



Rats' optimal choice behavior in a gambling-like task

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ABSTRACT

Among the different procedures that model gambling behavior in non-human animals, the “suboptimal choice procedure” has been extensively employed for analyzing the impact of environmental cues on choice behavior. It has been repeatedly demonstrated that pigeons prefer an alternative that infrequently presents a stimulus that signals a larger amount of reinforcement, than another alternative that always presents a stimulus associated with a smaller amount of reinforcement, even though the net rate of reinforcement is lower in the former. In the present study, we tested rats in the magnitude version of the suboptimal choice procedure. Eight rats were given a choice between two alternatives: a) one in which a stimulus predicting the delivery of ten pellets was presented with probability (p) = 0.2 and a stimulus predicting zero pellets was presented with p = 0.8, and b) one in which either of two stimuli predicted the delivery of three pellets with p = 1.0. Contrary to the consistent and robust suboptimal behavior of pigeons, rats preferred the optimal alternative. This effect occurred despite the high index of discrimination of the stimuli associated with the different outcomes shown by the rats. The relevance of this result to the development of animal models of gambling behavior is discussed.

1. Introduction

Gambling behavior is a complex phenomenon that can lead to serious deleterious consequences for an individual in the familial, social and financial spheres (for a review, see Raylu and Oei, 2002). A large body of research has identified a plethora of factors related to gambling, including social (Gupta and Derevensky, 1997) and neurobiological (Potenza, 2008; Goudriaan et al., 2004) factors, and pavlovian and operant conditioning (Horsley et al., 2012; Dickerson, 1979; James et al., 2016). A consistent feature of gambling behavior is the tendency to overvalue the occurrence of a win and to undervalue the (more frequent) occurrence of a loss. This tendency may have its roots in the availability heuristic (Tversky and Kahneman, 1974), according to which wins influence behavior more strongly than the losses because the former are easier to remember than the latter. This asymmetry between the influence of win and losses, in turn, may be derived from a pavlovian process that assigns a differential value to the stimuli according to their salience and to the outcomes they are associated with; while a strong and positive value (conditioned reinforcement) is ascribed to the highly salient environmental stimuli that accompany wins, the negative value (conditioned inhibition) assigned to the stimuli that are present when losses are experienced or wins are omitted is smaller, probably because those stimuli are less salient (Wagenaar, 1988). This pattern of higher sensitivity to stimuli associated with reward than to

stimuli associated with punishment, has been found in impulsive humans (Gray et al., 1983), which is relevant to the present analysis because of the relationship between gambling and impulsivity (Vitaro et al., 1999; Alessi and Petry, 2003).

Given the ethical and practical limitations inherent to the research performed with human participants, the development of animal models of gambling behavior is highly desirable. While to date there is no ideal animal model, different aspects of gambling have been successfully modelled in non-human animals (Rivalan et al., 2009; Zeeb et al., 2009; Clark, 2010; Madden et al., 2007; Scarf et al., 2011; de Visser et al., 2011; Proctor et al., 2014). One such model is the “suboptimal choice procedure” (For reviews, see Cunningham and Shahan, 2018; McDevitt et al., 2016), a choice task that models the impact on choice of the environmental cues associated with wins and losses. This procedure has been employed in many studies in which pigeons and other birds have been reported to behave in a way analogous to human gamblers.

In one version of this task (See Fig. 1, panel A), discriminative and non-discriminative alternatives are presented to pigeons. If the former is chosen, two possible scenarios may occur: 1) with probability 0.2, a stimulus is presented for 10 s followed by the delivery of a reinforcer, or 2) with a probability of 0.8, another stimulus is presented for 10 s, but no reinforcer is delivered; these conditions are those required for the stimuli becoming a conditioned reinforcer and a conditioned inhibitor, respectively. If the non-discriminative alternative is chosen, two

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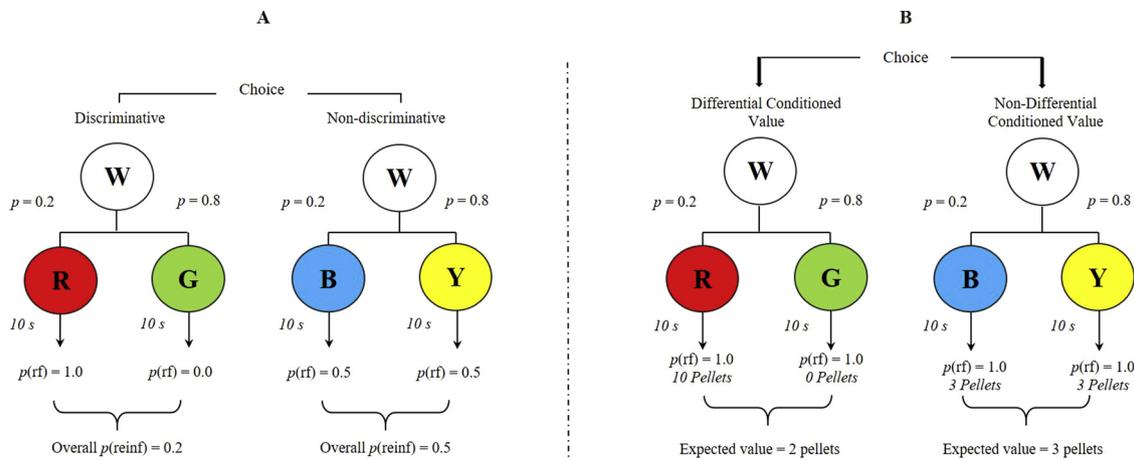


Fig. 1. Pigeons' suboptimal choice procedures. Panel A depicts the probability version: When pigeons choose the left white (W) key (discriminative option) then either a red light (R) always followed by a reinforcer turns on 20% of the time, or a green light (G) never followed by a reinforcer turns on 80% of the time; when pigeons choose the right white key (the non-discriminative option) then either a blue light (B) turns on 20% of the time, or a yellow light (Y) turns on 80% of the time. Both blue and yellow are followed by a reinforcer 50% of the time (see Stagner and Zentall, 2010). Panel B depicts the magnitude version: when pigeons choose the left White (W) key (Differential Conditioned Value) a red light (R) associated with the delivery of 10 pellets 10 s later is presented in 20% of the trials; in the other 80%, a green light (G) associated with zero pellets is presented. The expected value of this alternative is two pellets per trial. Choosing the other alternative (Non-Differential Conditioned Value) results in either of two stimuli (blue light (B), or yellow light (Y)), both associated with the delivery of three pellets 10 s later (expected value: three pellets per trial) (see Zentall and Stagner, 2011).

different stimuli may be presented (one with $p = 0.2$, the other with $p = 0.8$, so as to equate the probability of presentation of the stimuli in the two alternatives) and after 10 s in the presence of either stimulus, a reinforcer is delivered with $p = 0.5$; because these stimuli are less reliable predictors of reinforcement, they are assumed to become less powerful conditioned reinforcers than the perfectly reliable predictor of reinforcement from the discriminative alternative. The discriminative alternative is suboptimal as its probability of reinforcement (0.2) is smaller than the probability of reinforcement of the non-discriminative alternative (0.5). Pigeons, like human gamblers, show a preference for the suboptimal (and discriminative) alternative, i.e., that with the smaller expected earnings. Also, like human gamblers, pigeons seem to ignore the stimulus associated with no reinforcement or loses (Fortes et al., 2016; Laude et al., 2014b; McDevitt et al., 2016), so that the value of the discriminative alternative is determined exclusively by the stimulus associated with reinforcement (wins).

These similarities have encouraged some researchers to suggest that the same processes related to conditioned reinforcement influence the maladaptive-behavior of pigeons and humans (Zentall, 2011; Zentall and Stagner, 2011), an evolutionary-based account that allows the possibility that this behavioral pattern is also present in other species. However, the suboptimality shown by pigeons and other birds has not been replicated in rats (Martinez et al., 2017; Lopez et al., 2018; Trujano et al., 2016; Ojeda et al., 2018; Trujano and Orduña, 2015; Alba et al., 2018; c.f., Chow et al., 2017), questioning the wide generality implicated by the assumption of a common process as a cause of the similarity between the behavior of pigeons and humans. In spite of this absence of generality, the differences between the behavior of pigeons and rats could provide some insights in the search for the variables that determine gambling in humans. For example, the reported difference in behavior between pigeons and rats in the “suboptimal choice procedure” is consistent with the idea that these species differ in their sensitivity to the stimuli that predict the absence of reinforcement with certainty [conditioned inhibitors (for a theoretical analysis of the learning-mechanism that cause this differential sensitivity, see Daniels and Sanabria, 2018)]: while pigeons seem to ignore them (Laude et al., 2014b; McDevitt et al., 1997), rats strongly consider them when ascribing value to the discriminative alternative (Trujano et al., 2016). It is possible, then, that the sensitivity to conditioned inhibitors is a predictor of the tendency to gamble in humans.

Recently, it has been proposed (Zentall, 2011) that the procedure described above is not the best analogue of human gambling and that a better procedure should consider that in human gambling, the most relevant difference between the alternatives (gambling versus not gambling) does not lie in their probabilities of reinforcement, but in their amounts of reinforcement. Zentall and Stagner (2011) developed a new procedure that keeps the main characteristics of the aforementioned one, but presents two important modifications: a) the different stimuli associated with the discriminative alternative signal distinct amounts of reinforcement, besides different probabilities, b) in the non-discriminative alternative both stimuli signal the same amount, delivered with the same probability (1.0), therefore the uncertainty associated with this alternative is removed and its influence on suboptimal preferences may be discarded.

In this procedure (see Fig. 1, panel B), choice of one alternative (Differential Conditioned Value) results, in 20% of the trials, in a stimulus associated with the delivery of 10 pellets 10 s later, and in the other 80%, in a stimulus associated with zero pellets after the same delay (expected earnings: two pellets per trial). Choosing the other alternative (Non-Differential Conditioned Value) results in either of two stimuli associated with the delivery of three pellets 10 s later (expected earnings: three pellets per trial). Most of the pigeons quickly developed a strong preference for the suboptimal alternative (Zentall and Stagner, 2011; Laude et al., 2014a,b). Given that the preferred alternative, besides providing differential conditioned reinforcement, presented variable outcomes, it was necessary to analyze whether outcome variability or the differential conditioned reinforcement was the variable that determined pigeons' preference. For this reason, in a second experiment, the differential conditioned value was removed from the suboptimal alternative by providing 10 pellets with probability 0.2 (and 0 pellets with $p = .8$) 10 s after presentation of either of the two stimuli. Pigeons switched their preference to the optimal alternative, demonstrating that it was the differential conditioned value that determined their preference (Zentall and Stagner, 2011, exp 2).

Following up our idea that species-comparison could provide useful information about the variables controlling human gambling behavior, in the present study we evaluated rats in this version of the “suboptimal choice procedure”.

2. Method

2.1. Subjects

The subjects were sixteen experimentally naive, male Wistar rats obtained from the vivarium of the Institute of Cell Physiology, UNAM. The rats were 60 days old at the beginning of the experiment, were housed in groups of four, and were maintained at 85% of their free-body weight by providing food after each experimental session. Water was available ad lib in the home cage. The experiment followed the official Mexican norm NOM-062-ZOO-1999 'Technical Specification for Production, Use and Care of Laboratory Animals'. Half of the subjects participated in the main experiment, while the other half participated only in the Control condition (see below).

2.2. Apparatus

Four modified operant chambers (MED Associates, Inc., Model ENV 008-VP) were employed. Each chamber had two identical operative panels, one in the front side and the other in the back side. In each panel, a pellet receptacle (MED Associates, Inc., Model ENV-200R2M), provided with a head entry detector (MED Associates, Inc., Model ENV-254-CB) was mounted in the center, 2.5 cm above the floor. A nosepoke response device with a yellow stimulus light in its back (MED Associates, Inc., Model ENV-114BM) was mounted above food receptacle, and a retractable lever (MED Associates, Inc., Model ENV-112CM) on each side of it (for a detailed description of apparatus, see [Martinez et al. \(2017\)](#)).

2.2.1. Habituation and feeder training

Habituation to the operant chamber was achieved in 20-minute sessions during which there were 15 pellets available in each pellet receptacle. Habituation was considered complete when the subject ate all the pellets during a session. In the next session, subjects were exposed to a fixed-time 60 s schedule in which a pellet was delivered, every 60 s, in either of the two pellet receptacles, the probability of pellet delivery in either receptacle being 0.5. Session ended after 30 pellets had been delivered. No other stimulus was present during these sessions.

2.3. Nosepoke training

In each trial, one of the two nosepoke detector (randomly chosen, $p = 0.5$) was illuminated; when subject responded, a pellet was delivered, followed by a 10 s inter-trial interval (ITI). There were 50 trials in each session. This training finished when the latencies for responding on each nosepoke detector were shorter than 4 s and the difference between them was less than 1 s (approximately five sessions).

2.3.1. Sub-optimal choice: training

During 40 sessions, the differential conditioned value (DCV) alternative was located in the frontal panel and the non-differential conditioned value (NDCV) option in the back panel (see [Fig. 2](#), panel A). In each session there were 40 forced-choice trials and 20 free-choice trials. In half of the forced-choice trials, only the DCV alternative was available, which was signalled by the front nosepoke detector being illuminated. The first nosepoke response turned off the stimulus, and with $p = 0.2$ the left lever was presented and after 10 s was retracted and 10 pellets were delivered with an inter-pellet interval of 0.2 s; with $p = 0.8$, the right lever was presented and after 10 s this lever was retracted, and no pellet was delivered. In the other half of the forced-choice trials, only the NDCV alternative was available, signalled by the back nosepoke detector being illuminated. The first response in this detector led to the presentation of the left lever with $p = 0.2$ or the right lever with $p = 0.8$; after 10 s the lever presented was retracted and 3 pellets were delivered with $p = 1.0$. In free choice trials both

nosepoke detectors were illuminated and the first response on either presented the same contingencies of reinforcement that were described for the forced-choice trials. Trails were presented quasi-randomly, and were separated by 10-s ITIs.

After this condition was finished, a reversal condition was carried out in the following 40 sessions with the aim of detecting a potential position bias. In this condition, the location of DCV and NDCV alternatives was reversed and the position of the lever that was the predictor of 10 pellets in the DCV option, was also reversed. Therefore, the DCV alternative was now located in the back panel and the predictor of the larger amount of reinforcement was the right lever.

2.4. Control condition

In the procedure described above, the DCV alternative, besides being suboptimal, also implied risky outcomes; in contrast, the NDCV was the optimal alternative and was associated with the delivery of certain outcomes. Under these conditions, preference for the NDCV alternative could be mediated either by a preference for the higher expected value, or by risk-aversion. For analyzing the relative impact on choice of these variables, a control condition was conducted in which the DCV alternative continued to be risky, but now was the optimal alternative. In this condition, the probability of obtaining ten pellets after choosing the DCV alternative was changed from 0.2 to 0.5 (see [Fig. 2](#), panel B). The main difference from the main experimental condition was that the DCV alternative, while still risky, now was the optimal because its expected value was 5 pellets, while the NDCV continued providing 3 pellets.

3. Results

[Fig. 3](#) presents the mean proportion of choice for the option with differential conditioned value during each of the 40 sessions of training and the 40 sessions of the reversal phase, and the individual data. During the last five sessions of the training condition, when stability had been achieved, the mean proportion of choice for the differential conditioned reinforcement (suboptimal) alternative was 0.35 ± 0.07 (Mean \pm SEM). Although a *t*-test of the mean proportion of choice during the last five days against indifference did not reach statistical significance ($t(7) = 2.24$, $p = 0.059$, Cohen's $d = 0.79$), binomial tests on the individual preferences indicated that most of the subjects (6 out of 8) showed a significant preference for the optimal alternative (all p 's < 0.003); the other two subjects (R1 and R6) showed a significant preference for the suboptimal alternative (both p 's < 0.04). During reversal, the mean proportion of choice for the DCV alternative rapidly reached approximately the same levels as in the previous condition, and during the last five sessions the proportion was 0.34 ± 0.06 , which was significantly below indifference ($t(7) = 2.82$, $p < 0.05$, Cohen's $d = 0.99$); the pattern of individual preferences was similar to the training condition: 6 out of 8 subjects were optimal (all p 's < 0.003), one (R3) was indifferent ($p = 0.31$), and the other (R6) was suboptimal ($p = 0.01$).

[Fig. 4](#) shows the number of lever presses during the presence of the levers in forced trials in the DCV (top panel) and the NDCV alternative (lower panel). For the DCV alternative, the mean number of responses on the lever predicting reinforcement during the last five sessions in both conditions (10.36 ± 1.09) was higher than those on the lever associated with reinforcement omission (0.43 ± 0.16). No obvious differences between conditions were observed. An ANOVA performed to evaluate the effect of condition (training vs reversal) and stimuli (predictor of 10 pellets vs predictor of zero pellets) indicated that the factor stimuli was significant ($F(1, 7) = 70.20$, $p < 0.0001$; partial $\eta^2 = 0.91$), while the factor condition was not ($F(1, 7) = 0.05$, $p = 0.83$; partial $\eta^2 = 0.007$). The interaction of condition with stimuli was also non-significant ($F(1, 7) = 0.10$, $p = 0.76$; partial $\eta^2 = 0.01$). For the NDCV alternative ([Fig. 4](#), lower panel), during the last five

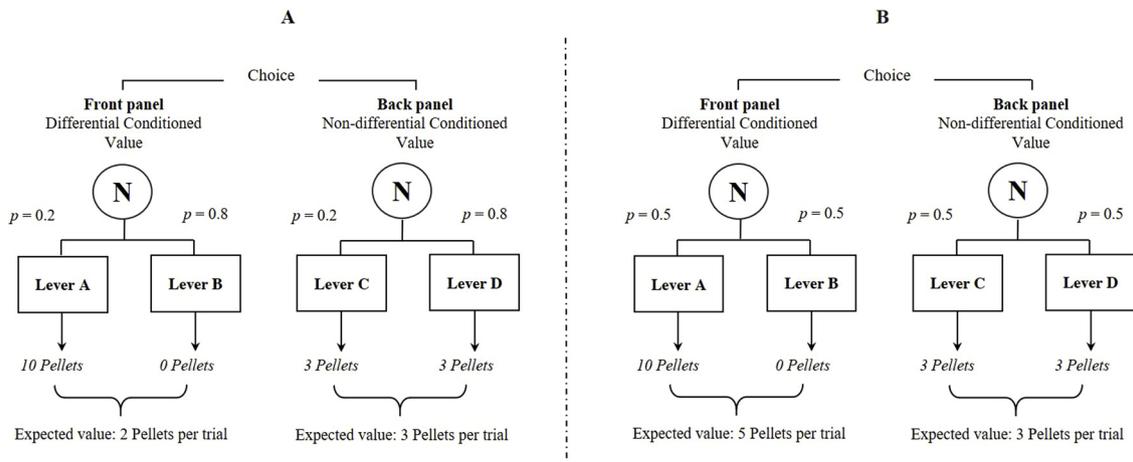


Fig. 2. Suboptimal choice procedure employed in the present experiment. Two alternatives, Differential Conditioned Value (DCV) and Non-differential Conditioned Value (NDCV), were presented in opposite panels. In the main condition (Panel A) Choosing the DCV option resulted with $p = .2$ in the presentation of lever A, which was a reliable predictor of the delivery of ten pellets, or with $p = .8$ of lever B, which was a reliable predictor of zero pellets. Choice of the NDCV option resulted in presentation of levers C or D (with $p = 0.2$ and 0.8 , respectively), both associated with the delivery of three pellets. NDCV was the optimal alternative. In the control condition (Panel B), after choosing the DCV alternative, the probability of presenting the stimulus leading to the larger amount of reinforcement (lever A) was changed from $.2$ to $.5$, in order to make the DCV alternative the optimal one.

sessions of each condition the mean number of responses was similar in the presence of the two stimuli that predicted three pellets. A separate ANOVA with the same factors revealed that there were no statistically significant effects of stimuli ($F(1, 7) = 0.004$, $p = 0.95$; partial $\eta^2 = 0.0005$) or condition ($F(1, 7) = 1.93$, $p = 0.21$; partial $\eta^2 = .22$), nor was the interaction significant ($F(1, 7) = 0.01$, $p = 0.92$; partial $\eta^2 = 0.001$).

The difference between the response rates in the presence of the stimulus predictor of the larger reinforcer and the predictor of no-reinforcement was not only statistically significant, but was very strong. Fig. 5 shows the index of discrimination for the DCV alternative during the entire experiment (responses on the reinforced lever / (responses on the reinforced lever + responses on the non-reinforced lever)). At the end of each condition, the discrimination was remarkably high (0.95 ± 0.03 and 0.96 ± 0.02 in training and reversal, respectively) and consistent among all the subjects (range $.84-.99$). In contrast, the same index for the NDCV alternative (responses in lever A / (responses on lever A + responses in lever B)) was around 0.5 in both conditions (0.50 ± 0.03).

3.1. Control condition results

Fig. 6 shows the proportion of choice for the DCV alternative across the 40 sessions of the condition. From the very first sessions, subjects rapidly departed from indifference and showed a reliable preference for the DCV alternative. During the last five sessions of this condition, the mean preference for this alternative was 0.74 ± 0.03 , which was significantly above indifference ($t(7) = 7.55$, $p < 0.001$, Cohen's $d = 2.66$). Binomial tests indicated that each of the 8 subjects showed a significant preference for the DCV alternative (all p 's < 0.03). The index of discrimination for responses in the two stimuli from the DCV alternative (data not shown) was 0.95 ± 0.03 (range $0.71-1$).

4. Discussion

In the present experiment, we evaluated rats' choice behavior in a procedure that has been regarded as an animal analogue of human gambling behavior. The results obtained here are relevant to the large body of data obtained with pigeons and other birds evaluated with similar procedures, and also to studies performed with rats in other gambling-like procedures.

The most direct comparison of the present data is with the results

obtained with pigeons using the same procedure (Laude et al., 2014a,b; Zentall and Stagner, 2011). Unlike the strong and consistent suboptimal preferences shown by pigeons, we found optimal choice in most of the rats (75%). A crucial aspect of these results is the finding that subjects discriminated the differential function of the stimuli (one associated with the delivery of ten pellets, the other with zero pellets), because it has been shown that pigeons make optimal choices when the suboptimal alternative is composed of two non-discriminative stimuli (Zentall and Stagner, 2011, exp.2). We found very high indexes of discrimination in all rats, with values similar to those obtained with pigeons (Laude et al., 2014b) and other birds (Vasconcelos et al., 2018), a fact that excludes the possibility that the optimal behavior was derived from an inability to discriminate the stimuli from the suboptimal alternative. In addition, data from the control condition suggest that the potential aversion to the risky outcome associated with the suboptimal alternative did not play a determinant role in the preference for the non-risky, optimal alternative. It should be acknowledged, however, that although the discriminative alternative continued being risky in the control condition, its coefficient of variation was smaller than in the main condition, possibly generating a decrement in the risk aversion (Weber et al., 2004).

Importantly, the optimal preference observed in the main condition occurred despite the discriminative stimuli (levers) had incentive salience; Chow et al (2017) hypothesized that the reason for the differences between pigeons and rats in the suboptimal choice procedure was that the illuminated keys employed in studies with pigeons had incentive salience, while the lights employed in the first studies with rats (Trujano et al., 2016; Trujano and Orduña, 2015) did not (for a related argument based on behavior systems theory, see Zentall et al., 2019). However, the present results, in conjunction with others (Lopez et al., 2018; Martinez et al., 2017; Ojeda et al., 2018; Alba et al., 2018), suggest that the incentive salience of the discriminative stimuli does not play such a major role in determining suboptimal choice.

The reasons for the strong differences between the behavior of pigeons and rats in the present procedure are not clear, but it is likely that they are related to the species-difference that has been demonstrated in the other version of the "suboptimal choice" procedure (currently the focus of deep theoretical analyses; see Cunningham and Shahan, 2018; Daniels and Sanabria, 2018): while pigeons prefer a discriminative (and suboptimal) alternative associated with probability of reinforcement = 0.2 over a non-discriminative alternative associated with probability of reinforcement = 0.5 (Stagner and Zentall, 2010), rats

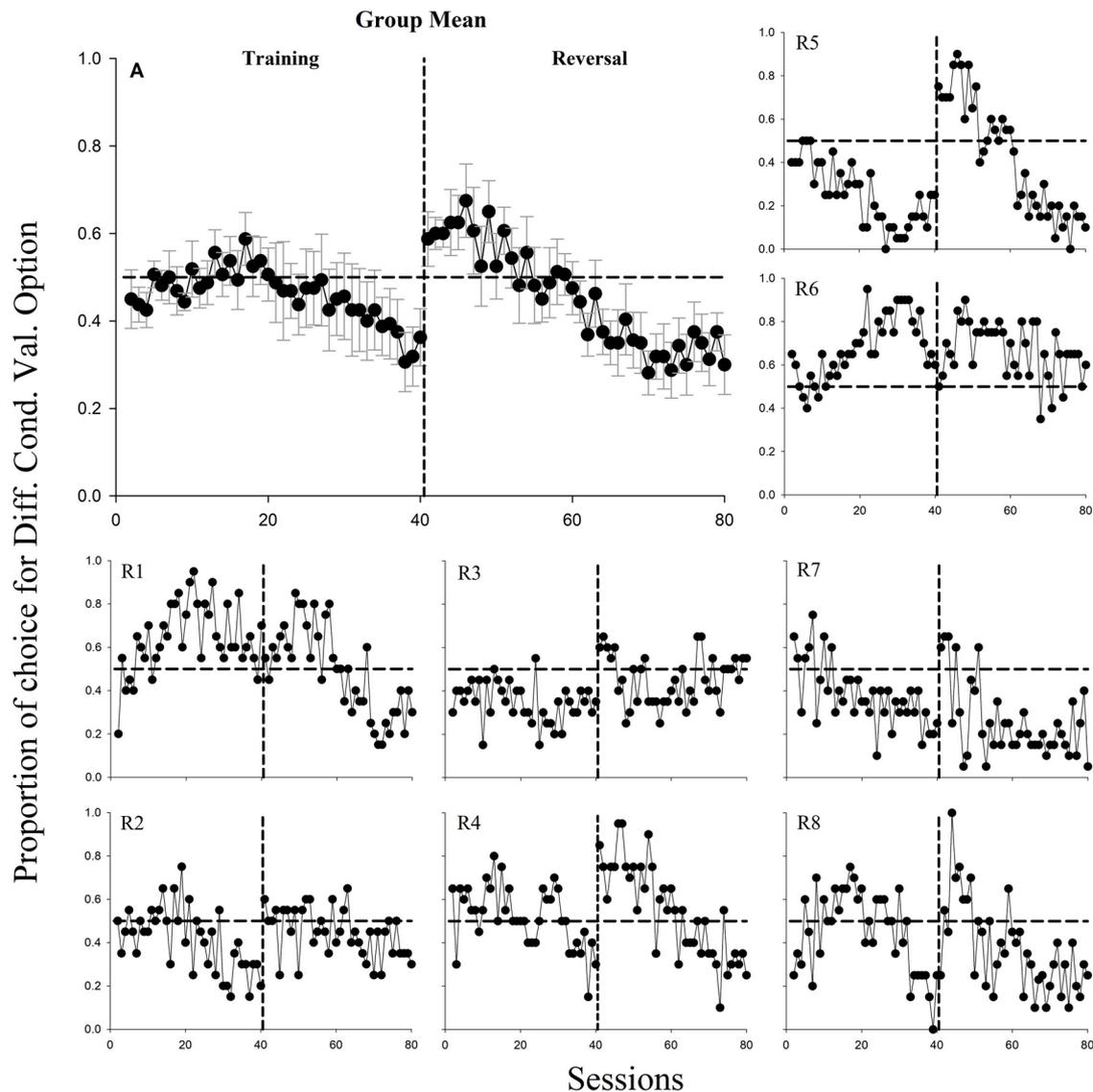


Fig. 3. Proportion of choice for the Differential Conditioned Value option along the 40 sessions of training in the suboptimal choice procedure, and the 40 sessions of the reversal phase of the main experimental condition. Horizontal dashed line denotes indifference between both options. Panel A shows the group mean \pm SEM; panels R1–R8 show data from each subject.

prefer the latter, optimal alternative (Alba et al., 2018; Trujano and Orduña, 2015; Ojeda et al., 2018; cf. Chow et al., 2017). Data from both procedures are consistent with the idea that rats are more sensitive to the conditioned inhibitor than pigeons. These data are not predicted by an extension to rodents of most theories of suboptimal choice, which were developed considering exclusively data from birds [SiGN (McDevitt et al., 2016), Contrast (Zentall, 2016), the Ecological Model (Vasconcelos et al., 2015; Fortes et al., 2017)]. The null influence that these theories ascribe to the stimulus that predicts no reinforcement is understandable, since until recently, the only data that suboptimal choice theories had to explain were those obtained with pigeons. The growing evidence that rats are optimal (Alba et al., 2018; Ojeda et al., 2018), and the demonstration that rats are persistently sensitive to the conditioned inhibitor (Trujano et al., 2016), pose a challenge to this aspect of the theories, but also suggest some possible ways for integrating the species-difference into a more general theory. More recent theories of suboptimal choice, developed after the difference between species was reported, have begun this integration. On the one hand, the temporal-information theoretic model (Cunningham and Shahan, 2018) proposes that the value of the discriminative and the non-discriminative alternatives is jointly determined by the temporal information that each

of its stimuli convey about food delivery, and by the rate of primary reinforcement associated with each alternative. Although this model has in common with previous theories the assumption of a null contribution of the predictor of no reinforcement to the value of the discriminative alternative, it can explain the species-difference in suboptimal choice by assuming a differential degree of competition between the rate of primary reinforcement and the value of the signals-defined by the temporal information they provide- as determinants of preference; it is possible that in contrast to pigeons, rats are more heavily influenced by primary reinforcement rate than by signal value. On the other hand, the Associability-decay model (Daniels and Sanabria, 2018) assumes that each terminal link stimulus and its related outcome influence initial link value according to an associability parameter, which in turn depends on the certainty of the relationship between terminal link and outcome presentation. Although in the suboptimal choice procedures, both stimuli from the discriminative alternative predict with certainty its outcome (reinforcer and no reinforcer, respectively) and therefore, the associability of both will be zero in steady state, the dynamics of this loss, together with the higher value of the positive stimulus, ascribe a higher value to the suboptimal alternative. When fitting the model to data from both pigeons and rats,

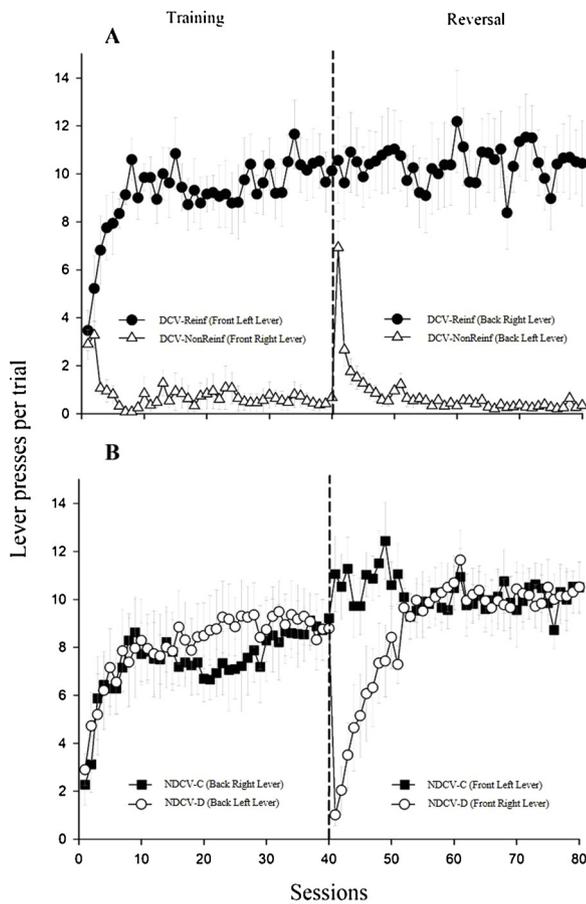


Fig. 4. Number of lever presses in forced trials (Mean \pm SEM) across all sessions during training and reversal phase of the main experimental condition. Panel A shows responses at the Differential Conditioned Value alternative. Closed symbols represent the number of responses during the stimulus associated with 10 pellets (DCV-Reinf) and open symbols represent responses during the stimulus associated with zero pellets (DCV-NoReinf). Panel B shows responses at the Non-Differential Conditioned Value alternative. Closed symbols represent responses on lever C (NDCV-C) and open symbols represent responses on lever D (NDCV-D).

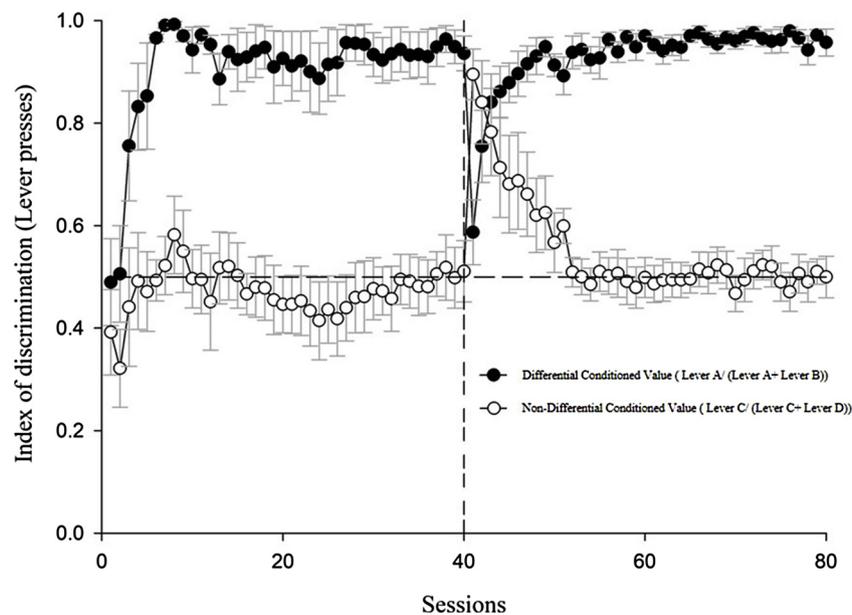


Fig. 5. Index of Discrimination (Mean \pm SEM) for the Differential Conditioned Value (closed symbols) and the Non-Differential Conditioned Value alternatives (open symbols) during the 40 sessions of training and the 40 sessions of reversal of the main experimental condition.

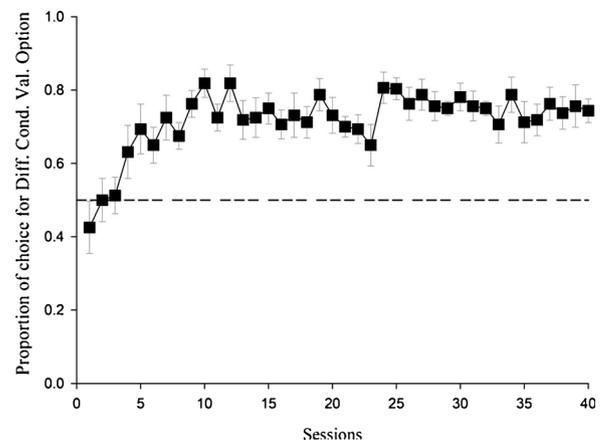


Fig. 6. Proportion of choice (Mean \pm SEM) for the Differential Conditioned Value option along the 40 sessions of training during the control condition. Horizontal dashed line denotes indifference between both options.

the model found a striking difference in the associability parameter for these species: while for pigeons the stimulus that predicted no reinforcement lost associability faster than the stimulus that predicted reinforcement, for rats there was no loss of associability for neither of these stimuli. Further research is needed to explore whether rats' optimality is more heavily influenced by the primary reinforcement rate, as assumed by the Temporal-information theoretic model, or by a stronger impact of the conditioned inhibitor, as suggested by the Associability-decay model.

The whole body of data obtained with rats, however, does not imply that the signalling effect is not present in this species; [Ojeda et al \(2018\)](#) demonstrated that rats prefer a discriminative alternative associated with probability of reinforcement 0.4, over a non-discriminative associated with $p = 0.5$, suggesting that the signaling effect is much weaker than it is in pigeons and other birds. This result is compatible with the assumption of the temporal-information theoretic model ([Cunningham and Shahan, 2018](#)), that although rats use both the value of the signals and the primary reinforcement rate for the calculation of value of the discriminative alternative, they give a higher weight to the primary reinforcement rate than pigeons.

Strong differences between pigeons and rats have also been noted in a modified version of the “probability discounting” procedure in which discriminative stimuli signalling the delivery or non-delivery of reinforcement were added to the basic procedure; in the basic procedure, a subject chooses between a smaller-certain and a larger-certain reinforcer. As both reinforcers have the same probability ($p = 1$), subjects show preference for the larger amount. Next the probability of the larger reinforcer is successively decreased resulting in a decrement in the preference for the this - now uncertain - reinforcer. The change in preference as a function of the decrement in probability is regarded as an index of risk-aversion: subjects that change their preference slower are more risk-prone than those showing a rapid change.

Although to our knowledge, rats and pigeons have not been explicitly compared in their degree of probability discounting, the analysis of the literature does not suggest obvious differences between them either in this task (Green et al., 2010; Simon et al., 2009; Cardinal and Howes, 2005; St Onge and Floresco, 2008) or in risk-sensitivity in general (Kacelnik and Bateson, 1996). Recently, in an effort to integrate the procedures of probability discounting and of suboptimal choice, both species were evaluated by the same research group in a probability discounting procedure in which choice of the risky alternative led to a different stimulus when the reinforcer was scheduled from when it was not. The results demonstrated that in pigeons probability discounting was completely eliminated, suggesting an increase in risk-proneness, and hence, suboptimality (Smith et al., 2017) while the effect in rats, although notable, was considerably smaller (Smith et al., 2018). A strong effect of the discriminative stimuli for pigeons, but not for rats, was also observed in a series of experiments by Mazur (Mazur, 1989, 1991, 2005, 2007) in which an adjusting-delay schedule was employed with both pigeons and rats to obtain the indifference point between a standard alternative that delivered a probabilistic reinforcer after 5 s delay and an adjusting-delay alternative that delivered a certain, but more delayed one. In some conditions, different stimuli presented during the standard delay signaled whether the reinforcer would be delivered or not. The results indicated that this manipulation increased the value of the standard alternative for pigeons, but not for rats, suggesting a stronger influence of conditioned reinforcement on the choice behavior of the first species. All these results are in agreement with the species-differences in the “signalling effect” mentioned above.

Our main result – that most of the rats chose optimally – is also in accordance with the results obtained in another of the most extensively employed animal models of gambling behavior, the rodent-adaptation of the Iowa Gambling Task (Rivalan et al., 2009; Zeeb et al., 2009; van den Bos et al., 2006; Pais-Vieira et al., 2007), originally developed for evaluating risky behavior in humans (Bechara et al., 1994).

In this procedure, subjects may respond in one of four alternatives that differ in both the amount of reinforcement provided and the severity and probability of losses (e.g., timeout from a time-restricted session). These variables are combined in a way that the alternative that delivers the largest rewards is also associated with largest losses that in the long term make this alternative non-optimal. In contrast, the other alternative delivers smaller reinforcers and smaller losses, a combination that makes this alternative the optimal one. A large number of studies has employed different variants of this procedure (for a review, see Van Den Bos et al., 2014), with the general findings being that most rats quickly learn to choose the most advantageous alternative and around 22–25% of subjects show a preference for the most disadvantageous alternative (Adams et al., 2017; Ferland and Winstanley, 2017; Rivalan et al., 2009, 2011; Di Ciano and Le Foll, 2016; Rivalan et al., 2013).

On the one hand, these results suggest –consistent with the results of the present study– that rats in general are capable of maximizing the reinforcement rate, and are sensitive to both the reinforcement rate and the timeouts associated with the different alternatives. On the other hand, the fact that a minority of subjects had a preference for the suboptimal alternative in the present report and in studies employing

the Iowa Gambling task could provide useful information about different sources of suboptimality: while in the suboptimal choice procedure, it appears to be primarily derived from ascribing a smaller weight to the conditioned inhibitor, in the Iowa Gambling Task it seems to be a result of heightened sensitivity to the reinforcer, and of a preference for immediate gratification, particularly related to the larger reinforcer (Rivalan et al., 2009).

Further research evaluating the same individuals in these two procedures is necessary to evaluate the potential correlation between these two different sources of suboptimality. The comparison between rats’ and pigeons’ performance in the Iowa Gambling Task and of pigeons’ behavior in both procedures could also inform on this point. To our knowledge, the Iowa gambling task has not been employed with pigeons, but a prediction can be made that they will be less sensitive to the timeout periods than rats, which will promote suboptimal behavior. Also relevant for increasing our understanding of the differences between pigeons and rats in models of gambling behavior is the evaluation of the signalling effect in the Iowa Gambling Task in both pigeons and rats. In this respect, it is likely that pigeons will be more sensitive to this manipulation than rats, as shown in the present study, and in other suboptimal choice procedures.

Animal models have undoubtedly contributed to understanding the roles played by stimuli signalling wins and losses. In particular, the analysis of the differences between rats and pigeons in the suboptimal choice procedure has highlighted some variables that have a rich potential for being incorporated into the study of gambling behavior in humans, for example, the incentive salience of the stimuli (Chow et al., 2017), the impact of the sensitivity to stimuli that signal losses (Laude et al., 2014b; Trujano et al., 2016), and – more closely related to the present results – the impact of the informativeness of the discriminative stimuli. In particular, the present results suggest that rats that displayed suboptimal choice behavior could represent an animal model of this aspect of gambling behavior in humans, supporting the idea that the study of spontaneous individual differences has a rich potential for advancing the study of suboptimal behavior (Rivalan et al., 2009).

While the present results suggest that the effect that discriminative stimuli has on gambling behavior is not as general across species (and across individuals within some species) as previously thought, the study of individual differences in the sensitivity to these stimuli seems to be a promising avenue for developing an improved animal model of gambling behavior.

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