

# Suboptimal choice by pigeons is eliminated when key-pecking behavior is replaced by treadle-pressing



Rodrigo González-Torres, Julio Flores, Vladimir Orduña\*

Facultad de Psicología, Universidad Nacional Autónoma de México, México, DF, 04510, Mexico

## ARTICLE INFO

### Keywords:

Suboptimal choice  
Incentive salience  
Treadle pressing  
Ambient lights  
Pigeons

## ABSTRACT

In the study of suboptimal choice, a reliable result is that pigeons strongly prefer an alternative that signals whether a reinforcer will be delivered or not over another alternative without that information even if the first provides a lower probability of reinforcement. In the aforementioned research, key pecking has been the operant response and illuminated keys the discriminative stimuli. In the present study we modified both of these aspects of the procedure in order to analyze the generality of suboptimal preferences of pigeons and to investigate the effect of changes in the incentive salience of the discriminative stimuli. To accomplish this, we presented pigeons a choice situation with the same parameters of reinforcement than previous research, but with treadle pressing as the choice response and ambient lights as discriminative stimuli. Under these conditions, most of the pigeons showed optimal behavior and a high degree of discrimination of the stimuli associated with the discriminative alternative. A control condition with key pecking as choice response and keylights as discriminative stimuli showed that the same pigeons turned to be suboptimal, a result that discards the possibility that the optimality found in the main condition was a consequence of a particular characteristic of our sample of subjects or of our procedure. We discuss the influence that the attribution of incentive salience to the discriminative stimuli has on suboptimal choice in both pigeons and rats.

## 1. Introduction

The suboptimal choice procedure has been employed in a long list of studies, with the objective of studying the determinants of choice and to model in animals some aspects of human gambling behavior. In the prototypical procedure (Stagner and Zentall, 2010), pigeons choose via a key peck between: a) an alternative (discriminative) that in 20 % of the trials presents a stimulus that predicts the delivery of a reinforcer 10 s later and that in 80 % of the trials presents another stimulus that predicts that 10 s later, no reinforcer will be delivered (overall probability of reinforcement = .20), and b) another alternative (non-discriminative) that presents either of two stimuli that equally predict that 10 s later a reinforcer will be delivered with  $p = .50$  (overall probability of reinforcement = .50). The name of the procedure is derived from the fact that pigeons have a strong preference for the first alternative, i.e., the discriminative and suboptimal.

Even though the strong preference for the suboptimal alternative has been replicated dozens of times in pigeons (for reviews, see Zentall, 2016; McDevitt et al., 2016), its generality remains largely unexplored as key pecking is the only response that has been studied in pigeons, and few experiments have studied other species. Performing research

with other responses and species would undoubtedly help to elucidate the mechanisms that promote suboptimal choice; an example of the usefulness of this approach is (though not consensual) the postulation of the incentive salience of the discriminative stimuli (Chow et al., 2017) as source of the difference between pigeons' suboptimality (Zentall, 2014) and rats' optimality (Trujano and Orduña, 2015). Incentive salience is a property of some conditioned stimuli (CS) which, due to their contingent pairing with an unconditioned stimulus (US), acquire the ability to attract behavior towards them, to function as secondary reinforcers, and to arouse complex emotional and motivational states related to the receipt of the US (Robinson et al., 2018). Incentive salience is not an absolute property of a CS, but depends, among other things, on its sensory properties (Singer et al., 2016; Meyer et al., 2014), the species used (Powell et al., 1975), and more generally, on the biological relatedness between the CS and the US for that particular species (Timberlake and Grant, 1975; Zentall et al., 2019). Interestingly, it has been reported that even when different organisms from the same species are exposed in a contingent way to the same pair of CS-US (e.g., lever-food), there are striking individual differences in the incentive salience attributed to the conditioned stimulus (Meyer et al., 2012). Incentive salience is a solid construct, with all its

\* Corresponding author.

E-mail address: [vladord@unam.mx](mailto:vladord@unam.mx) (V. Orduña).

<https://doi.org/10.1016/j.beproc.2020.104157>

Received 9 March 2020; Received in revised form 29 May 2020; Accepted 29 May 2020

Available online 01 June 2020

0376-6357/ © 2020 Elsevier B.V. All rights reserved.

causes (Killeen, 2001): final (Nesse and Berridge, 1997; Newlin, 2002), efficient (Tomie et al., 2014), material (Kuhn et al., 2018) and formal (Anselme, 2015; McClure et al., 2003; Zhang et al., 2009), as well as some of its implications in the promotion of maladaptive behavior (Meyer et al., 2018) extensively investigated.

When applied to the issue of between-species differences in sub-optimal choice, the incentive-salience hypothesis basically proposes that such differences are a byproduct of differences in the incentive salience of the discriminative stimuli employed with each species: while for pigeons the stimuli are usually illuminated keys which have high incentive salience for them and evoke sign-tracking responses that persist even when they cancel the presentation of food (Williams and Williams, 1969), the stimuli employed in the first studies with rats were lights (Trujano et al., 2016; Trujano and Orduña, 2015) or sounds (Ojeda et al., 2018), which do not have incentive salience for this species as they provoke goal-tracking behavior (Beckmann and Chow, 2015). The hypothesis that relates incentive salience of the stimuli with suboptimal preferences has been evaluated in rats, without conclusive results; although the first study reported that using levers as discriminative stimuli -which have been shown to be attributed with higher incentive salience than lights or tones (Beckmann and Chow, 2015)- promoted suboptimal choice (Chow et al., 2017), this result has not been replicated (Martínez et al., 2017; López et al., 2018; Orduña and Alba, 2019; Alba et al., 2018).

If we accept the idea that illuminated keys for pigeons and levers for rats have an equivalent level of incentive salience for the respective species, the results revised so far suggest that the incentive salience of stimuli is not the variable underlying their differential performance in the “suboptimal choice” procedure. It is possible, however, that although rats attribute more incentive salience to levers than to lights or tones (Beckmann and Chow, 2015), the level of incentive salience is lower than the level that pigeons attribute to illuminated keys, and does not reach the threshold for generating suboptimal choice. If pigeons preferences in the suboptimal choice procedure are actually influenced by the incentive salience of the stimuli, a decrement in pigeons’ sub-optimal behavior should be expected if the discriminative stimuli are separated from the response manipulandum (Tomie, 1996), and if the response manipulandum does not elicit the same consummatory behavior than the reinforcer. In support of this argument, different sources of evidence suggest that several instances of pigeons’ maladaptive key-pecking behavior are derived from the strong influence that Pavlovian contingencies have on pecking behavior; this influence is maximal in conditions in which the discriminative stimuli are presented on the response key (LoLordo, 1971; Boakes et al., 1975), smaller when the stimuli are separated from the response key (Westbrook, 1973), and is absent in conditions in which key pecking is replaced by foot-pressing a treadle (Westbrook, 1973; Green and Holt, 2003; LoLordo et al., 1974). It has been reported, for example, that pigeons are less efficient in differential reinforcement of low rates schedules when the operant response is key pecking than when it is treadle pressing (Hemmes, 1975). In a temporal discounting task, pigeons show a higher degree of discounting when the choice response is key pecking than when it is treadle pressing (Holt et al., 2013). The differences between these operant responses have also been noted in experiments exploring behavioral contrast: When pigeons are trained in multiple variable interval (VI)-VI schedules, and one of the schedules is changed to extinction, pigeons increase their response rate in the unchanged component when the operant response is key pecking, but show no changes when the operant response is treadle pressing (Hemmes, 1973).

The particularities of key pecking as an operant response have also been noted in the context of species differences in the sensitivity to the addition of free reinforcers to one of the components of a multiple schedule VI 2 min VI 2 min (Boakes et al., 1975); while pigeons’ key pecking increased during the component with free reinforcers added, rats’ lever pressing decreased in this component. In a similar experiment, the effect of adding free reinforcers was observed for pigeons’ key

pecking, but not for pigeons treadle pressing (Green and Holt, 2003; LoLordo, 1971; LoLordo et al., 1974).

All this evidence is compatible with the idea that key pecking is strongly influenced by the Pavlovian contingency between the stimuli displayed on the keys and the reinforcer, and less sensitive to the instrumental contingencies between key pecking and reinforcers than other responses like treadle pressing. Coherently with this line of arguments, it has been suggested that “treadle pressing in pigeons is more comparable to the operant behavior shown by other species than is key pecking” (Hemmes, 1975; p 356).

It is possible, then, that the mechanism by which the treadle-pressing response diminished maladaptive behavior in the studies described above was a decrement in the incentive salience, which was favored by both the separation between the discriminative stimuli and the response manipulandum, and by the dissimilarity in topography between the operant response and the consummatory responses originally elicited by the US (Zentall et al., 2019). In this context, we hypothesized that the suboptimal behavior of pigeons could be diminished by presenting ambient lights as discriminative stimuli, instead of the usual illuminated keys, and by replacing key pecking by treadle pressing as the choice response.

## 2. Method

### 2.1. Subjects

Eleven naive, domestic pigeons (*Columba livia*) of undetermined sex and between 1 and 2 years old served as subjects. Their weight when they were not food-restricted was  $402 \pm 77.3$  g (Mean  $\pm$  SD). At the beginning of the experiment, subjects were food deprived until they reached 80 % of their ad libitum weight; throughout the experiment subjects received food after the experimental sessions when needed to maintain the intended weight. All experimental protocols followed the Official Mexican Standard of Technical Specifications for the Production, Care and Use of Laboratory Animals (NOM-062-ZOO-1999).

### 2.2. Apparatus

#### 2.2.1. Treadle-pressing condition

Two modified operant conditioning chambers measuring 29.5 \* 23.5 \* 27.3 cm (large \* wide \* height) served as the experimental spaces. The floor was a stainless-steel grid composed of nineteen bars of 0.48 cm in diameter. Each chamber had two identical operative panels, one in the front side and the other in the back side. On each panel, a 5-cm square opening, located 1.3 cm above the floor and at the center of the panel, provided access to a solenoid-operated hopper (MED Associates, Inc., Model ENV-205 M) which contained a mixture of grains. The hopper was illuminated by a 1-W miniature lamp whenever it was raised. At the right of the hopper, and 2 cm above the floor, there was a 4.8 cm-wide retractable response lever (MED Associates, Inc., Model ENV-112CM) which was used as treadle. A houselight was mounted 24.5 cm above each lever. The visual stimuli used were 4 strips of ultra-brilliant LEDs that were attached to the ceiling of the chamber. Each of the 4 strips contained 5 LEDs of the same color (red, green, blue and white, respectively) which had a 4 cm separation between them. Each strip, when activated, provided illumination of the same color for the entire chamber.

#### 2.2.2. Control condition: key pecking

Four operant conditioning chambers measuring 35 \* 30 \* 37 cm (large \* wide \* high) were used as the experimental spaces. The floor was a stainless-steel grid composed of nineteen bars of 0.48 cm in diameter. A 5-cm square opening, located 9.5 cm above the floor in the front wall provided access to a solenoid-operated hopper filled with mixed grain. The hopper was illuminated by a 1-W miniature lamp

whenever it was raised. Three response keys, each measuring 2.5 cm in diameter, were located 23 cm above the floor; the center key was located directly above the hopper, with the additional two keys located 7.5 cm to the right and left of the center key, respectively. A force of approximately 0.15 N was required to operate each key, which could be illuminated with white, green or red light. A 1-W houselight was located at the center of the ceiling.

In both conditions, the chambers were enclosed in a sound attenuating box, with continually operating fans providing ventilation. The presentation of stimuli and the collection of data were controlled by personal computers using the Medstate programming language.

### 2.3. Procedure

#### 2.3.1. Treadle-pressing condition

**2.3.1.1. Habituation.** When the subjects were at 80 % of their ad-libitum weight, they were habituated to the experimental chamber for a single session 20 min long. During the first 5 min, both feeders were illuminated and provided access to a mixture of grains. If pigeons consistently approached to only one of the feeders, it was turned off, in order to allow exploration of the other feeder. During the remaining 15 min, an automated procedure was initiated, in which a fixed time 20 s schedule determined the activation of one of the feeders (quasi-randomly selected, with the only restriction that the same feeder could not be selected more than two times in a row) for 3 s.

**2.3.1.2. Treadle-pressing shaping.** Treadle pressing was shaped by the method of successive approximations during 1–5 sessions. Each of these sessions was 30 min long. Special attention was devoted to not reinforcing any treadle pressing that was made with a peck. During the entire session, both houselights were turned on. The criteria for ending this phase was that the latencies for pressing both treadles were less than 5 s.

**2.3.1.3. Pre-training.** Once pigeons consistently responded to both levers, pre-training sessions were carried out until similar latencies were observed for responses to both levers, in order to reduce the possibility of a position bias. These sessions were comprised of 4 blocks of 15 trials. In each of the blocks, the same lever was presented during 15 trials. In each trial, a single treadle press with duration > 0.2 s was required to give access to the reinforcer (2 s of access to the hopper); this duration requirement was implemented to avoid reinforcing presses that were performed with a peck and was maintained in all phases of the experiment. In successive blocks, both levers were presented twice in each session with strict alternation between them. The active lever in the first block was randomly selected. Trials and blocks were separated by 8 s intertrial intervals (ITI).

**2.3.1.4. Pre-exposure to stimuli.** Subjects were exposed to a single session in which they were required to press the treadle in the presence of the distinct stimuli that would be employed in the next phase. In this session, a trial initiated when one of the levers was extended and its associated houselight turned on. A single response extinguished the houselight and presented one of the four ambient lights (red, green, blue or white), in whose presence a reinforcer was delivered when a fixed ratio 3 was satisfied. Each color was presented 5 times in each of the levers, for completing 40 trials in the session.

**2.3.1.5. Training. Suboptimal choice procedure.** Each of the sessions in this phase was comprised of 40 forced-choice trials (20 for each alternative), and 20 free-choice trials. The start of a forced-choice trial (see Fig. 1, panel A) was defined by the presentation of a lever and its accompanying houselight. In the case of the discriminative alternative, a single treadle press turned on, in 20 % of the trials, the illumination of the chamber with red color for 10 s, after which the first treadle press was followed by reinforcement. In the remaining 80 % of

the trials, the chamber was illuminated with green color, and after 10 s, the trial ended without reinforcement. In this alternative the overall probability of reinforcement was 0.20. In the forced-choice trials of the non-discriminative alternative, a single treadle press turned on either blue or white color in 20 % and 80 % of trials, respectively. Irrespective of which of these colors was presented, reinforcement was provided with probability = .50 for the first response after 10 s had elapsed. In this alternative the overall probability of reinforcement was 0.50. In free-choice trials, both levers and both houselights were presented and the first treadle press on either lever initiated the same sequence of events than in forced-choice trials. The colors associated with the different outcomes and the position of the discriminative alternative (front panel or back panel) were counterbalanced among subjects. The trials were separated by 10 s ITIs, during which all stimuli were turned off. This phase was finished independently for each subject, when a visual stability criteria was satisfied: The subject must have had at least ten sessions, and during the last five, the last one could not have the higher nor the lower proportion of choice for the discriminative alternative, and no apparent upward or downward trend should be observed.

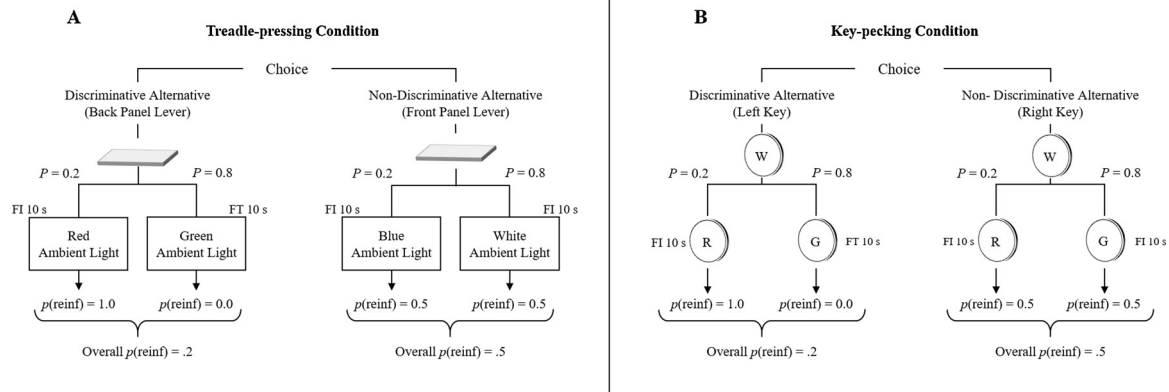
**2.3.1.6. Reversal training.** During this phase, the location of the discriminative and non-discriminative alternatives was reversed, in order to evaluate a potential position bias during the previous phase. The stability criteria were the same than in previous phase.

#### 2.3.2. Control condition: key pecking

**2.3.2.1. Key-pecking training.** Subjects were then exposed to seven sessions of autoshaping (Brown and Jenkins, 1968). At the beginning of each trial the central key was illuminated with white color for 8 s and was followed by 3 s of access to the hopper. After an ITI of 52 s, in which all stimuli were turned off, a new cycle began. This session was 1 h long. Subjects that did not acquire the key-pecking behavior were exposed to 3–7 sessions of manual shaping. After these sessions, all subjects reliably pecked the central white key.

**2.3.2.2. Pre-training.** Subjects were trained to peck the two lateral keys, which could be illuminated by any of three different colors (white, red or green). Each pretraining trial was as follows: one of the two lateral keys was illuminated by any of the three colors; the first response turned off the key and delivered the reinforcer. Three seconds later an ITI 7 s long followed, in which all lights were turned off, and a new trial began after that. Each of the 6 combinations of keys/colors was presented 12 times, for a total of 72 trials per session. These sessions were continued for each subject until their median latencies for key pecks on the two keys differed for less than 1 s. This phase lasted from 1 to 3 sessions.

**2.3.2.3. Training. Classical suboptimal choice procedure.** As in the previous condition, each session consisted of 60 trials that were divided into 20 forced-choice trials for each alternative and 20 free-choice trials, all presented in random order. In forced-choice trials, only one of the two lateral keys were illuminated with white color (see Fig. 1, panel B). If it was the discriminative option, a single peck illuminated the key with red color in 20 % of the trials, and reinforcement was delivered for the first key peck after 10 s had elapsed; in 80 % of the trials the key was illuminated with green color and 10 s later the trial ended without reinforcement (the colors were counterbalanced across subjects). If it was the non-discriminative option, a single peck illuminated the key with red color in 20 % of the trials and with green on the remaining 80 % (colors counterbalanced across subjects); in both cases, the first key peck after 10 s, led to the delivery of the reinforcer with  $p = 0.50$ . Trials were separated by 10 s ITIs. Assignment of option types to left-right sides was counterbalanced across subjects. In free-choice trials both options were simultaneously presented and a single peck initiated the



**Fig. 1.** Panel A depicts the procedure employed in the treadle-pressing condition. Two alternatives, Discriminative and Non-Discriminative, were presented in opposite panels. When pigeons chose the lever at the back panel (discriminative alternative), in 20 % of the trials the entire chamber was illuminated with a red color which was always followed by a reinforcer according to a FI 10 s; in the remaining 80 % of the trials, the chamber was illuminated with a green color during 10 s, and the trial ended without reinforcement. When pigeons chose the lever at the front panel (non-discriminative alternative) the entire chamber was illuminated with either a blue light or a white light in 20 % and 80 % of the trials, respectively; in either case, after satisfying a FI 10 s schedule the reinforcer was delivered with  $p = .50$ . Panel B depicts the procedure during the key-pecking condition. Two alternatives, Discriminative and Non-Discriminative, were presented in two adjacent keys. When pigeons pecked the left white (W) key (discriminative alternative) in 20 % of the trials a red (R) light was presented on it, and after completing a FI 10 s schedule, a reinforcer was delivered. In the remaining 80 % of the trials, the key was illuminated with a green (G) color during 10 s and the trial ended without reinforcement. When pigeons chose the right white key (W) (non-discriminative alternative) it was illuminated with either red (R) or green (G) colors in 20 % and 80 % of the trials, respectively; after satisfying a FI 10 s schedule, the reinforcer was delivered with  $p = .50$ .

same contingencies than in forced-choice trials. These sessions were conducted until the same stability criteria than for the treadle-pressing condition were satisfied.

**2.3.2.4. Reversal training.** The location of the discriminative and non-discriminative alternatives was reversed, in order to evaluate a potential position bias. The stability criteria were the same than in previous phase.

### 3. Results

#### 3.1. Treadle-pressing condition

Fig. 2 shows, for each subject, the proportion of choice for the discriminative alternative during each of the sessions of the “sub-optimal choice” training and its reversal phase in the condition in which the operant response was treadle pressing; once the stability criteria were met, the last five sessions of each phase were used for statistical purposes. The group’s proportion of choice for the discriminative alternative during the last five sessions of training was  $.23 \pm 0.10$  (Mean  $\pm$  SEM), which was statistically different from indifference, according to a two-tailed  $t$ -test ( $t(10) = -2.58$ ,  $p = .03$ ; Cohen’s  $d = -0.78$ ). During the reversal phase, most of the subjects recovered the preference for the alternative that was preferred in the training phase. The exception to this pattern were two subjects (PAL2 and PAL5) that in the training phase were optimal and in the reversal phase were indifferent. The group’s mean proportion of choice for the discriminative alternative during the last five sessions was  $.295 \pm .11$ , which was not statistically different from indifference ( $t(10) = -1.90$ ,  $p = .09$ ; Cohen’s  $d = -0.57$ ).

Excluding the subjects with an apparent side bias, and considering data from both training and reversal phases, 7 out of 9 subjects showed, according to binomial tests, a significant preference for the non-discriminative alternative. The two other subjects (PAL10 and PAL15), had a significant preference for the discriminative alternative.

Fig. 3 shows, for each subject, the mean number of treadle presses per trial during forced-choice trials of the discriminative alternative (top panel) and the non-discriminative alternative (lower panel) across all sessions of training and reversal. For the discriminative alternative, the responses on the treadle during the presence of the stimulus that

was predictor of reinforcement ( $S_+$ ) during the last five sessions from both phases ( $7.31 \pm 1.07$ ) were higher than those performed while the stimulus that predicted non-reinforcement ( $S_-$ ) was present ( $0.67 \pm 0.09$ ). An ANOVA indicated that this difference was statistically significant ( $F(1,10) = 42.30$ ,  $p < .001$ ; partial  $\eta^2 = .81$ ); no effect of phase (training vs reversal) nor of the interaction phase-stimuli were observed ( $F(1,10) = 0.75$ ,  $p = .41$ ; partial  $\eta^2 = .07$  and  $F(1,10) = 0.16$ ,  $p = .70$ ; partial  $\eta^2 = .02$ , respectively). An index of discrimination was calculated with these variables (Responses during  $S_+$  / (Responses during  $S_+$  + Responses during  $S_-$ )); its mean value was  $.90 \pm .02$  (range =  $.79$ – $.97$ ) and  $.93 \pm .01$  (range =  $.85$ – $1.0$ ) during the training and the reversal phases, respectively. Regarding the responses during the presence of the two non-discriminative stimuli (lower panel), an ANOVA showed null effects of stimuli ( $F(1,10) = 1.07$ ,  $p = .33$ ; partial  $\eta^2 = .10$ ), phase ( $F(1,10) = 0.04$ ,  $p = .85$ ; partial  $\eta^2 = .003$ ) and of the interaction phase-stimuli ( $F(1,10) = 3.03$ ,  $p = .11$ ; partial  $\eta^2 = .23$ ).

#### 3.2. Control condition: key pecking

Fig. 4 shows the individual proportion of choice for the discriminative alternative during each of the sessions of the training and reversal phases in the condition in which the operant response was key pecking. The group’s mean proportion of choice for this alternative was  $.87 \pm .07$ , which was significantly higher than indifference, according to a two-tailed  $t$ -test ( $t(10) = 5.58$ ,  $p < .001$ ; Cohen’s  $d = 1.68$ ). During the reversal phase, most of the subjects recovered their preference for the discriminative alternative. A two-tailed  $t$ -test indicated that the group’s preference for the discriminative alternative ( $.76 \pm .11$ ) was significantly above indifference ( $t(10) = 2.35$ ,  $p = .04$ ; Cohen’s  $d = 0.71$ ).

Excluding the subjects with an apparent side bias (PAL10, SSJ15), and considering data from both training and reversal phases, 8 out of 9 pigeons showed a significant preference for the discriminative alternative, according to binomial tests. The other subject showed a significant preference for the non-discriminative alternative.

Fig. 5 shows, for each subject, the number of key pecks performed during the forced-choice trials of the discriminative (top panel) and the non-discriminative (lower panel) alternatives. For the discriminative alternative, during the last five sessions from both conditions, key pecks

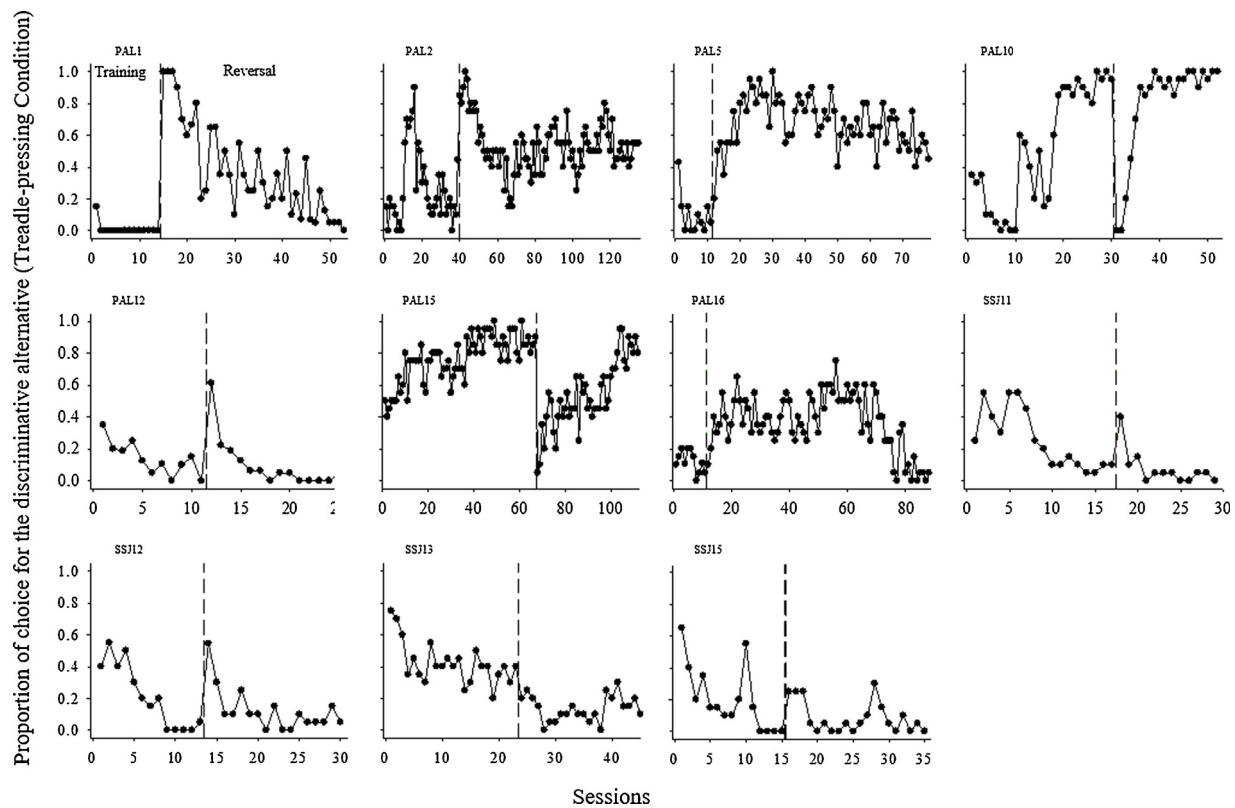


Fig. 2. Proportion of choice for the discriminative alternative during each of the sessions of the suboptimal choice training and its reversal phase in the treadle-pressing condition. Dashed line indicates the start of the reversal phase. Each panel represents data from an individual subject.

directed at the stimulus that was predictor of reinforcement ( $17.22 \pm 1.59$ ) were higher than those directed at the stimulus that predicted non-reinforcement ( $1.49 \pm .32$ ). An ANOVA indicated that this difference was statistically significant ( $F(1, 10) = 122.00$ ,  $p < .001$ ; partial  $\eta^2 = .92$ ), but no effect of phase (training vs reversal) nor of the interaction phase-stimuli were observed ( $F(1, 10) = 0.57$ ,  $p = .47$ ; partial  $\eta^2 = .05$  and  $F(1, 10) = 1.30$ ,  $p = .28$ ; partial  $\eta^2 = .11$ , respectively). The mean value of the index of discrimination during the training phase was  $.94 \pm .01$  (range =  $.84-.99$ ) and during the reversal phase  $.91 \pm .02$  (range =  $.82-.98$ ). Regarding the number of key pecks to the stimuli associated with the non-discriminative alternative, an ANOVA showed no differences due to stimulus ( $F(1, 10) = 0.05$ ,  $p = .83$ ; partial  $\eta^2 = .005$ ), phase ( $F(1, 10) = 0.08$ ,  $p = .79$ ; partial  $\eta^2 = .007$ ), or their interaction ( $F(1, 10) = 0.72$ ,  $p = .42$ ; partial  $\eta^2 = .07$ ).

### 3.3. Comparison between conditions

The proportion of choice for the discriminative alternative had lower values during the condition in which the operant response was treadle pressing ( $.23 \pm .10$  in the training phase, and  $.295 \pm .10$  in the reversal phase) than in the condition in which the operant response was key pecking ( $.87 \pm .07$  in the training phase and  $.76 \pm .11$  in the reversal phase). An ANOVA showed a significant effect of condition (treadle pressing vs key pecking:  $F(1, 10) = 16.62$ ,  $p < .01$ ; partial  $\eta^2 = .62$ ), but null effects of phase (training vs reversal:  $F(1, 10) = 0.31$ ,  $p = .59$ ; partial  $\eta^2 = .03$ ) and of the interaction condition-phase ( $F(1, 10) = 3.41$ ,  $p = .09$ ; partial  $\eta^2 = .25$ ). The response rate in the presence of the discriminative stimuli was lower for the treadle-pressing ( $7.31 \pm 1.07$ ) than for the key-pecking condition ( $17.22 \pm 1.59$ ); this was associated with longer times to complete the fixed interval schedule associated with the stimulus associated with reinforcer delivery in the treadle-pressing condition ( $16.35 \pm 1.94$  s) than in the key-pecking condition ( $10.60 \pm 1.14$  s). Notwithstanding these

differences, the index of discrimination was equally high across conditions ( $.91 \pm .009$  vs  $.92 \pm .010$  in the treadle-pressing and key-pecking conditions, respectively). An ANOVA showed null effects of condition ( $F(1, 10) = 0.85$ ,  $p = .38$ ; partial  $\eta^2 = .08$ ), phase ( $F(1, 10) < 0.01$ ,  $p = .98$ ; partial  $\eta^2 < .001$ ) and their interaction ( $F(1, 10) = 3.96$ ,  $p = .08$ ; partial  $\eta^2 = .28$ ).

## 4. Discussion

In the present study, we made a twofold modification of the classical procedure employed to study suboptimal choice by pigeons. On the one hand, we manipulated the operant response by which pigeons chose between a discriminative alternative associated with a lower probability of reinforcement and a non-discriminative alternative associated with a higher probability of reinforcement. On the other hand, we presented ambient stimuli, separated from the response manipulandum, instead of the localized, illuminated keys that are typically employed as discriminative stimuli in the suboptimal choice procedure in birds. Both manipulations were performed with the aim of decreasing the attribution of incentive salience to the discriminative stimuli, and as a consequence, for decreasing its Pavlovian influence on choice behavior.

We found that under these circumstances, most of the pigeons showed a preference for the alternative associated with the higher probability of reinforcement and with non-discriminative stimuli. In addition, all pigeons showed high levels of discrimination of the two stimuli associated with the discriminative alternative. The last finding is relevant because it has been shown that when pigeons choose between two non-discriminative alternatives, they prefer the alternative with the highest probability of reinforcement (Zentall and Stagner, 2011, exp 2; Stagner and Zentall, 2010). In this context, the fact that the index of discrimination was as high in the treadle-pressing condition as in the key-pecking condition allows us to discard the possibility that the optimality found was an artifact of an absence of discrimination.

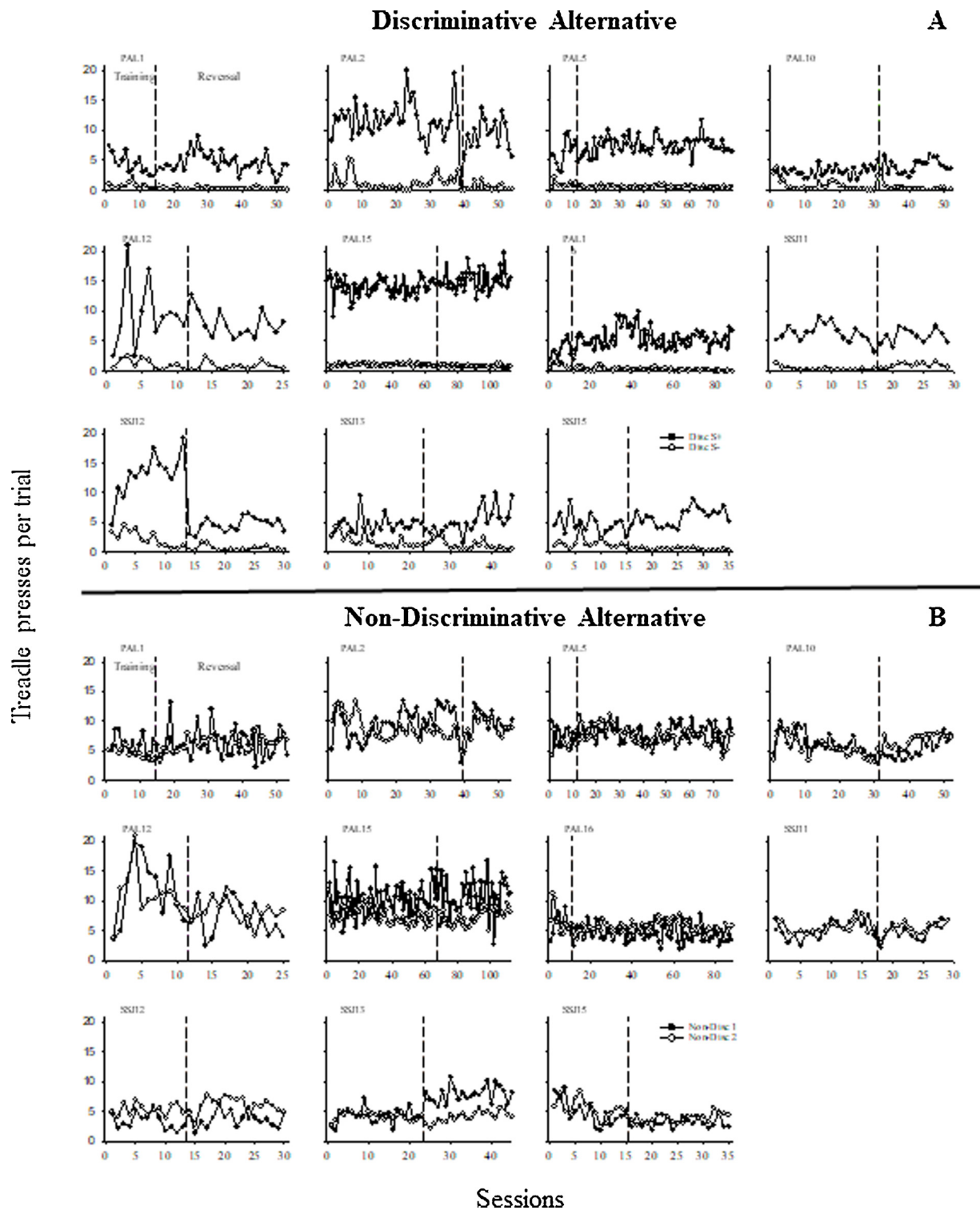


Fig. 3. Mean number of responses in forced-choice trials across all sessions during training and reversal phase of the treadle-pressing condition. Panel A shows data from the discriminative alternative: Closed symbols represent the number of responses during the stimulus associated with reinforcement (S+) and open symbols represent responses during the stimulus associated with the absence of reinforcement (S-). Panel B shows data from the Non-Discriminative alternative: Closed and open symbols represent responses under the presence of the two stimuli that were equally associated with probability of reinforcement .5. Dashed line indicates the start of the reversal phase. Each sub-panel represents data from an individual subject.

Considering the possible individual differences in the degree of suboptimal choice, we employed a control condition that presented the classical suboptimal choice procedure, with keylights as discriminative stimuli and key pecking as choice response. The results indicated that under the typical conditions in which suboptimal choice has been

demonstrated, most of the pigeons switched to suboptimal behavior.

In this study we presented in succession the treadle-pressing and the key-pecking conditions; a more desirable experimental design would have counterbalanced the order of exposure, but unfortunately, we were not able to perform the experiment in that fashion, since pilot

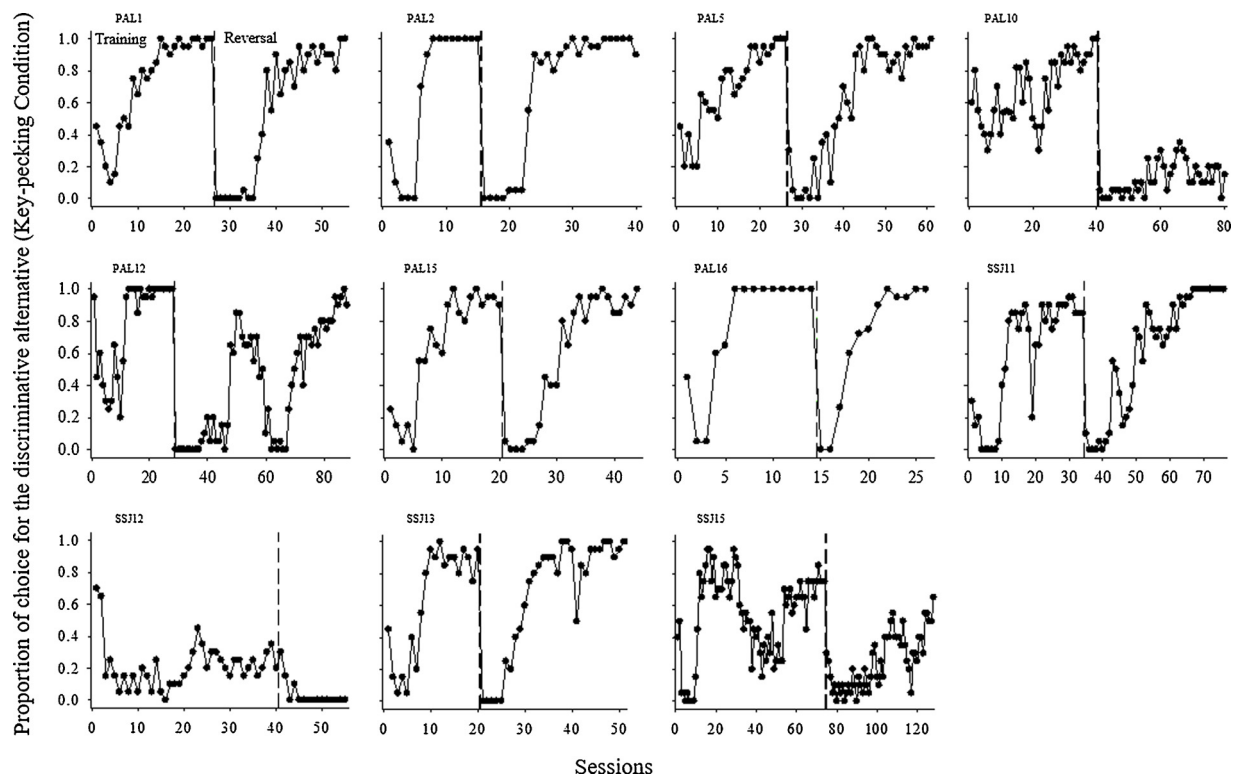


Fig. 4. Proportion of choice for the discriminative alternative during each of the sessions of the suboptimal choice training and its reversal phase in the key-pecking condition. Dashed line indicates the start of the reversal phase. Each panel represents data from an individual subject.

experiments showed that once pigeons' key-pecking behavior was shaped, it was very difficult to shape the treadle-pressing behavior because pigeons pecked the treadle instead of pressing it with their foot. However, it seems unlikely that the order had a determinant influence in our results, because in experiments in which key pecking is used in the entire experiment, pigeons show suboptimal behavior. Additionally, the optimality shown by some of the pigeons of the present report was maintained for a number of sessions well beyond those that have been required in other experiments to generate suboptimal behavior (Smith and Zentall, 2016).

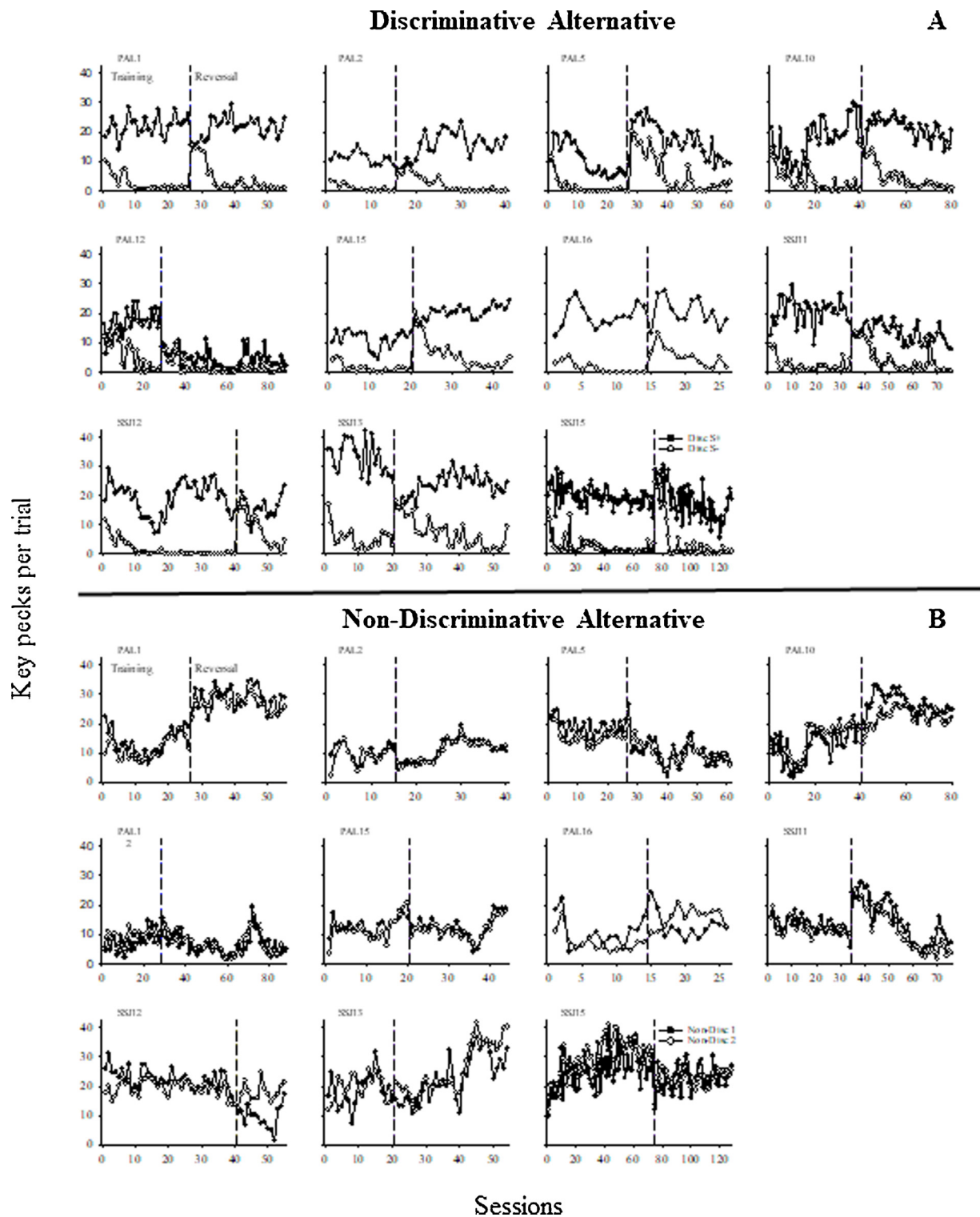
The preference for the optimal alternative in the treadle-pressing condition, together with the switch to suboptimal behavior in the key-pecking condition, supports the hypothesis that the degree of incentive salience that can be attributed to the discriminative stimuli is a strong determinant of the preference in the suboptimal choice procedure with pigeons as experimental subjects. A conflicting issue for this hypothesis, however, is its lack of generality across species, as the same relationship has not been demonstrated in rats. Although the first test of the hypothesis supported it, demonstrating that when the discriminative stimuli were levers (which were assumed to have high incentive salience) rats were suboptimal (Chow et al., 2017), subsequent experiments have demonstrated optimality even though the discriminative stimuli employed have been also levers (Martínez et al., 2017; López et al., 2018; Alba et al., 2018; Orduña and Alba, 2019). It is possible that the level of incentive salience attributed to levers by rats is far smaller than the level that pigeons attribute to illuminated keys. This possibility is supported by the comparison between the proportion of pigeons and rats that show sign-tracking behavior in autoshaping experiments: while practically 100 % of the pigeons rapidly develop sign-tracking behavior (Brown and Jenkins, 1968), approximately only 35 % of the rats show the same behavior (Meyer et al., 2012). It is possible, then, that the incentive salience of the stimuli could generate suboptimal behavior in rats if we could find stimuli with enough incentive salience for them.

Although our design does not allow to be certain about whether the

effect found was due to the replacement of localized keylights by ambient lights as discriminative stimuli or to the replacement of key pecking by treadle pressing, a brief review of the autoshaping literature would suggest that the latter is the relevant variable, as sign-tracking behavior to the key is maintained even when it is not associated with a primary reinforcer, but with a secondary one (Leyland, 1977), and even when this secondary reinforcer is an ambient stimulus like those employed in the present research (Patterson and Winokur, 1973; Rashotte et al., 1977; Green and Schweitzer, 1980). These studies suggest that employing ambient stimuli do not completely remove from the choice situation the attribution of incentive salience and therefore, it is more likely that the effect that we found was due to the substitution of the operant response.

Sign-tracking, one of the main properties of stimuli with incentive salience (Robinson et al., 2018), depends on the degree to which the capacity of an US for eliciting consummatory behaviors is transferred to the CS (Timberlake and Grant, 1975). Two examples of conditioned stimuli that after being contingently paired with food have this capacity are a keylight that elicits pigeons' pecking and a lever that elicits rats' biting and sniffing (Brown and Jenkins, 1968; Meyer et al., 2012). On the contrary, in situations in which the nature of the CS does not allow the expression of such consummatory behaviors, no attribution of incentive salience occurs, as suggested by the non-existence of sign-tracking behavior (Holland, 1977). In the case of the present study, the attribution of incentive salience was prevented in both the terminal and the initial links. In the former, using the illumination of the entire chamber as discriminative stimulus made it unlikely that the pigeons pecked the stimulus. In the latter, we prevented that the consummatory behavior of pecking were directed to the treadle by imposing a response duration requirement that was hard to be fulfilled by the pecking response.

The present results are consistent with a recent theoretical proposal for explaining the differences between pigeons and rats in the suboptimal choice procedure. Based on the general idea of Behavior Systems Theory (Timberlake, 1993), Zentall, Smith, and Beckmann



**Fig. 5.** Mean number of responses in forced-choice trials across all sessions during training and reversal phase of the key-pecking condition. Panel A shows data from the discriminative alternative: Closed symbols represent the number of responses during the stimulus associated with reinforcement (S+) and open symbols represent responses during the stimulus associated with the absence of reinforcement (S-). Panel B shows data from the Non-Discriminative alternative: Closed and open symbols represent responses under the presence of the two stimuli that were equally associated with probability of reinforcement .5. Dashed line indicates the start of the reversal phase. Each sub-panel represents data from an individual subject.

(2019) suggested that an interaction of the natural foraging sequence of an organism with the stimuli and responses available in the choice situation, determines its suboptimal or optimal preference. Because key pecking is related to pigeons' consummatory behavior, the stimuli that elicit it activate focal search for food, are attributed with incentive

salience, and promote suboptimal preferences. Generalizing these ideas to the present experiment, treadle pressing and its associated ambient stimuli activate general search (instead of focal search), are not attributed with incentive salience, and therefore should not promote suboptimal choice. Although the theoretical proposal of Zentall et al.



(2019) still has the challenge of explaining the optimal behavior by rats in several experiments in which the discriminative stimuli were levers (which activate focal search in this species, see Zentall et al., 2019) and there was no generalization between the levers associated with the positive and negative outcomes of the discriminative alternative, it succeeds in explaining the present results.

It is possible, however, that our manipulations, besides decreasing the incentive salience, affected other variables relevant to suboptimal choice as well. The difference in proportion of choice for the discriminative alternative between the treadle-pressing and the key-pecking conditions is consistent with the idea that in the former condition the ambient lights promoted a higher level of conditioned inhibition to the negative stimulus, favoring optimal choice. However, such hypothesis seems unlikely, since Stagner et al. (2011) presented an ambient light as a predictor of the absence of reinforcement in the discriminative alternative, without finding a decline in the level of suboptimal choice.

Our findings are also potentially related to a recent quantitative model of suboptimal choice, the Associability Decay Model (Daniels and Sanabria, 2018). For this model, the value of each alternative is determined by the value of its constituent terminal links, weighted by a dynamically-changing associability parameter that is inversely related to the certainty of the stimulus-reinforcer relationship. The model explains the differences between species based on differences in the associability of the terminal links: while pigeons' suboptimality was related to a faster decay of associability for the stimulus that predicted no reinforcement than for the stimulus that predicted reinforcement, rats' optimality was related to no loss of associability for neither of these stimuli. Therefore, there is the possibility that any of our manipulations for decreasing the incentive salience impacted also on the rate of decay of associability, maintaining the influence of the predictor of the absence of reinforcement at a higher level in the treadle-pressing condition than in the key-pecking condition.

Our results are relevant to some aspects of the temporal information-theoretic model (Cunningham and Shahan, 2018), a recent quantitative model on suboptimal choice. For this model, preference for the suboptimal alternative ( $p_{Sub}$ ) is determined by three main variables:

$$p_{Sub} = w \frac{H^{a_{sub}}}{H^{a_{sub}} + H^{a_{opt}}} + (1 - w) \frac{R^b_{sub}}{R^b_{sub} + R^b_{opt}} \quad (1)$$

1) the temporal information ( $H$ ) of the terminal links' stimuli associated with the discriminative (sub) and the non-discriminative (opt) alternative (for more details for its calculation, see Cunningham and Shahan, 2018); 2) the reinforcement rate ( $R$ ) associated with each of them, and 3) by the relative weight ( $w$ ;  $(1-w)$ ) that each of these variables have on preference for the suboptimal alternative. This weight, in turn, is calculated according to:

$$w = \frac{1}{1 + e^{-\beta(\frac{D_f}{D_s} - m)}} \quad (2)$$

Where  $D_f$  represents the average delay to food at the choice point,  $D_s$  represents the average delay between the choice point and the presentation of the discriminative stimuli,  $\beta$  represents sensitivity to the ratio between  $D_f$  and  $D_s$ , and  $m$  represents the bias against the influence of the temporal information of the stimuli. Because in the typical suboptimal choice procedure the discriminative alternative presents a stimulus that provides higher temporal information, but lower reinforcement rate, suboptimal preferences are predicted when  $w$  approaches 1 and optimal preferences when  $w$  approaches 0. With these assumptions, the model explains the differences between rats and pigeons as differences in the weighting mechanism, which could have been generated by the higher sensitivity to delay that has been reported for pigeons than for rats (Green et al., 2004). If these arguments are correct, suboptimal choice in rats could be promoted by increases in the length of the terminal links, which would increase  $D_f$  as well. Recently,

Cunningham and Shahan (2019) reported results consistent with this idea; in their study, rats were exposed across conditions to terminal links of varying duration, from 10 s to 50 s. Rats preferred the optimal alternative in the 10 s condition, but most of them preferred the suboptimal one when the length of the terminal links was 30 s or more. Although the change in preference in this study was assumed to result from the change in the length of the terminal links and not from a higher incentive salience of the discriminative stimuli, the authors suggested a possible interaction between these variables. Such an interaction would be consistent with the multifactorial nature of the weighting mechanism specified by Cunningham and Shahan (2018). More important to the present discussion is the suggestion that presenting the organisms with stimuli that elicit species-specific responses and therefore can be attributed with incentive salience should impact on the degree to which the temporal information of the stimuli determines preferences (Cunningham and Shahan, 2018). To our knowledge, our results provide the first evidence of this relationship with pigeons as subjects. Further research could focus on quantitative evaluations of the relationship between the incentive salience of the discriminative stimuli and the different parameters of the temporal information-theoretic model related to the weighting mechanism ( $\beta$  and  $m$ ).

Finally, our results highlight the need to reexamine some aspects of a set of suboptimal choice models (Vasconcelos et al., 2015; Iigaya et al., 2016; McDevitt et al., 2016; Zhu et al., 2017) that have as a common characteristic the assumption that the value of the discriminative alternative is strongly influenced by the positive value of the stimulus predictor of reinforcement and much less (or nothing at all) by the negative value of the predictor of absence of reinforcement. Although an important set of data supports these arguments (Laude et al., 2014; McDevitt et al., 1997; Vasconcelos et al., 2015; Fortes et al., 2016, 2017), it should be considered that such data were obtained exclusively with key pecking as an operant response so that their generality awaits further experiments with other operant responses.

In conclusion, the present experiment showed that pigeons' suboptimality was eliminated when key pecking was replaced by treadle pressing as choice response, and that the optimality in the treadle-pressing condition was not the product of failures in discrimination between the positive and the negative stimuli associated with the discriminative alternative. Further research is needed to evaluate the generality across species of this effect and to analyze the potential applicability of manipulations based on changes in the incentive salience related to the choice situation for decreasing human maladaptive behaviors.

#### Author contributions

V.O. conceptualized the experiments, developed the experimental design and wrote the manuscript. R.G. and J.F. contributed to the development of the experimental design, performed the experiment, analyzed the data and reviewed the manuscript.

#### Acknowledgements

This research was supported by grants 281548 from CONACYT and IN306818 from PAPIIT-DGAPA. We thank Fernando Salinas for technical assistance, Enrique Rivera for assistance in data collection and experimental design of pilot experiments, and Rodrigo Alba for help in animal care and data analysis.

#### References

- Alba, R., Rodriguez, W., Martinez, M., Orduna, V., 2018. Rats' preferences in the suboptimal choice procedure: evaluating the impact of reinforcement probability and conditioned inhibitors. *Behav. Processes* 157, 574–582. <https://doi.org/10.1016/j.beproc.2018.04.013>.

- Anselme, P., 2015. Incentive salience attribution under reward uncertainty: a Pavlovian model. *Behav. Processes* 111, 6–18. <https://doi.org/10.1016/j.beproc.2014.10.016>.
- Beckmann, J.S., Chow, J.J., 2015. Isolating the incentive salience of reward-associated stimuli: value, choice, and persistence. *Learn. Mem.* 22, 116–127. <https://doi.org/10.1101/lm.037382.114>.
- Boakes, R.A., Halliday, M.S., Poli, M., 1975. Response additivity: effects of superimposed free reinforcement on a variable-interval baseline. *J. Exper.* 23, 177–191. <https://doi.org/10.1901/jeab.1975.23.177>.
- Brown, P.L., Jenkins, H.M., 1968. Auto-shaping of the pigeon's key-peck. *J. Exp. Anal. Behav.* 11, 1–8. <https://doi.org/10.1901/jeab.1968.11.1>.
- Chow, J.J., Smith, A.P., Wilson, A.G., Zentall, T.R., Beckmann, J.S., 2017. Suboptimal choice in rats: incentive salience attribution promotes maladaptive decision-making. *Behav. Brain Res.* 320, 244–254. <https://doi.org/10.1016/j.bbr.2016.12.013>.
- Cunningham, P.J., Shahan, T.A., 2018. Suboptimal choice, reward-predictive signals, and temporal information. *J. Exp. Psychol. Anim. Learn. Cogn.* 44, 1–22. <https://doi.org/10.1037/xan0000160>.
- Cunningham, P.J., Shahan, T.A., 2019. Rats engage in suboptimal choice when the delay to food is sufficiently long. *J. Exp. Psychol. Anim. Learn. Cogn.* 45, 301–310. <https://doi.org/10.1037/xan0000211>.
- Daniels, C.W., Sanabria, F., 2018. An associability decay model of paradoxical choice. *J. Exp. Psychol. Anim. Learn. Cogn.* 44, 258–271. <https://doi.org/10.1037/xan0000179>.
- Fortes, I., Vasconcelos, M., Machado, A., 2016. Testing the boundaries of “paradoxical” predictions: pigeons do disregard bad news. *J. Exp. Psychol. Anim. Learn. Cogn.* 42, 336–346. <https://doi.org/10.1037/xan0000114>.
- Fortes, I., Machado, A., Vasconcelos, M., 2017. Do pigeons (*Columba livia*) use information about the absence of food appropriately? A further look into suboptimal choice. *J. Comp. Psychol.* 131, 277–289. <https://doi.org/10.1037/com0000079>.
- Green, L., Holt, D.D., 2003. Economic and biological influences on key pecking and treadle pressing in pigeons. *J. Exp. Anal. Behav.* 80, 43–58. <https://doi.org/10.1901/jeab.2003.80.43>.
- Green, L., Schweitzer, L., 1980. Second-order conditioning of the pigeon's key-peck using an autoshaping procedure. *Am. J. Psychol.* 93, 25–39. <https://doi.org/10.2307/1422102>.
- Green, L., Myerson, J., Holt, D.D., Slevin, J.R., Estle, S.J., 2004. Discounting of delayed food rewards in pigeons and rats: is there a magnitude effect? *J. Exp. Anal. Behav.* 81, 39–50. <https://doi.org/10.1901/jeab.2004.81.39>.
- Hemmes, N.S., 1973. Behavioral reinforcement in pigeons depends upon the operant. *J. Comp. Psychol.* 85, 171–178. <https://doi.org/10.1037/h0034883>.
- Hemmes, N.S., 1975. Pigeons' performance under differential reinforcement of low rate schedules depends upon the operant. *Learn. Motiv.* 6, 344–357. [https://doi.org/10.1016/0023-9690\(75\)90014-4](https://doi.org/10.1016/0023-9690(75)90014-4).
- Holland, P.C., 1977. Conditioned stimulus as a determinant of the form of the Pavlovian conditioned response. *J. Exp. Psychol. Anim. Behav. Process.* 3, 77–104. <https://doi.org/10.1037/0097-7403.3.1.77>.
- Holt, D.D., Carlson, J.D., Follett, V.L., Jerdee, N.J., Kelley, D.P., Muhich, K.M., Tiry, A.M., Retz, N.K., 2013. Response factors in delay discounting: evidence for Pavlovian influences on delay discounting in pigeons. *Behav. Processes* 98, 37–43. <https://doi.org/10.1016/j.beproc.2013.04.009>.
- Igaya, K., Story, G.W., Kurth-Nelson, Z., Dolan, R.J., Dayan, P., 2016. The modulation of savouring by prediction error and its effects on choice. *eLife* 5, e13747. <https://doi.org/10.7554/eLife.13747>.
- Killeen, P.R., 2001. The four causes of behavior. *Curr. Dir. Psychol. Sci.* 10, 136–140. <https://doi.org/10.1111/1467-8721.00134>.
- Kuhn, B.N., Campus, P., Flagel, S.B., 2018. 3. The neurobiological mechanisms underlying sign-tracking behavior. *Sign Track. Drug Addict.* 35.
- Laude, J.R., Stagner, J.P., Zentall, T.R., 2014. Suboptimal choice by pigeons may result from the diminishing effect of nonreinforcement. *J. Exp. Psychol. Anim. Learn. Cogn.* 40, 12–21. <https://doi.org/10.1037/xan0000010>.
- Leyland, C.M., 1977. Higher order autoshaping. *Q. J. Exp. Psychol.* 29, 607–619. <https://doi.org/10.1080/14640747708400636>.
- LoLordo, V.M., 1971. Facilitation of food-reinforced responding by a signal for response-independent food. *J. Exp. Anal. Behav.* 15, 49–55. <https://doi.org/10.1901/jeab.1971.15.49>.
- LoLordo, V.M., McMillan, J.C., Riley, A.L., 1974. The effects upon food-reinforced pecking and treadle-pressing of auditory and visual signals for response-independent food. *Learn. Motiv.* 5, 24–41. [https://doi.org/10.1016/0023-9690\(74\)90035-6](https://doi.org/10.1016/0023-9690(74)90035-6).
- López, P., Alba, R., Orduña, V., 2018. Individual differences in incentive salience attribution are not related to suboptimal choice in rats. *Behav. Brain Res.* 341, 71–78. <https://doi.org/10.1016/j.bbr.2017.12.028>.
- Martinez, M., Alba, R., Rodriguez, W., Orduña, V., 2017. Incentive salience attribution is not the sole determinant of suboptimal choice in rats: conditioned inhibition matters. *Behav. Processes* 142, 99–105. <https://doi.org/10.1016/j.beproc.2017.06.012>.
- McClure, S.M., Daw, N.D., Read, M.P., 2003. A computational substrate for incentive salience. *Trends Neurosci.* 26, 423–428. [https://doi.org/10.1016/S0166-2236\(03\)00177-2](https://doi.org/10.1016/S0166-2236(03)00177-2).
- McDevitt, M., Spetch, M., Dunn, R., 1997. Contiguity and conditioned reinforcement in probabilistic choice. *J. Exp. Anal. Behav.* 68, 317–327. <https://doi.org/10.1901/jeab.1997.68.317>.
- McDevitt, M.A., Dunn, R.M., Spetch, M.L., Ludvig, E.A., 2016. When good news leads to bad choices. *J. Exp. Anal. Behav.* 105, 23–40. <https://doi.org/10.1002/jeab.192>.
- Meyer, P.J., Lovic, V., Saunders, B.T., Yager, L.M., Flagel, S.B., Morrow, J.D., Robinson, T.E., 2012. Quantifying individual variation in the propensity to attribute incentive salience to reward cues. *PLoS One* 7. <https://doi.org/10.1371/journal.pone.0038987>. e38987-e38987.
- Meyer, P.J., Cogan, E.S., Robinson, T.E., 2014. The form of a conditioned stimulus can influence the degree to which it acquires incentive motivational properties. *PLoS One* 9, e98163. <https://doi.org/10.1371/journal.pone.0098163>.
- Meyer, P.J., Tripi, J.A., Tomie, A., Morrow, J., 2018. Sign-tracking, response inhibition, and drug-induced vocalizations. *Sign-Track. Drug Addict.*
- Nesse, R.M., Berridge, K.C., 1997. Psychoactive drug use in evolutionary perspective. *Science* 278, 63–66. <https://doi.org/10.1126/science.278.5335.63>.
- Newlin, D.B., 2002. The self-perceived survival ability and reproductive fitness (SPFit) theory of substance use disorders. *Addiction* 97, 427–445. <https://doi.org/10.1046/j.1360-0443.2002.00021.x>.
- Ojeda, A., Murphy, R.A., Kacelnik, A., 2018. Paradoxical choice in rats: subjective valuation and mechanism of choice. *Behav. Processes* 152, 73–80. <https://doi.org/10.1016/j.beproc.2018.03.024>.
- Orduña, V., Alba, R., 2019. Rats' optimal choice behavior in a gambling-like task. *Behav. Processes* 162, 104–111. <https://doi.org/10.1016/j.beproc.2019.02.002>.
- Patterson, D.D., Winokur, S., 1973. Autoshaping pigeons' keypecking with a conditioned reinforcer. *Bull. Psychon. Soc.* 1, 247–249. <https://doi.org/10.3758/BF03333358>.
- Powell, R.W., Kelly, W., Santisteban, D., 1975. Response-independent reinforcement in the crow: failure to obtain autoshaping or positive automaintenance. *Bull. Psychon. Soc.* 6, 513–516. <https://doi.org/10.3758/BF03337554>.
- Rashotte, M.E., Griffin, R.W., Sisk, C.L., 1977. Second-order conditioning of the pigeon's keypeck. *Anim. Learn. Behav.* 5, 25–38. <https://doi.org/10.3758/BF03209127>.
- Robinson, T., Carr, C., Kawa, A., 2018. The Propensity to Attribute Incentive Salience to Drug Cues and Poor Cognitive Control Combine to Render Sign-Trackers Susceptible to Addiction. *Sign-Tracking and Drug Addiction Vol. A. Ann Arbor, MI: Maize Books*, pp. 10.
- Singer, B.F., Bryan, M.A., Popov, P., Scarff, R., Carter, C., Wright, E., Aragona, B.J., Robinson, T.E., 2016. The sensory features of a food cue influence its ability to act as an incentive stimulus and evoke dopamine release in the nucleus accumbens core. *Learn. Mem.* 23, 595–606. <https://doi.org/10.1101/lm.043026.116>.
- Smith, A.P., Zentall, T.R., 2016. Suboptimal choice in pigeons: choice is primarily based on the value of the conditioned reinforcer rather than overall reinforcement rate. *J. Exp. Psychol. Anim. Learn. Cogn.* 42, 212.
- Stagner, J.P., Laude, J.R., Zentall, T.R., 2011. Sub-optimal choice in pigeons does not depend on avoidance of the stimulus associated with the absence of reinforcement. *Learn. Motiv.* 42, 282–287. <https://doi.org/10.1016/j.lmot.2011.09.001>.
- Stagner, J.P., Zentall, T.R., 2010. Suboptimal choice behavior by pigeons. *Psychon. Bull. Rev.* 17, 412–416. <https://doi.org/10.3758/PBR.17.3.412>.
- Timberlake, W., 1993. Behavior systems and reinforcement: an integrative approach. *J. Exp. Anal. Behav.* 60, 105–128. <https://doi.org/10.1901/jeab.1993.60.105>.
- Timberlake, W., Grant, D.L., 1975. Auto-shaping in rats to the presentation of another rat predicting food. *Science* 190, 690–692. <https://doi.org/10.1126/science.190.4215.690>.
- Tomie, A., 1996. Locating reward cue at response manipulandum (CAM) induces symptoms of drug abuse. *Neurosci. Biobehav. Rev.* 20, 505–535. [https://doi.org/10.1016/0149-7634\(95\)00023-2](https://doi.org/10.1016/0149-7634(95)00023-2).
- Tomie, A., Brooks, W., Zito, B., 2014. Sign-tracking: the Search for Reward. *Contemporary Learning Theories: Volume II: Instrumental Conditioning Theory and the Impact of Biological Constraints on Learning*. pp. 108.
- Trujano, R.E., Orduña, V., 2015. Rats are optimal in a choice task in which pigeons are not. *Behav. Processes* 119, 22–27. <https://doi.org/10.1016/j.beproc.2015.07.010>.
- Trujano, R.E., Lopez, P., Rojas-Leguizamon, M., Orduña, V., 2016. Optimal behavior by rats in a choice task is associated to a persistent conditioned inhibition effect. *Behav. Processes* 130, 65–70. <https://doi.org/10.1016/j.beproc.2016.07.005>.
- Vasconcelos, M., Monteiro, T., Kacelnik, A., 2015. Irrational choice and the value of information. *Sci. Rep.* 5, 13874. <https://doi.org/10.1038/srep13874>.
- Westbrook, R.F., 1973. Failure to obtain positive contrast when pigeons press a bar. *J. Exp. Anal. Behav.* 20, 499–510. <https://doi.org/10.1901/jeab.1973.20.499>.
- Williams, D.R., Williams, H., 1969. Auto-maintenance in the pigeon: sustained pecking despite contingent non-reinforcement. *J. Exp. Anal. Behav.* 12, 511–520. <https://doi.org/10.1901/jeab.1969.12.511>.
- Zentall, T.R., 2014. Suboptimal choice by pigeons: an analog of human gambling behavior. *Behav. Processes* 103, 156–164. <https://doi.org/10.1016/j.beproc.2013.11.004>.
- Zentall, T.R., 2016. An animal model of human gambling. *Int. J. Psychol. Res.* 9, 96–112.
- Zentall, T.R., Stagner, J., 2011. Maladaptive choice behaviour by pigeons: an animal analogue and possible mechanism for gambling (sub-optimal human decision-making behaviour). *Proc. R. Soc. Lond., B, Biol. Sci.* 278, 1203–1208. <https://doi.org/10.1098/rspb.2010.1607>.
- Zentall, T.R., Smith, A.P., Beckmann, J., 2019. Differences in rats and pigeons suboptimal choice may depend on where those stimuli are in their behavior system. *Behav. Processes* 159, 37–41. <https://doi.org/10.1016/j.beproc.2018.11.012>.
- Zhang, J., Berridge, K.C., Tindell, A.J., Smith, K.S., Aldridge, J.W., 2009. A neural computational model of incentive salience. *J. PLoS Computat. Biol.* 5, e1000437. <https://doi.org/10.1371/journal.pcbi.1000437>.
- Zhu, J.-Q., Xiang, W., Ludvig, E.A., 2017. Information seeking as chasing anticipated prediction errors. In: *CogSci 2017: 39th Annual Meeting of the Cognitive Science Society*. London, UK.