate novelty seeking procedure for exploration and locomotor activity would be required.

The present work shows that a phenotypic classification based on novelty-seeking is associated with rats' preferences in a risk-sensitivity procedure. At least in this experiment we didn't find that the level of food deprivation – one of the most widely investigated variables in risk-sensitivity – account for preference for the variable option. The correlation we found was at least partially mediated by differences in spontaneous alternation, and thus suggests that individual differences should be considered in the study of choice in risk-sensitivity procedures.

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References

Blanchard, M.M., Mendelsohn, D. & Stamp, J. A. (2009). The HR/LR model: Further evidence as an animal model of sensation-seeking. Neuroscience and Biobehavioral Reviews, 33, 1145-1154. doi: 10.1016/j.neubiorev.2009.05.00

Brogan, A., Hevey, D., O'Callaghan, G., Yoder, R. & O'Shea D. (2011). Impaired decision making among morbidly obese adults. Journal of Psychosomatic Research, 70, 189-196. doi: 10.1016/j.jpsychores.2010.07.012

Cabrera, F., Robayo-Castro, B. & Covarrubias, P. (2010). The 'Huautli' alternative: amaranth as reinforcer in operant procedures. Mexican Journal of Behavior Analysis, 36(2), 71-92.

Cain, M.E., Smith, C.M. & Bardo, M.T. (2004). The effect of novelty on amphetamine self-administration in rats classified as high and low responders. Psychopharmacology, 176, 129-138. doi: 10.1007/s00213-004-1870-2

Caraco, T., Martindale, S. & Whittam, T. S. (1980). An empirical demonstration of risk-sensitivity foraging preferences. Animal Behavior, 28, 820-830. doi: 10.1016/S0003-3472(80)80142-4

de Visser, L., van der Knaap, L.J., van den Loo, A.J.A.E., van der Weerd, C.M.M., Ohl, F., & van den Bos, R. (2010). Trait anxiety affects decision-making differently in healthy men

and women: towards gender-specific endophenotypes of anxiety. Neuropsychologia, 48, 1598-1606. doi: 10.1016/j.neuropsychologia.2010.01.027
Einat, H. & Szechtman, H. (1995). Perseveration without hyperlocomotion in spontaneous alternation task in rats sensitized to the dopamine agonist quimpirole. Physiology and Behavior, 57 (1), 55-59. doi: 10.1016/0031-9384(94)00209-N
Flagel, S.B., Robinson, T.E., Clark, J.J., Clinton, S.M., Watson, S.J., Seeman, P., Philips P.E. & Akil H. (2010). An animal model of genetic vulnerability to behavioural disinhibition and responsiveness to reward-related cues: implications for addiction. Neuropsychopharmacology. 35, 388-400. doi: 10.1038/npp.2009.142
Gaffan, E.A., & Davies, J. (1982). Reward, novelty and spontaneous alternation. The Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology. 34 (1), 31-47. doi: 10.1080/14640748208400888.
Gancarz, A.M., Robble, M.A., Kausch, M.A., Lloyd, D.R. & Richards, J. B. (2012). Association between locomotor response to novelty and light reinforcement: sensory reinforcement as a rodent model of sensation seeking. Behavioral Brain Research, 230, 380-388.
García-Leal, O., Saldivar, G. & Lemus, C.A. (2008). Efecto de la disponibilidad de recursos energéticos en la sensibilidad al riesgo en ratas (Energy Budget effect over risk-sensitivity in rats). Acta Comportamentalia, 16(1), 25-40.
Graham, L.K., Yoon, T. & Kim, J.J. (2010). Stress impairs optimal behavior in a water-foraging choice in rats. Learning & Memory, 10, 1-14. doi: 10.1101/lm.1605510
Hughes, R.N. (2007). Neotic preferences in laboratory rodents: Issues, assessment and substrates. Neuroscience and Biobehavioral reviews, 31, 441-464. doi: 10.1016/j.neubiorev.2006.11.004
Kacelnik, A. (2006). Meanings of rationality. En M. Nudds & S. Hurley (Eds.), Rational Animals? (pp. 87-106). Oxford: Oxford University Press.
Kacelnik, A. & Bateson, M. (1996). Risky theories- The effects of variance in foraging decisions. American Society of Zoology, 36, 402-434. doi: 10.1093/icb/36.4.402
Kaminski, B.J. & Ator, N.A. (2001). Behavioral and pharmacological variables affecting risky choice in rats. Journal of the Experimental Analysis of Behavior, 75, 275-297. doi: 10.1901/jeab.2001.75-275
Loewenstein, G. (1996). Out of control: Visceral influences on behaviour. Organizational Behavior and Human Decision Processes, 65 (3), 272-292. doi:10.1006/obhd.1996.0028
Mazur, J.E. (2004). Risky choice: Selecting between certain and uncertain outcomes. The Behavior Analyst Today, 5 (2), 190-230.
Mueller, E.M., Nguyen, J., Ray, W J.,& Borkovek, T.D. (2010). Future-oriented decision-making in generalized anxiety disorder is evident across different versions of the Iowa gambling task. Journal of Behavior Therapy and Experimental Psychiatry, 41, 165-171. doi: 10.1016/j.jbtep.2009.12.002
Pawlak, C.R., Ho, Y.-J., & Schwarting, R.K.W. (2008). Animal models of human psychopathology based on individual differences in novelty-seeking and anxiety. Neuroscience and Biobehavioral Reviews, 32 (8), 1544-1568. doi: 10.1016/j.neubiorev.2008.06.007
Pyke, G.H. (1984). Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics, 15, 523-575. doi: 10.1146/annurev.es.15.110184.002515
Richman, C.L., Kim P., & Dember, W.N. (1986). Spontaneous Alternation Behavior in Animals: A Review. Current Psychological Research & Reviews, 5 (4), 358-391. doi: 10.1007/BF02686603
Rivalan, M., Ahmed, S.H., & Dellu-Hagedon, F. (2009). Risk-prone individuals prefer the wrong options on a rat version of the IOWA gambling task. Biological Psychiatry, 66, 743-749. doi: 10.1016/j.biopsych.2009.04.008
Roussos, P., Giakoumaki, G., & Bitsios P. (2009). Cognitive and emotional processing in high novelty-seeking associated with the L-DRD4 genotype. Neuropsychologia, 47, 1654-1659. doi: 10.1016/j.neuropsychologia.2009.02.005

Stead, J.D.H., Clinton, S., Neal, C., Schneider, J., Jama, A., Miller, S., Vazquez, D.M., Watson, S.J., & Akil, H. (2006). Selective breeding for divergence in novelty-seeking traits: heritability and enrichment in spontaneous anxiety-related behaviors. Behavior Genetics, 36 (5), 697-712. doi: 10.1007/s10519-006-9058-7

Stephens, D.W. (1981). The logic of risk-sensitivite foraging preferences. Animal Behaviour, 29, 628-629.

Stephens, D.W., & Krebs, J.R. (1986). Foraging theory. New Jersey. Princeton University Press.

Wooters, T.E., Dwoskin, L.P., & Bardo, M.T. (2006). Age and sex differences in the locomotor effect of repeated methylphenidate in rats classified as high- or low-novelty responders. Psychopharmacology, 188, 18.27. doi: 10.1007/s00213-006-0445-9

Yechiam, E., Busemeyer, J.R., Stout, J.C. & Bechara, A. (2005). Using cognitive models to map relations between neuropsychological disorders and human decision-making deficits. Psychological Science, 16 (12), 973-978. doi: 10.1111/j.1467-9280.2005.01646.x

Zabludoff, S.D., Wecker J., & Caraco T. (1988). Foraging choice in laboratory rats: constant versus variable delay. Behavioral Processes, 16, 95-110. doi: 10.1016/0376-6357(88)90021-6

Zhu, J., Bardo, M.T., Bruntz, R.C., Stairs, D.J. & Dwoskin, L.P. (2007). Individual differences in response to novelty predict prefrontal cortex dopamine transporter function and cell surface expression. European Journal of Neuroscience, 26, 717-728. doi: 10.1111/j.1460-9568.2007.05690.x

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