Universidade de Aveiro
Ano 2020

JOSÉ ALEJANDRO MACÍAS AYALA

O EFEITO DAS CONSEQUÊNCIAS SINALIZADAS NA ESCOLHA

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THE EFFECT OF SIGNALED OUTCOMES ON CHOICE

Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Psicología, realizada sob a orientação científica do Doutor Marco Alexander Barbosa de Vasconcelos Professor Auxiliar do Departamento de Educação e Psicología da Universidade de Aveiro e do Doutor Armando Batista Domingos Machado, Professor Catedrático do Departamento de Educação e Psicología da Universidade de Aveiro

Esta tesis es posible gracias al apoyo brindado por el Consejo Nacional de Ciencia y Tecnología de México a través de la Beca para estudios en el Extranjero: 438354

Dedico este trabajo a mi familia, especialmente a mis padres

o júri

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agradecimentos

A mis orientadores, Marco Vasconcelos y Armando Machado. Gracias por todo el esfuerzo y dedicación puestos en este trabajo.

A la Universidad de Minho, particularmente al Centro de Investigación en Psicología (CIPsi) y al Laboratorio de Comportamiento y Aprendizaje Animal por todo el apoyo brindado para la realización de este trabajo.

A mi familia. A mis padres quienes me han dado tanto. Por su amor, su paciencia, su apoyo, sus enseñanzas, sus risas. Nada de lo alcanzado sería posible sin ustedes. Mamá, por tu lucha incansable por tu familia y tus hijos, por todo tu amor en cada pozole, tus risas en cada momento. Papá, por tu paciencia y bondad, tu cariño, tu sentido del humor siempre. A los dos por siempre quererme y cuidarme, en las buenas y en las más oscuras. Son mi mayor ejemplo y mi mayor fuente de inspiración. Mis hermanos, Marco, Mario y Gris. Mis compañeros de travesuras, de risas, pero también de mucho cariño. Gracias por su apoyo incondicional siempre. No podía pedir mejor familia que ustedes. Los amo.

A mis amigos, lo mejor de este doctorado. Especialmente a quienes me acompañaron en esta etapa. Cristina, gracias por cada una de las risas, de lo que nos acordamos y de lo que no. Por todo el apoyo en cada momento, con paciencia y con cariño, por tu disposición a siempre ayudarme, resolverme, por cuidarme, por todo. Eres lo mejor del doctorado, una hermana. No puedo esperar a que te mudes a Puebla. Te quiero mucho.
Val, gracias por tu acompañamiento siempre. Te toca estar en el párrafo de orientadores. Gracias por las conversaciones, los desvelos y la escucha paciente. Sobre todo, gracias por tu amistad, lo más valioso que gané de ti. Te quiero.
Harry, gracias por tu amistad, tu paciencia. Por el acompañamiento en lo difícil y en lo divertido: las cervezas, los veranos y el coronavirus. Te quiero.
A todos los que me apoyaron siempre: Cat, gracias por tu amistad, risas y ayuda incondicional; Jairo, gracias por ser la persona más luminosa que he conocido. Los quiero mucho.
A todos los amigos del laboratorio: Carlos, Inés, Renata. Gracias por todo su apoyo.

A mis amigos a lo lejos, siempre presentes. Ale, Alan, Andrés, Cucho, Damián, Gaby, Gil, Kkis, Mike, Montse yTania.

To Randy. Thank you very much for opening your lab to me, for the meetings and all the advice. Thank you also for the beers and the talks. I cannot imagine a better lab for my period abroad. I had a great adventure.

Al Consejo Nacional de Ciencia y Tecnología por la Beca para Estudios en Extranjero 438354

palavras-chave

Informação, escolha subótima, valor preditivo, consequências sinalizadas, hipótese Δ-Σ, pombos

resumo

Pombos e outros animais preferem consequências sinalizadas a não sinalizadas em diferentes situações de escolha, mesmo que isso signifique não maximizar a taxa de retorno. O procedimento experimental de escolha subótima é um exemplo prototípico. Nesta tarefa, os pombos escolhem entre duas alternativas associadas a diferentes probabilidades de recompensa com atraso. Escolher a opção informativa (mas mais pobre) conduz a estímulos diferenciados que sinalizam de imediato se o ensaio resultará em comida ou não; escolher a opção não informativa (mas mais rica) também conduz a diferentes estímulos, no entanto, estes não sinalizam qual será a consequência. Os pombos preferem a opção informativa apesar da sua taxa de recompensa ser menor. A presente dissertação aprofunda o nosso conhecimento acerca deste fenómeno. No primeiro estudo, comparamos duas versões coexistentes da tarefa de escolha subótima que geralmente são consideradas equivalentes. No segundo, exploramos o efeito de atrasar a desambiguação da consequência, comida ou não, na opção informativa. Também estudamos se e como é que a preferência varia em função da duração da certeza ou incerteza acerca da consequência.

No terceiro estudo, analisamos a escolha ao sinalizar diferentes atrasos na recompensa; também estudamos se a preferência varia em função de quão diferentes os atrasos sinalizados são. Dos três estudos, concluímos que: (1) as duas versões da tarefa são equivalentes; (2) atrasar o momento de desambiguação da consequência reduz o valor da opção informativa; e que esse valor varia com o atraso da informação; e (3) quando as opções conduzem a múltiplos atrasos até à recompensa, os pombos preferem conhecer antecipadamente o atraso em vigor, mas essa preferência varia de acordo o rácio entre os atrasos possíveis. Em termos teóricos, analisamos os nossos resultados do ponto de vista funcional e mecanicista. Do ponto de vista funcional, assumimos que a evolução modelou a preferência pela informação porque esta pode ser usada pelos animais para ajustar o seu comportamento (e.g. a perseguir recompensas mais valiosas e a evitar as menos valiosas). Do ponto de vista mecanicista, expandimos a hipótese Δ-Σ (González et al., 2020) de forma a dar conta dos nossos resultados. O modelo propõe que a preferência pela informação surge de duas variáveis de ordem superior: o contraste entre as consequências sinalizadas dentro de cada opção e a taxa geral da recompensa associada a cada opção. As duas abordagens teóricas aproximam-nos da aspiração de Tinbergen (1963) de ilustrar como é que explicações funcionais e mecanicistas se complementam.

keywords

Information, suboptimal choice, predictive value, Δ-Σ hypothesis, signaled outcomes, pigeons

abstract

Pigeons and other animals prefer signaled over unsignaled outcomes in different choice situations, even if by doing so they fail to maximize their rate of return. The suboptimal-choice procedure is a prototypical example. In this task, pigeons choose between two options associated with different probabilities of delayed food reward. Choosing the *informative* (but leaner) option leads to differential stimuli that immediately signal whether the outcome of the trial will be food or no-food; choosing the *non-informative* (but richer) option leads to different stimuli too, but they do not reliably signal the outcome. Pigeons prefer the informative option despite its lower rate of reinforcement.

The present dissertation furthers our knowledge of this phenomenon. In the first study, we compared two coexisting versions of the suboptimal-choice task that are usually regarded as equivalent. In the second study, we explored the effect of delaying the disambiguation of the food or no-food outcome in the informative option; also, we studied if and how preference varies with the time under certainty and uncertainty about the outcome. In the third study, we analyzed the effect of signaling different delays to food reward on choice; also, we studied if preference varied with how different the signaled delays were. From the three studies, we concluded that: (1) the two coexisting versions are equivalent; (2) delaying the moment of disambiguation of the outcome reduces the value of the informative option; this value varies with the delay to information, and; (3) when the options lead to multiple delays to food, pigeons prefer to know in advance the delay in effect, but this preference varies with the ratio of the possible delays. Theoretically, we tackled these findings from both a functional and a mechanistic standpoint. Functionally, we assumed that evolution shaped preference for information because information can be used by animals to adjust their behavior (e.g., chasing valuable outcomes and avoiding less-valuable ones). Mechanistically, we expanded the Δ-Σ hypothesis (González et al., 2020) to account for our findings. The model proposes that preference for information arises from two higher-order variables: a contrast between the signaled outcomes within each option and the overall rate of reinforcement offered by each option. These two theorethical approaches to the same findings bring us closer to Tinbergen’s (1963) desideratum to illustrate how functional and mechanistic explanations complement each other.

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Abbreviations, Acronyms and Symbols

Δ	Delta
Σ	Sigma
cm	Centimiter
DGAV	Directorate-General for Food and Veterinary
d_{IL}	Initial link duration
d_{TL}	Terminal link duration
FR	Fixed Ratio
FT	Fixed Time
IQR	Interquartile Range
ITI	Inter-Trial Interval
Ln	Natural logarithm
msec	Milliseconds
p	Probability
SCM	Sequential Choice Model
sec	Seconds
t_s	Switching time
W	Watt

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Chapter I: Introduction

Animals live in a complex and uncertain environment. They face choices on a daily basis that are critical to most imaginable aspect of their life. When and whom to fight or mate with, where and when to search for food, and how long to persist in their searches are only a few examples of their vast challenges. The issue is important because the outcomes of these choices most likely impact the ability of animals to survive and reproduce. Hence, it seems reasonable to assume that natural selection has pruned contemporary behavioral mechanisms such that they are adaptive, on the average. In that sense, an animal capable of identifying information about future events and use that information to improve the outcomes of such events would, everything else equal, have greater chances of surviving and reproducing.

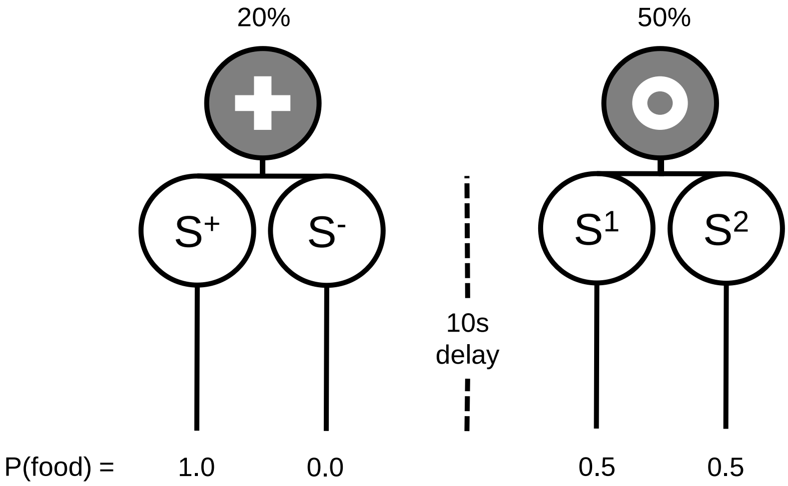
Take, for instance, foraging decisions. To guarantee survival, most animals must ensure a minimum amount of daily energy. To accomplish this, an animal must decide when to search for food; once it finds a possible source, it must decide whether to pursue it and exploit it or keep looking; and once exploiting a source, it must decide when to abandon it. Moreover, when it encounters two or more options, it must choose one and reject the alternatives. Since less time searching for food entails more time for other vital activities (like reproduction) and fewer chances of predation, we expect these foraging decisions to be sensitive to their long-term rate of return (Stephens & Krebs, 1986). From a normative standpoint, foraging activities ought to optimize the rate of energetic gain. Because the outcomes of each of these decisions are not certain, one way to maximize the rate of energy intake is to learn the properties of patches, including food density and quality, travel distance, and the arbitrary cues that signal such properties. This ability provides an advantage because this information can be used to optimize choice.

To illustrate, consider an animal facing binary choices. If the alternatives differ only in their rate of return, animals do learn the cues associated with each option and, once learned, prefer cues signaling the higher rate of return. If the options differ only in the amount of food, animals generally choose the one with the larger amount; if they differ only in the delay to food, animals prefer the one with the shorter delay; and if options differ only in the probability of food, they tend to prefer the one with higher odds (Bailey & Mazur, 1990; Green & Myerson, 2004; Mazur, 1985, 1997; Rachlin & Green, 1972). Under these conditions, choice is relatively predictable because options only differ in the rate of food offered.

However, animals sometimes seem to disregard the rate of return when the alternatives differ in the information they convey, preferring options yielding less food overall but more information. Take for instance the experimental situation depicted in Figure 1. In this task, a pigeon chooses between two alternatives that deliver food with different probabilities after the same delay. One option (cross symbol) yields food on 20% of the occasions; the other option (circle symbol) yields the same amount of food on 50% of the occasions. Animals should prefer the circle because it is objectively more profitable. Suppose now that, when the cross option is chosen, one cue signals that the delay will end with food (S^+) and a different cue signals that the delay will not end with food (S^-); hence, the cross option becomes *informative* in the sense that the stimuli are perfectly correlated with the outcome: when the S^+ is shown, reward is certain; when the S^- is shown instead, the absence of reward of certain [p(food)|$S^+ = 1.0$ and p(food)|$S^- = 0.0$]. On the other hand, when the circle option is chosen, cues are also presented (S^1 or S^2), but they do not reliably signal whether the delay will end with food or not (reward occurs on 50% of these trails, independently of which stimulus, S^1 or S^2, is presented).The circle option is *non-informative* because it does not 'inform' the animal about the forthcoming outcome [p(food)|S^1 = p(food)|$S^2 = 0.5$]. When the cross option is chosen, distinctive stimuli signal trials ending with food (S^+) and trials ending with No Food (S^-). When the circle option is chosen, stimuli are presented (S^1 or S^2) but do not reliable signal whether the trial outcome.

Figure 1

Experimental task



Note. Pigeons choose between a cross option with 20% chances of food or a circle option with 50% chances.

This feature does not change the fact that the overall chances of getting food are 2.5 larger when the circle is chosen. Yet, contrary to a maximization policy, pigeons and other animals strongly prefer the cross option (for reviews, see Cunningham & Shahan, 2018; McDevitt et al., 2016; Vasconcelos et al., 2018; Zentall, 2011, 2016). Why do animals prefer information despite it provides a lower rate of return? Why do animals prefer informative options when that information cannot be used?

The present dissertation addresses these questions from both a mechanistic and a functional perspective. On the one hand, it describes the ultimate causes that apparently make information valuable. The main argument is that, in nature, information is instrumental to maximize the rate of food intake because animals can adapt their behavior accordingly. If a cue informs that a particular option is ‘good’ relative to the background, an animal can purse that opportunity; if a cue informs that the option is ‘bad’ relative to the background, the animal can avoid the option and continue searching for alternatives. Previous research by Vasconcelos et al. (2015), Fortes et al. (2016) and Fortes et al. (2018) suggests that such a strategy may have been pruned by natural selection and is in fact adaptive under ecological conditions; yet, it may backfire in laboratory tasks where information cannot be used to adjust behavior. In other words, there is a mismatch between the circumstances in which the strategy evolved (the domain of selection) and the situation where the strategy is studied (the domain of testing) (Stevens & Stephens, 2010): In the latter, the animal cannot use the information to avoid a ‘bad’ option, hence being forced to pay the price of waiting in the presence of such option.

On the other hand, the dissertation studies the proximate causes driving choice in situations with asymmetric information. A recently proposed model, the Δ-Σ hypothesis (González et al., 2020) is contrasted with the data observed in the studies reported. The model proposes that the value of each option arises from two higher-order variables: Delta (Δ) and Sigma (Σ). Δ is the contrast between the probabilities of food within each option and is expressed as the difference in the probabilities associated with each stimulus. For example, the contrast in the cross option in Figure 1 is 1.0, because the S^+ signals a probability of food of 1.0 and the S^- a probability of 0.0 [1.0 – 0.0 = 1.0]; on the other hand the contrast in the circle option is 0.0 because both the S^1 and the S^2 signal the same probability of reward [0.5 – 0.5 = 0.0]. Σ is the overall probability of food offered by the option. In Figure 1, Σ = 0.2 for the cross option (0.2 x 1.0 + 0.8 x 0.0) and 0.5 for the circle option (0.2 x 0.5 + 0.8 x 0.5). The general idea of the model is that the value of an option increases with both Δ and Σ.

Together, the functional and mechanistic approaches serve as the theoretical and mathematical foundations of the three studies that follow. In the first study, we compare two experimental tasks that have co-existed in the research on preference for informative options and that are often referred to as equivalent. The tasks differ primarily on the number of stimuli signaling the outcomes in each alternative. One task comprises two stimuli in the informative option and two in the non-informative option. The other task involves two stimuli in the informative option, but only one in the non-informative. The aims of this this study were two-fold: (1) to test the equivalence between the tasks with constant parameters, and; (2) to test whether two stimuli associated with the same probability of food ($\Delta = 0$) are equivalent to only one stimulus associated with that same probability, a crucial assumption of the Δ-Σ hypothesis. This first study also served an unexpected purpose. The latencies to choose observed in this study resulted in a fruitful test of a more general model of choice, the Sequential Choice Model (SCM). SCM proposes that any choice between alternatives is the result of a valuation process occurring in parallel for each option. The fastest process is expressed behaviorally as a choice (SCM, Kacelnik et al., 2011; Shapiro et al., 2008).

In the second study, we deferred the moment at which the stimuli on the informative option disambiguated the outcome (food or no-food) and studied its effects on choice. In one experiment, choosing the informative option led to a stimulus that could remain throughout the entire delay and end with food, or it could change to a different stimulus and end with no-food. In the next experiment, the complementary manipulation was implemented: Choosing the informative option led to a stimulus that could remain throughout the entire delay ending with no-food or change to a different stimulus and end with food. That is, in Experiment 1, food was lost when the stimulus changed; in Experiment 2, food was guaranteed when the stimulus changed. The aim of these experiments was to test if and how preference would vary when the stimuli on the informative option increased or decreased the time under uncertainty about the trial outcome. The experiments also tested a modified version of the Δ-Σ hypothesis that included the role of this temporal certainty/uncertainty variable.

Finally, in the third study, we investigated the value of information about delays to food. In this experiment, choosing any of two alternatives led to food after a short or a long delay. Similar to the previous studies, one option was informative and the other non-informative, but instead of probabilities, information was about the delay in effect: In the informative option, the short delay was signaled by one stimulus and the long delay by a different stimulus; in the non-informative option, the stimuli presented did not reliably signal whether the delay was short or long. We tested whether choice favored information about the delays, and if so, whether this preference varied depending on the ratio of the delays. Our aims were: (1) to test preference for a different type of information, yet with a putative similar function; (2) to test whether the value of information depended on the ratio of delays, and; (3) to extend the Δ-Σ hypothesis to a situation where the contrast is not between the probabilities of reinforcement, but between the delays to reinforcement.

Together, these three studies attempt to broader our understanding of the role played by signaled outcomes on choice. Particularly, we aim to understand the proximate and ultimate causes for the value that informative cues seem to hold. We expect that the present dissertation extends this knowledge both empirically and theoretically.

Chapter II: The functional equivalence of two variants of the suboptimal choice task

Abstract

In the suboptimal choice task, birds systematically choose the leaner but *informative* option over the richer but *non-informative* option. The task has two variations. In the standard task, the non-informative option includes two terminal link stimuli. In the original task, it includes a single terminal link stimulus. For theoretical and empirical reasons, we tested whether these two variations are functionally equivalent. One group of pigeons was trained with the standard procedure, another group with the original procedure, and a third group was trained with a hybrid of the other two (i.e., the two options were the non-informative links of the standard and original procedures). Our findings indicate that the number of terminal link stimuli in the non-informative option is inconsequential *vis-à-vis* choice. Moreover, our findings also indicate that latencies to respond are a sensitive metric of value and choice. As predicted by the Sequential Choice Model, we were able to predict choices from latencies and observed a substantial shortening of latencies during simultaneous choices.

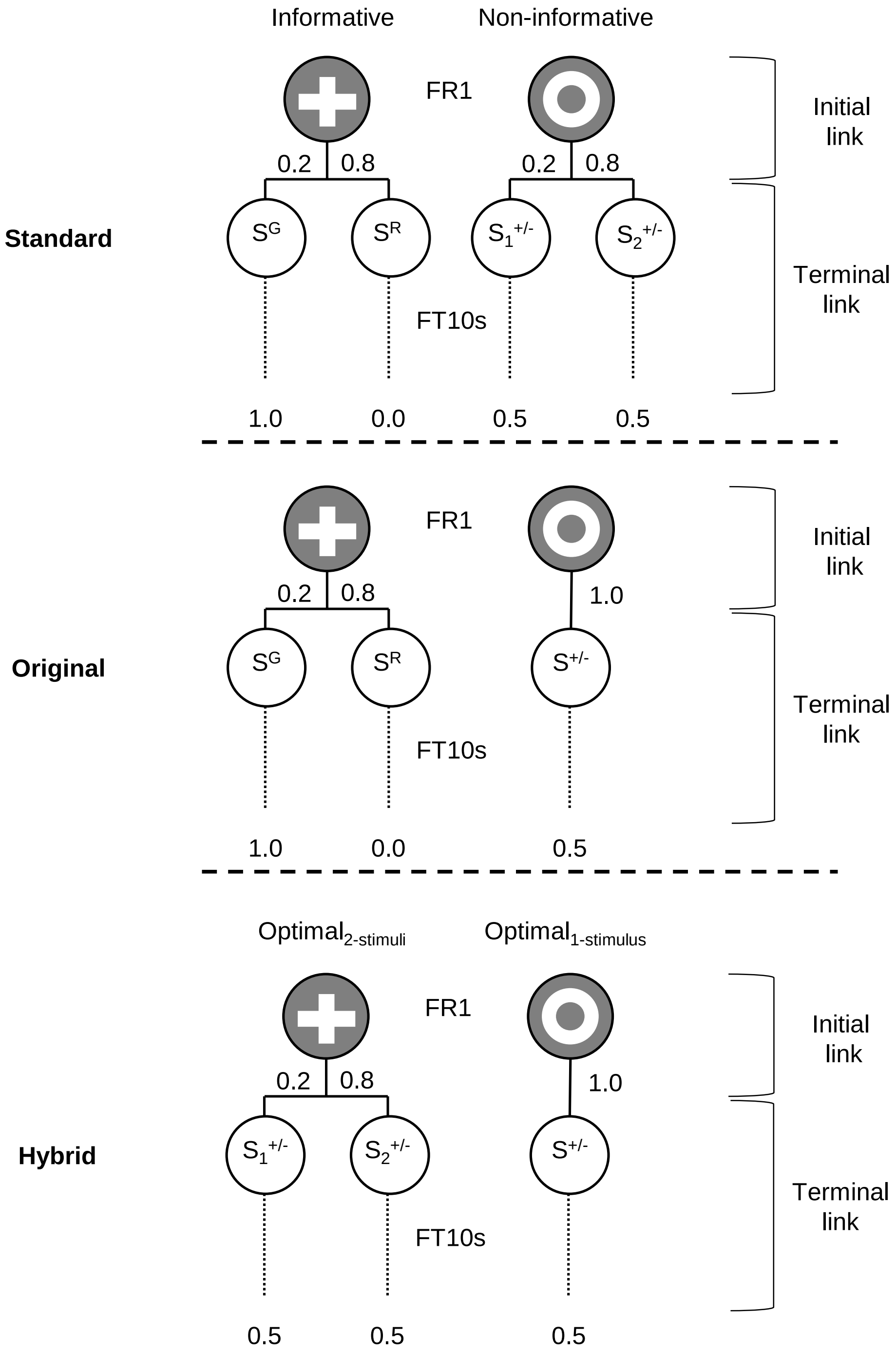
Introduction

The idea that psychological mechanisms are the product of the same evolutionary process as any other biological traits has often led to the expectation that behavior ought to maximize benefits and minimize costs in every conceivable circumstance. Even though behavior and its underpinning mechanisms must be adaptive on the average, (otherwise they would be selected against), evolutionarily minded researchers are well aware that animals will and do fail to maximize well-known benefits under some circumstances (e.g., McNamara et al.,, 2014; Vasconcelos et al., 2017). The optimizing agent is natural selection not the behaving organism.

A noticeable example of a situation wherein animals utterly deviate from optimality is the suboptimal choice task. The top panel of Figure 1 shows the prototypical procedure. Two options are presented either individually or simultaneously. Responding on the informative alternative turns on a positive discriminative stimulus (S^+) on 20% of these trials, a stimulus that is then followed by food reinforcement after 10 seconds; on the remaining 80% of these trials, a negative discriminative stimulus (S^-) is turned on and the trial ends without reinforcement after 10 s have elapsed. Alternatively, pecking on the non-informative alternative leads to one of two terminal stimuli ($S_1^{+/-}$ on 20% of these trials and $S_2^{+/-}$ on the remaining 80%) and after 10 s the trials end in food reinforcement 50% of the time regardless of the stimulus presented. Even though the overall probability of food in the informative alternative is 2.5 times lower than in the non-informative alternative (20 vs. 50%, respectively), birds strongly prefer the former (e.g. Fortes et al., 2017; Fortes et al., 2018; Fortes et al., 2016; Laude et al., 2014; Stagner & Zentall, 2010; Vasconcelos et al., 2015; for an example with rats, see Cunningham & Shahan, 2019; for reviews, see Cunningham & Shahan, 2018; McDevitt et al., 2016; Vasconcelos et al., 2018; Zentall, 2011, 2016).

Figure 1

Standard, Original and Hybrid procedures



Note. Experimental design for the Standard, Original, and Critical procedures. Solid lines represent no delay between consecutive events; dotted lines represent a10 s delay; *p* indicates probability of occurrence.

Numerous studies have now proposed that the critical ingredients of the suboptimal choice task lay in the signaling properties of the terminal stimuli (S^+, S^-, $S_1^{+/-}$, and $S_2^{+/-}$). Despite its probabilistic nature, the task contains a pivotal asymmetry: whereas uncertainty about the trial outcome (food vs. no food) disappears once one of the terminal stimuli is presented in the informative alternative (the S^+ or the S^-), uncertainty remains until the end of the trial regardless of the terminal stimulus presented in the non-informative alternative ($S_1^{+/-}$ and $S_2^{+/-}$). The particulars of how the signaling properties of the terminal stimuli influence choice remain under dispute. Cunningham and Shahan (2018), for example, propose suboptimal choice occurs when two conditions are met: S^+ conveys more temporal information about reinforcement (i.e. *when* food will occur) than $S_1^{+/-}$and $S_2^{+/-}$, and when animals ignore the S^-. This last condition is shared by other proposals (Gipson et al., 2009; Roper & Zentall, 1999; Mazur, 1996; Vasconcelos et al., 2015).

The newly proposed Delta-Sigma hypothesis (González et al., 2020), on the other hand, suggests that the contrast, defined as the difference between the two reinforcement probabilities associated with each terminal link within an alternative (*Delta*, Δ), and the overall reinforcement probability of each alternative (*Sigma*, ∑) are the main determinants of choice. In the standard task (see Figure 1, top panel), the contrast is 1 in the informative alternative [$p(\text{food}|\ S^+) - p(\text{food}|\ S^-) = 1 - 0 = 1$] and 0 in the non-informative alternative [$p(\text{food}|\ S_1^{+/-})$.– $p(\text{food}|\ S_2^{+/-}) = .5 - .5 = 0$] The hypothesis assumes that, everything else equal, the value of an alternative varies directly with both Δ (greater differences between the two terminal link probabilities mean greater value of the alternative) and with ∑ (greater overall reinforcement probability means greater value of the alternative).

Independently of the particulars of each proposal, the terminal stimuli and their associated properties (i.e., probability of reinforcement) consistently play center stage. Yet, two versions of the suboptimal choice task have co-existed in the literature and have been usually treated as equivalent: the aforementioned standard task (see Figure 1, top panel) and the original version of the task (see Figure 1, middle panel). These two versions differ only in the number of terminal stimuli in the non-informative alternative: whereas in the standard procedure the partially reinforced stimuli, $S_1^{+/-}$ and $S_2^{+/-}$, appear on 20 and 80% of the occasions, respectively, in the original procedure the same terminal stimulus, $S^{+/-}$, is always presented and is also partially reinforced.

The difference between these two procedures goes beyond a mere methodological curiosity. Theoretically, changing the number of terminal stimuli has implications for some of the accounts advanced so far. For instance, Cunningham and Shahan (2018) presupposes that an option with two terminal stimuli associated with the same probability of reinforcement (as $S_1^{+/-}$ and $S_2^{+/-}$ in the top panel) is functionally equivalent to an option with a single terminal stimulus with the same probability of reinforcement (as $S^{+/-}$ in the middle panel). Yet, one could also hypothesize that the number of terminal stimuli is not inconsequential. The presence of two putative conditioned reinforcers ($S_1^{+/-}$, and $S_2^{+/-}$) would accrue more value than the presence of one ($S^{+/-}$). On the other hand, applying the Δ-$\sum$ hypothesis to the non-informative alternative in the original procedure is not straightforward because, with only one terminal link stimulus, we cannot compute Δ. For simplicity, González et al. (2020) tentatively assumed that $\Delta = 0$ whenever a single terminal stimulus was used (see their Table 7), but this assumption clearly needed further support. Finally, as response-dependent sensory changes have been shown to be reinforcing (e.g., Kish, 1966; Osborne, 1977), one could argue that presenting one of two possible stimuli ($S_1^{+/-}$, $S_2^{+/-}$) ought to be more reinforcing than presenting always the same one ($S^{+/-}$).

Empirically, preferences observed with the two procedures tend to be somewhat dissimilar, but comparisons are clouded by differences in other important variables (e.g., probabilities of reinforcement, length of terminal links, etc.). For example, Kendall (1974) reported the first experiments using a single terminal stimulus in the non-informative alternative (original task). The procedure was similar to that depicted in the middle panel of Figure 1, except that (a) all terminal stimuli stayed on for 15 s, (b) the S^+ and the S^- appeared equally often when the informative alternative was chosen, and (3) the terminal stimulus of the non-informative alternative was always reinforced. Overall, pigeons preferred the informative alternative over 80% of the time, despite the concomitant loss of many available reinforcers. Further attempts to replicate these findings faced unexpected difficulties mostly due to within and between subjects' variability. Dunn and Spetch (1990, Experiment 3) used the same procedure as Kendall, but with 50-s long terminal stimuli, and found preferences between 13% and 95% for the informative alternative (see also Gipson et al., 2009). This degree of variability is hardly ever seen in the standard procedure. Overall, the original procedure appears to engender inconsistent and highly variable preferences both within and across subjects (e.g., Dunn & Spetch, 1990; Fantino et al., 1979; Kendall, 1974; Spetch et al., 1990; Spetch et al., 1994), whereas the standard procedure usually generates high and consistent preferences for the informative alternative (e.g., Fortes et al., 2016; Stagner et al., 2011; Stagner & Zentall, 2010; Vasconcelos et al., 2015; Zentall & Stagner, 2011).

In sum, a formal test of the pre-supposed equivalence between the standard and the original procedures remains to be implemented with exactly the same parameters (i.e., with the same initial-link schedules, the same probabilities of reinforcement with each terminal stimulus, and the same terminal link duration). The experiment detailed below presents such a test. We compared three versions of the task: One group of pigeons experienced the standard task with the parameters depicted in the top panel of Figure 1; a second group of pigeons experienced the original task as depicted in the middle panel of Figure 1; finally, a third group of pigeons experienced an hybrid task wherein choices involved the non-informative alternatives from the standard and original procedures (see Figure 1, bottom panel). The hybrid task was thought as a critical equivalence test. If the tasks are indeed equivalent and the number of terminal stimuli is irrelevant for choice, then (1) pigeons in the standard and original procedures ought to show a strong and *comparable* preference for the informative alternative, and (2) pigeons in the hybrid procedure ought to be indifferent between the two non-informative alternatives.

To analyze the value of the alternatives in each procedure, we focused not only on choice itself but also on latencies to respond. Latencies have been shown to be inversely related with value in a variety of procedures (e.g., Bateson & Kacelnik, 1995; Killeen & Hall, 2001; Lagorio & Hackenberg, 2012; Reboreda & Kacelnik, 1991; Shull et al., 1990) and may provide convergent evidence regarding the assumed equivalence. If the standard and the original procedures are indeed equivalent, then the preferred option should engender shorter latencies to respond; if the two non-informative options presented in the hybrid procedure are indeed similarly valued, then latencies to respond must not differ.

Two other latency-related predictions derive from the Sequential Choice Model (SCM; Kacelnik et al., 2011; Shapiro et al., 2008). For evolutionary and ecological reasons, the model proposes that contemporary decision mechanisms were pruned to deal with sequential-choice situations where animals decide whether to pursue a prey, rather than with simultaneous-choice situations where animals decide which of two preys to pursue. According to the SCM, animals assign value to each sequentially encountered item depending on a) the item's absolute properties such that, integrated over encounters, more profitable items become more valued (Bateson & Kacelnik, 1996; Shapiro et al., 2008; Vasconcelos et al., 2010); b) the animal's energetic state during learning such that items found under greater need become more valued (Aw et al., 2011; Marsh et al., 2004; Pompilio et al., 2006; Vasconcelos & Urcuioli, 2008); and c) the value of alternative items such that an item becomes less valued as the environment becomes globally richer (the average gain in the envirionment increases) (Fantino & Abarca, 1985; Pompilio & Kacelnik, 2010; Vasconcelos et al., 2013). Overall, animals end up with a "library" of latencies that are on average shorter for more valued options. The critical feature of the SCM is seen in the sporadic simultaneous encounters: there is no explicit deliberation between the options; instead, each option triggers an independent, non-interfering sequential process, but the option generating the shorter latency "censors" the alternative and is expressed behaviorally as a choice. This proposal has two consequences: First, we ought to be able to predict simultaneous choice from the latency distributions observed in sequential encounters because the distributions themselves reflect the value of the alternatives. Second, latencies observed during simultaneous choices should be shorter than latencies observed during sequential encounters (Kacelnik et al., 2011; Shapiro et al., 2008). This counterintuitive shortening should be particularly noteworthy for the non-preferred options because their associated latencies during sequential encounters tend to be longer and thus more likely to be censored during simultaneous choices.

Several studies have now confirmed that simultaneous choice can indeed be predicted from latencies collected during sequential encounters with the same options (e.g., Freidin et al., 2009; Ojeda et al., 2018; Shapiro et al., 2008; Vasconcelos et al., 2010; Vasconcelos et al., 2013; Vasconcelos et al., 2015). The evidence for shortening latencies is somewhat mixed. To date, only two studies have reported latency shortening for the non-preferred option (Ojeda et al., 2018; Shapiro et al., 2008), three have failed to find it (Aw et al., 2012; Vasconcelos et al., 2010; Vasconcelos et al., 2013), and no study has reported shortening for the preferred option. The shortening prediction has proven difficult to test because, when animals favor one of the alternatives, the latency distribution of the preferred option is hardly censored. Because this option is highly valued, latencies are already at floor with very limited room for further shortening. On the other hand, the sample size of latencies for the less preferred option is too small to allow a formal test (i.e., the less preferred option is chosen too infrequently). The most promising approach to overcome these practical limitations is to arrange a critical test wherein both options have similar value, thus avoiding a floor effect in the latency distributions and ensuring that they overlap substantially, thus allowing plenty of room for the cross-censorship mechanism to operate. If the two non-informative options presented in the hybrid procedure are indeed equivalent, this preparation may contain the necessary ingredients to observe the shortening of latencies during simultaneous choices.

In summary, our main goal was to test whether the standard and the original suboptimal-choice procedures are functionally equivalent resorting to two measure of value: choice proportions and response latencies. In parallel, we test the SCM’s counterintuitive prediction of latency shortening during simultaneous-choice situations.

Method

Subjects

Twelve pigeons (*Columba livia*), with 80% to 85% of their free feeding body weights, participated in the experiment. The pigeons had no experience with the present task. They were housed individually in a temperature-controlled room (around 21° C) on a 13:11 hour light/dark cycle (lights on at 8:00). Grit and water were always available in their home cage. The pigeons were cared for in accordance with the animal care guidelines of the Directorate-General for Food and Veterinary (DGAV), the Portuguese national authority for animal health, and the University of Minho. All experimental procedures were conducted in agreement with European (Directive 2010/63/EU) and Portuguese law (Ordinance 1005/92 of October 23), and were approved by DGAV (Authorization #024946).

Apparatus

Three Med Associates operant boxes for pigeons were used. The boxes were 28.5-cm high, 24-cm long, and 30-cm wide. The response panel had three centrally aligned keys, with the side keys 6 cm apart from the center key. The circular keys were 2.5 cm in diameter and were located 21 cm above the floor grid. The grain hopper opening (5-cm high x 6-cm wide) was located below the central key, 4 cm above the floor. When activated, the food hopper was raised and illuminated with a 1.1-W light. On the opposite wall, a 2.8-W houselight, located centrally 23 cm above the floor, illuminated the entire box. Each box was enclosed by a sound-attenuating chamber, equipped with a fan to circulate air and mask outside noises. A personal computer controlled all three boxes. The events were controlled, and the data recorded using ABET II software (Lafayette Instruments).

Procedure

*Pre-training***.** Pigeons were first trained on Fixed-Ratio (FR) schedules with the six stimuli used in the experiment: red, green, yellow, blue, cross, and circle. Each stimulus was presented randomly four times on the left and right keys for a total of 48 trials per session. Once the FR schedule was completed, the key was turned off and the feeder was activated. Feeder duration was adjusted for each pigeon to reduce the amount of food given outside the experimental session, while maintaining the pigeon's weight; during the experiment it ranged from 2 to 5 s. Delivery of food was followed by a 10-s Inter-Trial Interval (ITI) with the houselight on. Pigeons received two sessions with a FR-1 schedule followed by one session with a FR 5 schedule in the first half and a FR 10 schedule in the second half.

*Training***.** Pigeons were randomly divided into three groups of four birds each, and then the groups were randomly assigned to the three task variants, the standard procedure (Figure 1, top panel), the original procedure (Figure 2, middle panel), or the hybrid procedure (Figure 1, bottom panel). All groups faced two types of trials: sequential-choice trials wherein only one option was available and simultaneous-choice trials wherein pigeons were free to choose between the two options. For the original and standard procedures, a simultaneous-choice trial started with the informative and non-informative alternatives randomly presented on the left and right. A single peck at one of the keys determined choice and turned both keys off. Choosing the informative alternative led to the same events in the original and standard procedures: On 20% of these trials, a stimulus that ended with food after 10 sec (S^+) was presented at the pecked location; on the remaining 80%, a different stimulus that ended without food (S^-) after 10 sec had elapsed was presented at the same location. The consequences differed when the non-informative alternative was chosen instead: whereas in the standard procedure, $S_1^{+/-}$ or $S_2^{+/-}$, was presented, on 20% and 80% of the occasions, respectively, in the original procedure the same stimulus ($S^{+/-}$) was always presented. Each of these stimuli: $S_1^{+/-}$, $S_2^{+/-}$, or $S^{+/-}$, stayed on for 10 sec and was followed by food 50% of the time. In the hybrid procedure, simultaneous choice trials required a choice between the non-informative options from the original and standard procedures, one involving a single terminal stimulus ($S^{+/-}$) and the other involving two terminal stimuli ($S_1^{+/-}$ and $S_2^{+/-}$). Sequential-choice trials were similar to simultaneous-choice trials, except that only one option was available at trial outset (i.e., only one side key was illuminated). In the original and standard procedures, either the non-informative or the informative alternative was turned on; in the hybrid procedure, one of the two non-informative alternatives was turned on.

Each session comprised 120 trials, 80 sequential- and 40 simultaneous-choice trials, randomly interspersed, all with side key allocation counterbalanced across trials. Both the initial stimuli (circle or cross) and the terminal stimuli (red, green, blue or yellow) were counterbalanced across pigeons, with the constraint that when an option was followed by two possible terminal stimuli (S^+ and S^-, or $S_1^{+/-}$ and $S_2^{+/-}$,) red always paired with green, and blue with yellow. The stimulus for $S^{+/-}$ was chosen randomly from one of the remaining hues (for instance, if a bird had red and green as S^+ and S^-, $S^{+/-}$ could be either blue or yellow). The houselight was on during the ITI and off during the trials. The time between the onset of the options (either one or two depending on the trial type) and the peck at one of the side-keys corresponded to the latency to respond collected on each trial. Training continued for 24 sessions.

Reversal. Immediately after training, the stimuli that identified each option (i.e., circle and cross) were interchanged. All other details remained unaltered. The reversal lasted for another 24 sessions.

Data analysis

In the original and standard procedures, we measured preference in simultaneous choice trials as the proportion of choices for the informative alternative. In the hybrid procedure, preference corresponded to the proportion of choices for the alternative that comprised two terminal stimuli ($S_1^{+/-}$ and $S_2^{+/-}$; i.e., the non-informative alternative from the standard procedure). The SCM's predictions were calculated using latencies from sequential-choice trials preceding simultaneous-choice trials. To minimize the influence of temporal fluctuations in the subjects' state, we predicted each simultaneous-choice trial based on the average latency from the preceding four sequential-choice trials with each option (e.g., Kacelnik et al., 2011; Vasconcelos et al., 2010; Vasconcelos et al., 2015). The predicted choice was the option with the shorter average latency. Analyses of preference at stability used the last six sessions of each phase (e.g. training and reversal).

To test the SCM's shortening prediction, we used separate permutation tests for each subject and phase (for extensive treatments, see Edgington, 1995; Manly, 2007). These tests are distribution free and make fewer assumptions than traditional parametric tests. Under the null hypothesis, any latency collected in the experiment is equally likely to be from sequential- or simultaneous-choice trials. Thus, any difference between the average latencies from sequential- and simultaneous-choice trials (used here as our test statistic) is due only to chance. To test the hypothesis, we generated 10,000 random permutations of all the latencies collected for a given option (say n latencies from sequential-choice trials and m latencies from simultaneous-choice trials). For each permutation, we computed the difference between the median latency to respond in the first n latencies and the median latency to respond in the last *m* latencies. We used the set of all such differences as the permutation distribution of our test statistic. We then computed the proportion of differences that were as extreme as or more extreme than the observed difference. This proportion yielded the *p*-value of the test. Latencies collected at stability (last six sessions) for each option in each phase were collapsed to run the tests. Tests were only performed when at least 30 latencies were available for sequential- and simultaneous choice trials. Non-parametric tests were used in all statistical comparisons, with the Type-1 error rate set at .05.

Results

Figure 2 (black dots) shows the median preference (IQR) in simultaneous-choice trials across blocks of two sessions, both in training and reversal phases (left and right panels, respectively). Median choice data for each bird during the last 6 sessions of each phase is shown in Table 1. During training, a strong preference for the informative alternative developed in the standard and in the original procedures (top and middle panels, respectively). Conversely, in the hybrid procedure (bottom panel), preference remained stable with minor deviations from indifference.

Table 1

Individual median preferences in each group

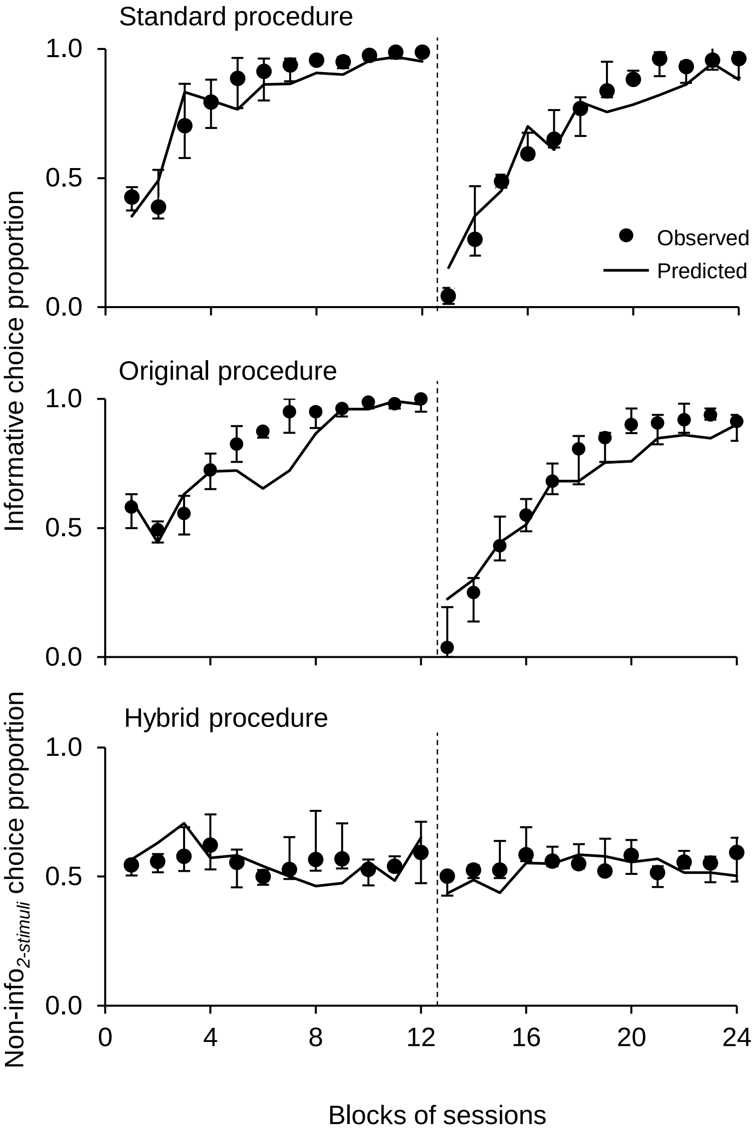
Group		Training			Reversal		
	Pigeon	Median	Max	Min	Median	Max	Min
Standard	449	0.913	1.000	0.825	0.925	1.000	0.900
	458	1.000	1.000	1.000	0.950	1.000	0.925
	519	0.988	1.000	0.975	1.000	1.000	0.975
	860	0.975	1.000	0.950	0.863	0.900	0.700
Original	161	0.800	0.900	0.775	0.825	0.900	0.675
	286	1.000	1.000	0.975	0.888	0.950	0.850
	918	1.000	1.000	0.975	0.950	0.975	0.925
	967	0.988	1.000	0.975	0.975	1.000	0.950
Hybrid	157	0.500	0.575	0.425	0.438	0.500	0.400
	444	0.413	0.475	0.375	0.625	0.750	0.575
	724	0.663	0.900	0.525	0.575	0.725	0.550
	G39	0.600	0.750	0.525	0.575	0.625	0.500

Note. (with maximum and minimum) for the Informative alternative (Standard and Original procedures) and for the Non-informative alternative with two stimuli (Critical procedure) during the last 6 sessions of training and reversal.

The pattern of findings in the reversal phase was similar (see Figure 2, right panels). After an initial and expected reversal of preference, pigeons in the original and standard procedures re-acquired a strong preference for the informative alternative comparable to the one observed at the end of training. Preference in the hybrid procedure did not show any systematic variation in the reversal. Separate Friedman tests for preference across sessions in each phase confirmed these visual impressions. Preference increased significantly in both training and reversal phases in the standard [smaller $\chi^2(11) = 31.710$, $p = .001$] and in the original procedure [smaller $\chi^2(11) = 35.618$, $p < .001$], whilst it remained stable in the hybrid procedure [larger $\chi^2(11) = 8.841$, $p = 0.637$]. By the end of training (last six sessions), median (IQR) preferences in the standard, original and hybrid procedures were 98.50% (93.13 % to 99.75%), 99.5 % (84.75% to 100.00%), and 55.25% (43.63% to 65.00%), respectively. The corresponding preferences by the end of reversal were 94.00% (88.13% to 98.75%), 92.00% (84.50% to 97.25%), and 57.75% (47.38% to 61.75%), respectively. Mann-Whitney tests revealed that preference at stability was comparable in the standard and the original procedures, irrespective of phase (smaller $U = 6.5$, $p = .655$, $r = .16$), and that preference was significantly lower in the hybrid procedure when compared with the standard (larger $U = 0.0$, $p = .021$, $r = .82$) and with the original procedure (larger $U = 0.0$, $p = .021$, $r = .82$). In summary, while a similar, systematic, and strong preference for the informative alternative developed in the original and standard procedures, no systematic departures from indifference were observed in the hybrid procedure.

Figure 2

Proportion of choices for the Informative option in the Standard and original procedures, and Non-info$_{2stimuli}$ in the hybrid procedure



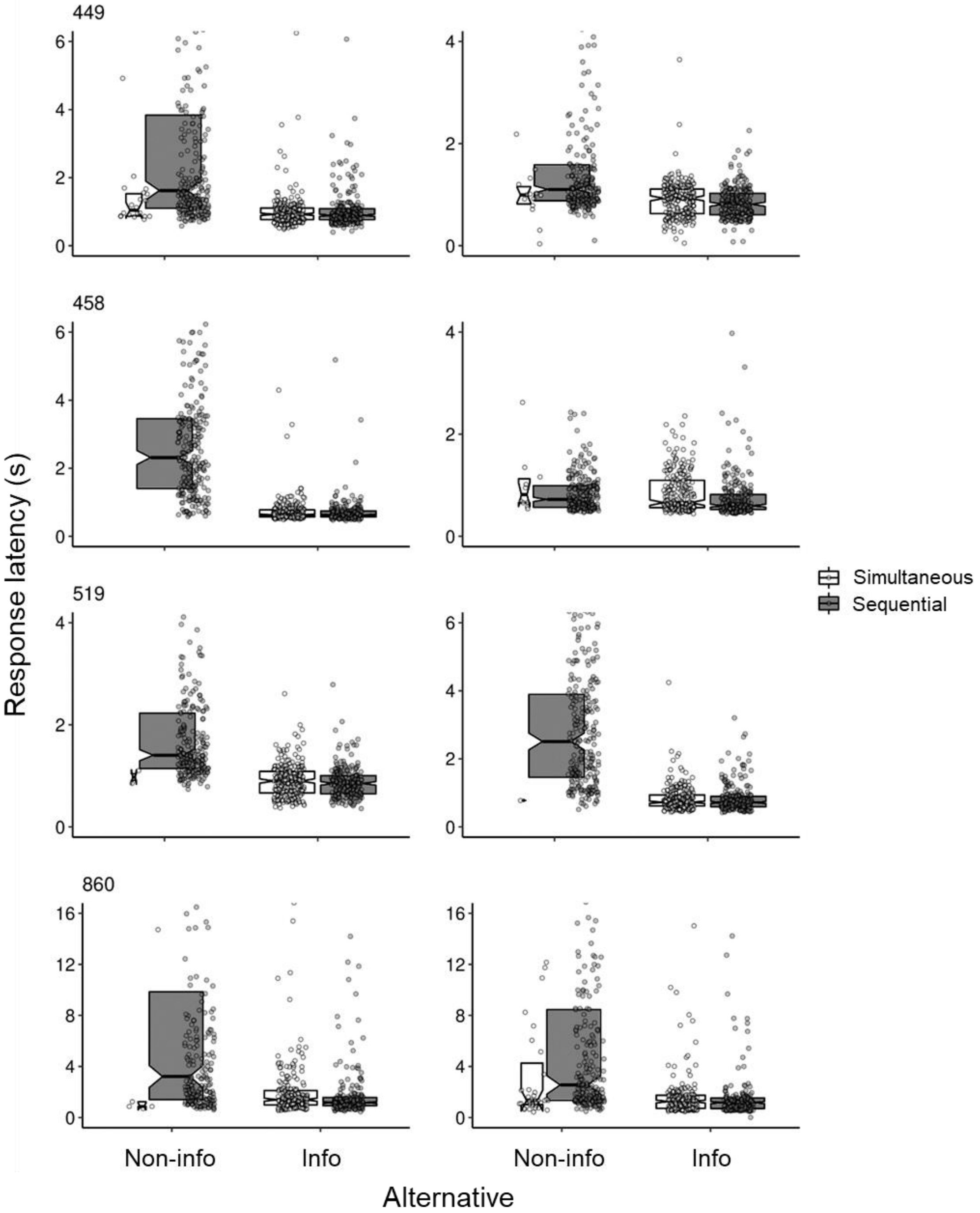
Note. Median proportion of observed choices and preference predicted by the SCM for the Informative option in the standard and the original procedures (upper and middle panel, respectively) and for the Non-informative option with two terminal stimuli in the Critical procedure (bottom panel). Error bars represent the interquartile range.

The lines in Figure 2 represent the preferences predicted by the SCM. Overall, choices in simultaneous-choice trials closely matched the predictions generated from latencies collected during sequential-choice trials in the three procedures, both during training and reversal phases. Despite a tendency to slightly underpredict choice in the standard and original procedures, latencies and preference covaried systematically throughout acquisition even when sudden and large shifts in preference were observed as in the first few blocks of the reversal (R^2 = .93 and for all the blocks of sessions in the standard procedure; R^2 = .89 for the corresponding data of the original procedure).

The foregoing analyses suggest that latencies are indeed a sensitive metric of value. To explore the issue further, we restricted our assessment to the last segments of each phase when preference and presumably latencies were stable (i.e., the last six sessions of training and the last six sessions of reversal). Figure 3 shows the latencies collected from each bird in the standard procedure both in training (left panel) and reversal (right panel) phases for each of the options. Figures 4 and 5 show the corresponding data for the original and hybrid procedure, respectively. The width of the boxes is proportional to the square root of the number of observations, dots represent individual latencies, horizontal lines correspond to the median, boxes span the interquartile range, and notches represent the 95% CI for the median. Because birds strongly preferred the informative option in simultaneous-choice trials, we expected that they should also exhibit shorter latencies to accept this option in sequential-choice trials relative to the non-informative alternative. Figures 3 and 4 confirm this prediction for each of the birds (cf. grey boxes always shorter and with lower median for the informative option). Overall, in sequential-choice trials, latencies to respond on the informative (but preferred) alternative were shorter than latencies to respond on the non-informative (but non-preferred) alternative, both in training and reversal (median latencies across the last 6 sessions of the standard and original procedures in training: 0.873 vs. 2.081 sec, respectively; corresponding median latencies in reversal: 0.766 vs. 1.102 sec, respectively). Wilcoxon Signed-ranks tests ran with birds in the standard and in the original procedure collapsed into a single group confirmed that these differences were significant both in training and reversal (both *z'*s = -2.521, *p* = .012).

Figure 3

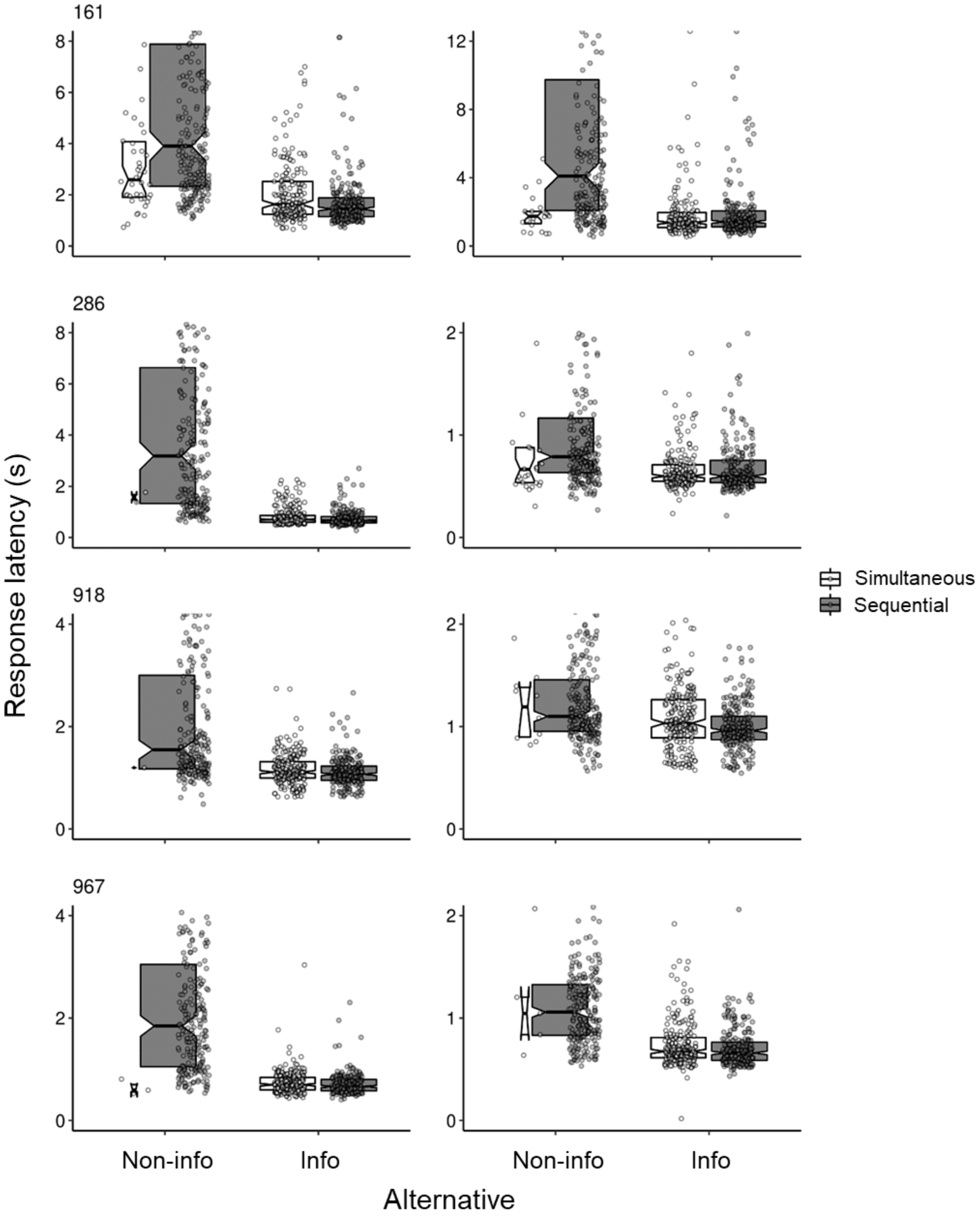
Individual latencies for the informative and non-informative options in the Standard group



Note. Individual latency data for *Standard* group during the last six sessions in sequential and simultaneous encounters for the informative and non-informative alternatives. Left panel = training; right panel = Reversal. Each data point represents one latency; box represents 50%of the data (being the box limits the 25th and 75th percentiles determined by R software); notches represent the 95% confidence interval for the median; black lines at the center of the notches represent the medians. Width of box is proportional to the square root of observations (n).

Figure 4

Individual latencies for the informative and non-informative options in the Original group

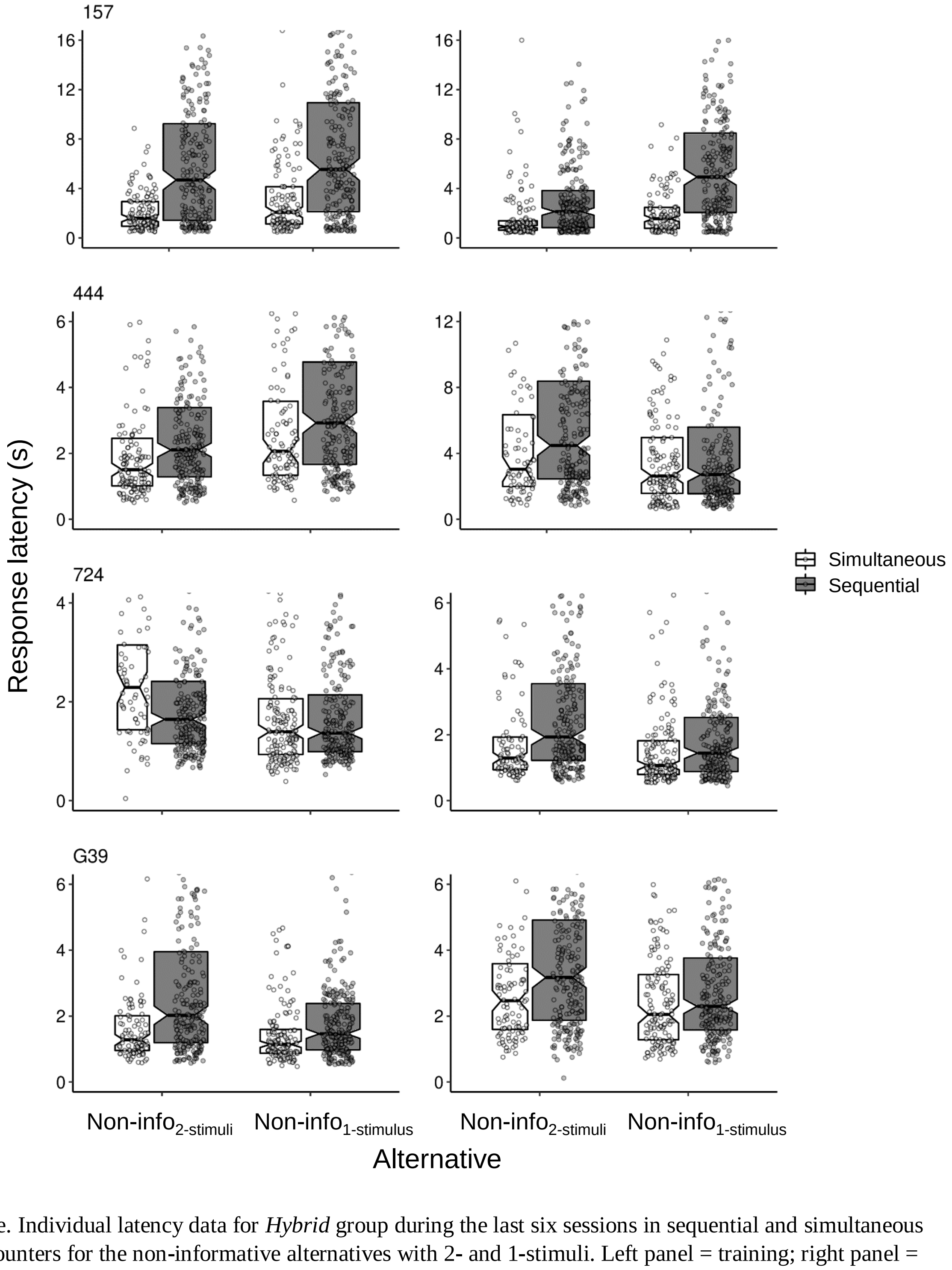


Note. Individual latency data for *Original* group during the last six sessions in sequential and simultaneous encounters for the non-informative and non-informative alternatives. Left panel = training; right panel = Reversal. Each data point represents one latency; box represents 50%of the data (being the box limits the 25th and 75th percentiles determined by R software); notches represent the 95% confidence interval for the median; black lines at the center of the notches represent the medians. Width of box is proportional to the square root of observations (n).

For the hybrid procedure, we predicted no systematic differences in latencies from the two non-informative options within sequential- and simultaneous-choice trials because preference did not deviate substantially from indifference in simultaneous-choice trials. Figure 5 confirms this prediction for each of the birds (cf. no systematic differences within white boxes, and no systematic differences within grey boxes). Median latencies to accept each option were comparable both during training and reversal (2.195 sec for Non-info$_{2\text{-stimuli}}$ vs. 2.064 sec for Non-info$_{1\text{-stimulus}}$, and 2.503 sec vs. 2.652 sec, correspondingly). Wilcoxon Signed-ranks tests confirmed these non-significant findings (largest $z = -0.730$, $p = .465$).

Figure 5

Individual latencies for the non-informative options with 2- and 1- stimuli in the Hybrid group



Note. Individual latency data for *Hybrid* group during the last six sessions in sequential and simultaneous encounters for the non-informative alternatives with 2- and 1-stimuli. Left panel = training; right panel = Reversal. Each data point represents one latency; box represents 50%of the data (being the box limits the 25th and 75th percentiles determined by R software); notches represent the 95% confidence interval for the median; black lines at the center of the notches represent the medians. Width of box is proportional to the square root of observations (n).

Finally, to test SCM's shortening hypothesis we compared, for each subject, latencies collected during sequential-choice trials (grey boxes in Figures 3, 4, and 5) and latencies collected during simultaneous-choice trials (white boxes in Figures 3, 4, and 5) at stability of each phase. As expected from the strong preference for the informative alternative, the test of the shortening hypothesis was hindered by the near exclusive preference observed in the standard and original procedures. As Figures 3 and 4 show, the latencies for the informative (but preferred) alternative in sequential-choice trials (grey) were already at floor, and the corresponding latencies in simultaneous-choice trials (white) appeared indistinguishable from them. The permutations tests confirmed that the median differences in latencies to respond to the informative option when alone and when part of a choice set were not statistically significant in any subject in the standard and original procedures (smallest *p's* = .738 and .874, respectively).

The strong preference for the informative alternative also reduced the number of latency samples from the non-informative (but non-preferred) option in the simultaneous-choice trials thus rendering most tests mute. Formal permutation tests were performed only for subjects 449 and 860 from the standard procedure, and 161 from the original procedure. All tests revealed that latencies were significantly shorter in simultaneous-choice trials (largest *p* = .011).

As expected, the hybrid procedure offered good conditions to test the shortening hypothesis: because preference was intermediate, latencies in sequential choices were not at floor and the number of latencies collected for each option during simultaneous choices was substantial. Except for bird 724 in the training phase, Figure 5 shows a widespread shortening of latencies to respond to both options in simultaneous-choice trials relative to sequential-choice trials (cf. light vs. dark grey symbols). Except for pigeon 724 that showed no evidence of shortening in the 2-stimuli non-informative option (*p* = .243), but did show it in the 1-

stimulus non-informative option (*p* = .034), the permutation tests revealed significant evidence for shortening for both options in all other pigeons (*p's* < .025 for the 2-stimuli option, and *p's* < .001 for the 1-stimulus option).

Discussion

Animals systematically prefer options with informative rather than non-informative terminal link stimuli (e.g., Bower et al., 1966; Prokasy, 1956; Roper & Zentall, 1999). This fact *per se* is unsurprising for information can be used to adapt behavior under normal circumstances. However, when information is not useful as in the choice procedure discussed here, it generates ostensive suboptimal preferences, with animals preferring an option that, although informative, yields a much lower rate of reinforcement (McDevitt et al., 2016; Zentall, 2016).

In this paper, we compared two variations of the suboptimal choice task: one where the best, but usually not preferred option includes two non-informative terminal stimuli, and another where this same option includes only one equally non-informative terminal stimulus (cf. top and middle panels of Figure 1). Historically, these variations have been considered interchangeable, but a definite clarification was needed, for both theoretical and empirical reasons. Thus, we analyzed the two versions resorting to different measures. One group of pigeons faced choices between the informative option and a non-informative option with two terminal stimuli (the standard procedure); another group faced choices between the informative option and a non-informative option with one terminal stimulus (the original procedure); and still another group faced choices between the two variations of the non-informative option (hybrid procedure). Besides choices proportions, we also analyzed response latencies for they have been shown to be a sensitive metric of value (e.g., Bateson &

Kacelnik, 1995; Killeen & Hall, 2001; Lagorio & Hackenberg, 2012; Reboreda & Kacelnik, 1991; Shull et al., 1990).

Altogether, our findings support the claim that the two procedures are equivalent. First, pigeons in the standard and original procedures developed a strong and comparable preference for the informative option. Second, pigeons in the hybrid procedure remained indifferent between the options. Third, when a systematic preference for the informative option developed, latencies to respond were systematically shorter for the preferred option. Lastly, when no preference emerged, latencies to respond to the two options were similar. In fact, choices and latencies were so closely interrelated that we were able to predict choices from latencies in the three procedures as suggested by the SCM (see also Vasconcelos et al., 2015).

While our findings do not demonstrate that non-informative options with one- or two-terminal stimuli are perceived equally by pigeons, they do suggest that the two options have the same attractiveness or value. Other studies have changed key features of the task, including the probability of occurrence of each terminal stimulus and the overall probability of reinforcement in each option (e.g., Belke & Spetch, 1994; Case & Zentall, 2018; Dunn & Spetch, 1990; Fantino et al., 1979; Smith & Zentall, 2016; Spetch et al., 1990; Spetch et al., 1994; Zentall et al., 2017) along with the number of terminal stimuli, and have usually credited their findings to the former rather than the latter. Our results rule out the possible confounding effect of the number of terminal stimuli and support the notion that at least pigeons do not have specific preferences for stimulus variety per se (e.g., Catania, 1975; Catania & Sagvolden, 1980).

These results have also theoretical implications for the recently proposed Delta-Sigma hypothesis (González, et al., 2020). The model predicts animals should prefer the option with a greater difference between the reinforcement probabilities associated with each terminal link stimuli within each option or Delta (Δ), and modulated by the overall probability of reinforcement (Sigma, $\sum$) associated with each alternative. When the non-informative option comprised 2-stimuli the probabilities $\Delta = 0$ [p(food| [p(food| $S_1^{+/-}$) .– p(food| $S_2^{+/-}$) = .5 – .5 = 0]; however, when only one terminal link stimulus exists, the authors assumed these was equivalent to a $\Delta = 0$ to test the model. The present results provide empirical validity to their assumption.

This study also set the ideal stage to test the counterintuitive prediction of latencies shortening during simultaneous-choice trials. Choice data confirmed that pigeons in the hybrid procedure were effectively choosing between similarly valued options which, in and of itself implied that latency distributions from sequential-choice trials were not at floor and overlapped substantially. Except for one bird and one option, we obtained widespread evidence for shortening in the critical procedure. Further, some evidence for shortening was observed also for the non-preferred option of the standard and original procedures. As expected, the strong preference for the informative option in the latter procedures prevented any shortening of latencies to respond to this option.

These findings are in direct opposition with the dominant intuition that choice is both cognitively demanding and time consuming. The Buridan's ass paradox, wherein a donkey finds himself midway between two piles of hay and eventually starves to death unable to decide, illustrates well this line of reasoning (see also Schwartz, 2004). At the heart of these models lies the speed-accuracy trade-off (Pachella, 1974; Wickelgren, 1977) according to which more time invested into a decision yields a more accurate choice. Nevertheless, more accurate decisions are not necessarily more profitable. Value-based decisions wherein the animal collects the chosen item pose a challenge because, from an economic and optimal-foraging perspectives, preference should be based on the maximization of the ratio of expected gains from the item to expected time to receive it, or equivalently on the minimization of lost opportunity (Stephens & Krebs, 1986; see also Stephens et al., 2007). This means that the profitability of the chosen option decays hyperbolically with the time taken to choose. While this loss in profitability may be overcome by the benefits of a ‘wise’ choice when the alternatives have different value, the scenario is more problematic when the alternatives have similar value.

Intuitively, latencies to respond should vary inversely with the options’ similarity in value. In other words, difficult decisions (i.e., those involving options with similar return) should take more time even though choosing the best option yields only a minimal increase in profitability. Why lean towards accuracy when speed would pay off? The paradox would vanish if, as the SCM shows, we assume that choice does not involve any comparison between alternatives and is therefore neither cognitively demanding nor time-consuming.

For the moment, we are left with yet another paradox: On the one hand our findings with pigeons and previous ones with starlings (Shapiro et al., 2008) and rats (Ojeda et al., 2018) seem to support the cross-censorship mechanism imposed by the non-interfering sequential processes envisaged by the SCM; on the other hand, both humans and other primates do indeed take longer to choose when the alternatives have smaller differences in value (Birnbaum & Jou, 1990; Dashiell, 1937; Henri-Bhargava et al., 2012; Oud et al., 2016; Padoa-Schioppa et al., 2006; Robles et al, 2011; Robles & Vargas, 2007). The reasons for these apparent inconsistencies have yet to be unraveled.

Chapter III: Time, uncertainty, and suboptimal choice

Abstract

In some concurrent-chain schedules, pigeons prefer the initial link option that is followed by informative terminal-link stimuli over the initial-link option that is followed by uninformative terminal-link stimuli even when the latter offers a higher overall rate of reinforcement. In the former, the terminal stimuli immediately disambiguate the delayed trial outcome, say S^G for reinforcement and S^R for non-reinforcement; in the later, the terminal stimuli, say S^B and S^Y, remain ambiguous about the delayed trial outcome. In two experiments, we studied the effect of deferring the moment at which the terminal stimuli disambiguate the trial outcome on the informative option. In Experiment 1, S^G was always presented when the informative option was chosen. On 20% of these trials, S^G remained on throughout the delay and the trial ended with reinforcement; on the remaining 80% of these trials, S^G changed to S^R after t_s sec and the trial ended with no reinforcement. Parameter t_s varied across conditions from 0 to10 sec. In Experiment 2, the complementary manipulation occurred: When the informative option was chosen, S^R was initially shown; on 80% of these trials it remained on throughout the delay and ended with no reinforcement; on the remaining 20% of these trials, S^R changed to S^G after t_s sec and the trial ended with reinforcement. In both experiments, preference for the informative option decreased with t_s, but the effect was sharper in Experiment 1. A modified version of the Δ-Σ hypothesis (González et al., 2020) accounted well for our findings.

Introduction

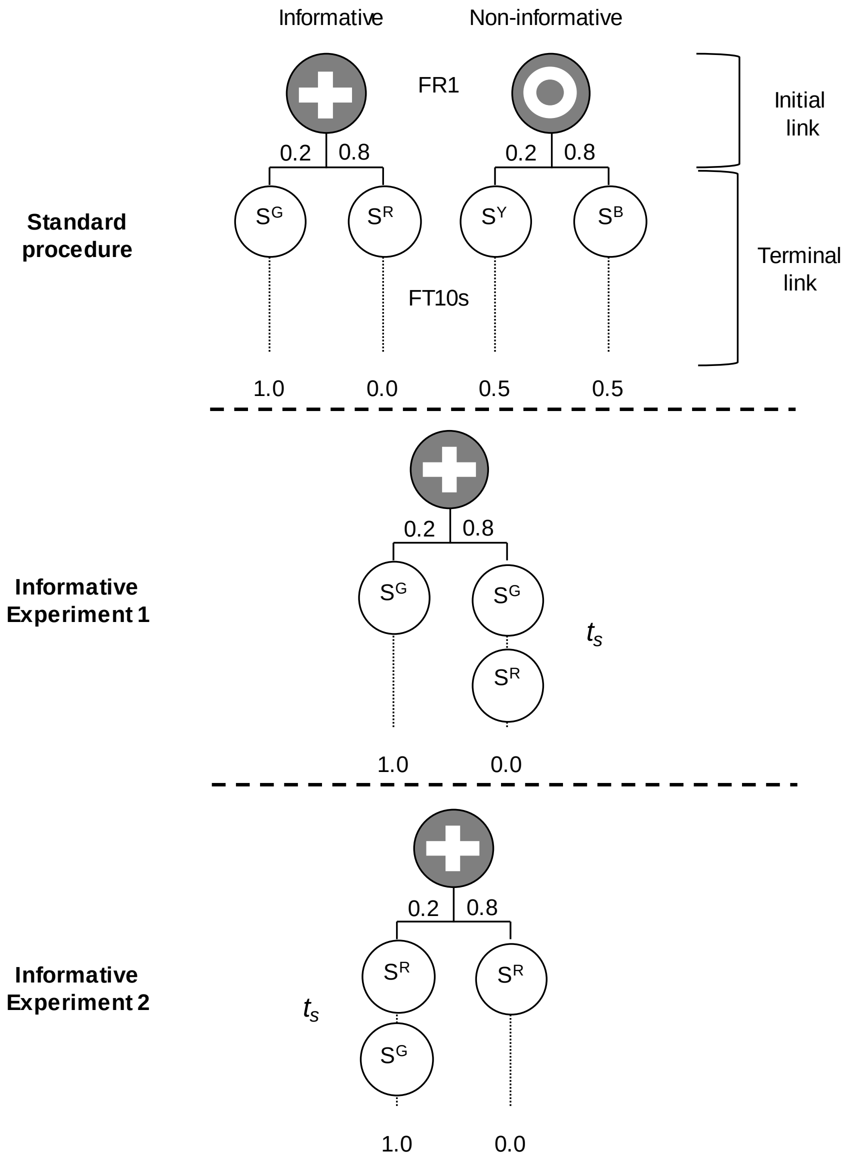
In uncertain environments, animals should value any sign that disambiguates the outcome of their foraging bouts. Why pursue a prey when it is clear it will escape? This premise has been studied systematically in the laboratory using a discrete-choice procedure commonly known as the suboptimal choice task (Stagner & Zentall, 2010). The interesting feature of this procedure is that animals do appear to attend to the signaling properties of stimuli but to the extent that they forego food in order to be informed about the forthcoming trial outcome. The top panel of Figure 1 shows a schematic of the typical procedure: In a concurrent-chain schedule, pigeons choose between two alternative keys (cross and circle as initial-link stimuli) leading to differential and probabilistic outcomes. Choosing one option (cross in the figure) leads to informative terminal-link stimuli, in the sense that one stimulus, typically the color of the key (e.g. Green, S^G), is always followed by reinforcement after a d = 10 sec delay and another stimulus (e.g. Red, S^R) is never followed by reinforcement after the same delay. Choosing the other option (plus in the figure) leads also to one of two terminal-link stimuli (Blue, S^B or Yellow, S^Y) but in this case they are both non-informative in the sense that neither reliably indicates whether reinforcement will be delivered after the same d = 10 sec delay; each is followed by reinforcement on 50% of the trials. We refer to these two options as *informative* and *non-informative*, respectively.

When the stimulus followed by reinforcement in the informative option (S^G in Figure 1) appears on 20% of the occasions (and therefore the other stimulus, S^R, appears on the remaining 80%), the informative option yields 2.5 times less reinforcement than the non-informative option. Yet, after minimal training, pigeons, starlings and sometimes rats develop a strong preference for the informative option (Cunningham & Shahan, 2019; Fortes et al., 2017, 2018; González et al., 2020; Ojeda et al., 2018; Smith et al., 2016; Stagner et al., 2012; Stagner & Zentall, 2010; Vasconcelos et al., 2015; Zentall, 2015; Zentall & Stagner, 2011).

The analysis of such paradoxical preferences generated an intense empirical effort (Cunningham & Shahan, 2018; Daniels & Sanabria, 2018; M. A. McDevitt et al., 2016; Vasconcelos et al., 2018; Zentall, 2016). Yet, the issue remains controversial.

Figure 1

Suboptimal choice procedure and Informative option in Experiment 1 and 2



Note. Top: The prototypical Suboptimal Choice procedure. Middle: Informative option in Experiment 1. Bottom: Informative option in Experiment 2. FR 1 = fixed ratio 1; FT 10 s = fixed time 10 s.

The search for the ultimate and proximate causes of such suboptimal preferences converged on the asymmetry in the *predictive value* of the terminal stimuli (S^G, S^R, S^B, and S^Y): both terminal stimuli of the informative option (S^G and S^R) disambiguate the trial outcome upon presentation, whereas the terminal stimuli of the non-informative option (S^B and S^Y) do not, maintaining uncertainty about the outcome until the trial ends. Consider Vasconcelos and colleagues functional account based on evolutionary theory (e.g., Fortes et al., 2017, 2018; Fortes, Vasconcelos, & Machado, 2016; Vasconcelos et al., 2015; for a review, see Vasconcelos, Machado, & Pandeirada, 2018). Using the formalism of classical foraging theory (Stephens & Krebs, 1986), the authors proposed that natural selection ought to favor a preference for informative cues provided that the information is usable and indeed used to maximize inclusive fitness. The argument is that under natural circumstances any information can be used to modulate behavior; for instance, an animal will actively pursue a prey if the available cues indicate some probability of success, but it will disengage if that probability drops do zero. In other words, the animal pays the energetic and temporal costs of chasing (the opportunity cost) when the cues indicate some possibility of success, but not when they indicate certain failure. This strategy will, on the long run, maximize the profitability of its foraging cycles. Yet, in the artificial laboratory preparation depicted in the top panel of Figure 1, this strategy will backfire. Here, the information afforded by choice cannot be used to adjust behavior: the animal is forced to endure all the waiting times (i.e., to pay the opportunity cost), including those leading to certain failure (i.e., when S^R is shown). Although the animal learns the contingencies associated with each stimulus, it does not change its preference for the suboptimal option because natural settings do not usually contain informative but unusable stimuli. In other words, given an informative stimulus (e.g. the prey will not be caught), the predator never experiences the opportunity cost of being unable to initiate another foraging bout. Thus, the paradoxical choice behavior in the experimental condition (domain of testing) reflects what the animal would normally do under natural circumstances (domain of selection) (Stevens & Stephens, 2010) The animal behaves as if information were usable, when the peculiarity of the experimental task makes it unusable.

The question of how animals choose here and now —the mechanism— led many authors to suggest that suboptimal choice is an effect of the differential conditioned reinforcement value of the terminal stimuli (Case & Zentall, 2018; Cunningham & Shahan, 2019; Dunn & Spetch, 1990; M. McDevitt et al., 1997; Pisklak et al., 2015; Smith et al., 2016; Smith & Zentall, 2016; Spetch et al., 1990; Zentall et al., 2015). According to this perspective, S^G, the terminal stimulus reliably signaling reinforcement, acquires conditioned reinforcing properties due to its predictive relation with food, and it apparently drives preference for the informative option. Yet, why this conditioned reinforcer overrides the possible weight on choice of S^R, the terminal stimulus that reliably signals the absence of food remains an unresolved topic (Cunningham & Shahan, 2019; Daniels & Sanabria, 2018; Laude et al., 2014; Smith et al., 2016; Trujano et al., 2016).

Regardless of how such differential conditioned reinforcing properties may drive preference (see, for example, Cunningham & Shahan, 2018; Daniels & Sanabria, 2018; McDevitt et al., 2016; Roper & Zentall, 1999), the role of the terminal stimuli predictive value is testable and the evidence of its importance has been mounting. For instance, preference for the informative, yet suboptimal option ought to decrease if its terminal stimuli become less reliable predictors of the outcome. When Stagner et al. (2012) set the probability of reinforcement following S^G and S^R to .2, a change that maintained the overall rate of reinforcement on this option as in the original task, pigeons reversed their preference. When these two probabilities were set to .5, thus equalizing the overall probability of reinforcement with each option, pigeons became indifferent between them (Smith & Zentall, 2016). Finally, González et al. (2020) degraded the reliability of the informative option terminal stimuli while maintaining the overall probability of reinforcement of each option (the probabilities of reinforcement following S^G and S^R were set at .75 and.25, respectively) and still found a reliable, though weaker, preference for the informative option (roughly 70%). To summarize, when the non-informative option remains unchanged, preference for the informative option can vary widely depending on the probabilities of reinforcement associated with S^G and S^R. This supports the notion that the predictive value of the terminal stimuli plays a pivotal role in choice.

In the two experiments reported below, we further explored the role of such predictability but focused not on the probabilities of reinforcement associated with S^G and S^R but on the moment when such stimuli disambiguate the trial outcome. In the typical task, the onset of either S^G or S^R signals immediately the outcome and eliminates uncertainty for the entire duration of the terminal link. Here, we explore the effect of increasing the time under uncertainty once the terminal stimuli are presented. To clarify, consider the modification of the informative option in our first experiment (see middle panel of Figure 1): When the animal chooses the informative option, it always sees S^G. On 80% of the trials, S^G remains present up to t_s sec into the terminal link delay, then it is turned off and S^R is presented for the remaining $10 - t_s$ sec, after which the trial ends without food; on the remaining 20% of the trials, S^G remains throughout the 10-s delay and is then followed by food. This procedural change implies that the terminal link remains uninformative up to t_s sec, at which time it is either s replaced by S^R or it remains on, thus disambiguating the trial outcome, non-reinforcement or reinforcement, respectively. In our second experiment, we implemented the complementary manipulation (bottom panel of Figure 1): When the animal chooses the informative option, it always sees S^R. On 20% of the trials, the S^R stays on up to t_s sec into the terminal link delay, then it is turned off, S^G is presented for the remaining $10 - t_s$ sec, and it is then followed by food; on the remaining 80% of the trials, the S^R remains throughout the 10-s delay and the trial ends without food. Thus, the terminal link also remains uninformative up to t_s sec, at which time either S^G replaces S^R and signals food, or S^R remains on and signals no food. In both experiments, the non-informative option remained unchanged.

We examined the effect of these two manipulations by varying *S* across conditions. When $t_s = 0$ sec, the task corresponds to the prototypical suboptimal choice procedure, with each terminal stimulus signaling food or no-food immediately upon choice of the informative option. When $t_s = 10$ sec, only one partially reinforced stimulus was presented on every trial. We predict that preference for the informative option ought to decrease monotonically with t_s—the longer the t_s, the longer the trial outcome remains uncertain, and therefore the lower the preference for the informative option ought to be.

To conceptualize the foregoing reasoning, we assume that the initial link persists until the disambiguating event, t_s sec into the delay. Hence, increasing t_s should be functionally similar to increasing the initial link duration of the option. Prior findings about the effects of the initial- and terminal links duration seem to support our conceptualization. Preference for the informative option increases with the terminal link delay, *d* (e.g., Kendall, 1985; Spetch et al., 1994, Spetch et al., 1990), but the effect appears to depend on the initial link duration: longer initial links tend to decrease suboptimal choice. For example, Spetch et al., (1990) found that pigeons showed a low preference for the informative option when terminal-link durations were relatively short (i.e., 5 to 10 s) but increased their preference when the terminal-link durations were longer (i.e. 30 s, 50 s, and 90 s). On the other hand, Dunn and Spetch (1990) found that pigeons preferred the informative option when the initial link was short, but decreased their preference with longer initial-link durations. Overall, preference for the informative option appears to hinge upon short initial-link durations and relatively long-term durations (McDevitt et al., 2016; Spetch et al., 1994; for a review, see Cunningham & Shahan, 2018).

To guide our analyses, at least at an ordinal level, we resorted to a modified version of the recently proposed Δ - ∑ hypothesis (González et al., 2020). According to this hypothesis, two higher-order variables drive preference in the task, Δ and ∑. The first, Δ, is intimately related to the signaling properties of the terminal stimuli; it corresponds to the difference between the two reinforcement probabilities associated with the terminal-link stimuli of each option. In the standard task (see top panel of Figure 1), Δ = 1 – 0 = 1 for the informative option, and Δ = .5 - .5 = 0 for the non-informative option. The assumption is that the value of each option varies directly with delta. On the other hand, ∑ corresponds to the overall probability of reinforcement of an option. In the standard task, ∑ = .2 x 1 + .8 x 0 = .2 in the informative option and ∑ = .2 x .5 + .8 x .5 = .5 in the non-informative option. Again, the assumption is that the value of each option varies directly with ∑.

According to the hypothesis, the value of option *i* is given by

$$V_i = (\Sigma_i)^c * e^{\beta * \Delta_i}, \qquad \text{(Eq. 1)}$$

with the parameters *c* and β both > 0. Using Luce's ratio rule, preference for the informative option is given by

$$P_{info} = \frac{V_{info}}{V_{info}+V_{noninfo}} \qquad \text{(Eq. 2)}$$

By substituting Eq. 1 into Eq. 2 and simplifying we obtain

$$= \frac{1}{1+\left(\frac{\Sigma_{noninfo}}{\Sigma_{info}}\right)^{c} e^{-\beta\left(\Delta_{info}-\Delta_{noninfo}\right)}}. \qquad \text{(Eq. 3)}$$

Thus, preference for the informative option increases with the difference between the Δ's and with the ratio between the ∑'s. Equation 3 integrates most of the ingredients of the suboptimal-choice task: the probabilities of entering each of the four terminal stimuli and the probability of reinforcement associated with each of the latter. Conspicuously absent from the equation are the initial- and terminal-link durations, which are paramount in our manipulations.

To overcome this limitation, we advance a modified version of the Δ-∑ hypothesis sensitive to both the initial- and terminal-link durations, d_{IL} and d_{TL} respectively. Our proposal is that the $d_{\mathrm{TL}}/d_{\mathrm{IL}}$ ratio modulates the effect of Δ, with greater ratios magnifying the effects of Δ. Specifically, we propose that the value of alternative i is given by

$$V_i = (\Sigma_i)^c * e^{\beta * \left(\frac{d_{TL}}{d_{IL}}\right)^{\alpha} * \Delta_i}, \qquad \text{(Eq. 4)}$$

with parameters c, α, and $\beta > 0$. This new formulation implies that the effect on value of the difference in terminal-link reinforcement probabilities, Δ, is amplified by the relative time spent in the terminal and initial links. Using the same ratio rule, preference for the informative option is given by Equation 5.

$$P_{info} = \frac{1}{1+\left(\frac{\Sigma_{noninfo}}{\Sigma_{info}}\right)^{c} e^{-\left[\beta\left(\frac{d_{TL}}{d_{IL}}\right)^{\alpha}(\Delta_{info}) \quad -\beta\left(\frac{d_{TL}}{d_{IL}}\right)^{\alpha}(\Delta_{noninfo})\right]}} \qquad \text{(Eq. 5)}$$

When $\Delta_{\mathrm{noninfo}} = 0$, as in the present experiments, Eq. 5 simplifies to

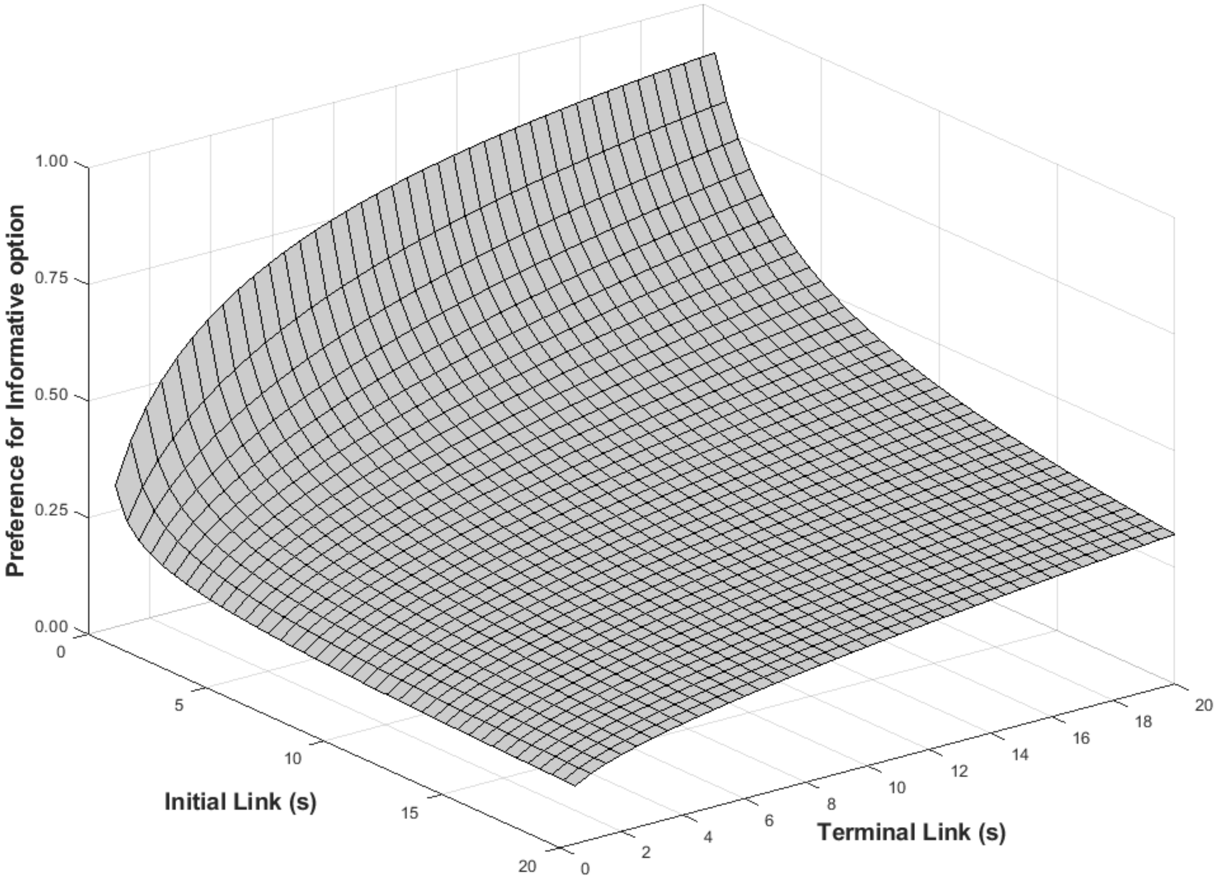
$$P_{info} = \frac{1}{1+\left(\frac{\Sigma_{noninfo}}{\Sigma_{info}}\right)^{c} e^{-\beta\left(\frac{d_{TL}}{d_{IL}}\right)^{\alpha} \Delta_{info}}} \qquad \text{(Eq. 6)}$$

where preference depends on the ratio of the Σs, the ratio of the terminal to initial link delays, and Δ_{info}.

Figure 2 illustrates how this modified version of Δ-∑ hypothesis captures the effect on choice of the link durations, for a particular set of parameters c, α, and β, when all other task ingredients remain as described in the top panel of Figure 1. Consistent with previous findings, preference for the informative option varies directly with the terminal-link duration and inversely with the initial-link duration.

Figure 2

Preference for the informative option as a function of the initial- and terminal-link durations according to the modified Δ-∑ *hypothesis.*



Note. The task parameters are as depicted in the top panel of Figure 1 except that the initial- and terminal-link durations were varied; c= 3.0, α = 0.25, β = 2.0.

Experiment 1 - Temporarily reducing the reliability of S^G

Experiment 1 explored the effect of temporarily reducing the reliability of S^G. Every trial with the informative option started with S^G, which could change to S^R after t_s sec into the terminal link delay. We hypothesize that the predictive value of the informative option should decline because the onset of S^G no longer signals the outcome immediately.

Method

Subjects

Seven pigeons (*Columba livia*), maintained between 80% and 85% of their free feeding weights, participated in the experiment. The pigeons had no experience with the present task. They were individually housed in a temperature-controlled room (around 21º C) on a 13:11 hour light/dark cycle (lights on at 8:00). Grit and water were always available in the home cage. The pigeons were cared for in accordance with the animal care guidelines of the Directorate-General for Food and Veterinary (DGAV), the Portuguese national authority for animal health, and the University of Minho. All experimental procedures were conducted in agreement with European (Directive 2010/63/EU) and Portuguese law (Ordinance 1005/92 of October 23), and were approved by DGAV (Authorization #024946).

Apparatus

Three Med Associates® operant boxes were used. The boxes were 28.5 cm high, 24 cm long, and 30 cm wide. The response panel had three centrally aligned circular keys, each with a 2.5 cm diameter. The keys were located 21 cm above the floor grid, with the side keys 6 cm apart from the center key. The grain hopper opening (5 cm high x 6 cm wide) was located below the central key, 4 cm above the floor. When activated, the food hopper opening was illuminated with a 1.1-W light. On the opposite wall, a houselight (2.8 W), centrally located 23 cm above the floor, illuminated the entire chamber. Each chamber was enclosed by a sound-attenuating box, equipped with a fan to mask outside noises. A personal computer controlled all three boxes. The events were controlled, and the data recorded using ABET II software (Lafayette Instruments).

Procedure

Pretraining. First, pigeons were trained on different fixed-ratio (FR) schedules with the six stimuli used in the experiment: red, green, yellow, blue, plus and circle. Each stimulus was presented randomly four times on each side key (left or right) for a total of 48 trials in one session. Once the FR schedule was completed, the pecked key turned off and the feeder was raised for 3 to 5 sec (adjusted individually to maintain the bodyweight stable). Food delivery was followed by a 10-sec Inter-Trial-Interval (ITI) with only the houselight on. The houselight was turned off for a new trial. Pigeons were exposed to two sessions with a FR1 schedule and one session with a FR5 schedule on the first half and a FR10 schedule on the second half.

Training. After pretraining, each pigeon went through four different conditions, each with a different t_s. Each condition was in effect for a minimum of 12 sessions and continued until stability was reached. Stability was assumed when: (a) there was no increasing or decreasing trend in the proportion of choices for the informative option in the preceding three sessions (i.e., three increasing or decreasing values), and (b) the difference between the highest and lowest preference in the preceding three sessions was at most 10%.

Each session comprised 120 trials, 40 choice and 80 forced trials. Choice trials started with the simultaneous illumination of the left and right keys with a symbol (Cross and Circle), with side counterbalanced across trials. A single peck on any of the side-keys turned the other key light off and initiated the terminal link of the chosen key. If the Non-informative option was chosen, one of the terminal stimuli S^Y or S^B was shown, 20% and 80% of the times, respectively. Once 10 sec elapsed in the presence of the terminal stimulus, the key turned off and food was presented with a probability of .5. If, on the other hand, the informative option was chosen, S^G was presented for t_s s; on 20% of these trials, S^G remained on for the remaining 10 - t_s sec, after which it was turned off and food was delivered; on the remaining 80% of these trials, the S^G was turned off at t_s sec and S^R was presented for the remaining 10 - t_s sec. After the 10 - t_s sec elapsed, S^R was turned off and the trial ended without food.

Forced trials had the same structure as choice trials, except that only one of the options was available. They were pseudorandomly distributed such that 40 occurred on the left- and 40 on the right-key. Symbols (cross and circle) and colors (green, red, blue, and yellow) were counterbalanced across pigeons, with the constraint that red and green were jointly assigned to one option and blue and yellow were jointly assigned to the other. The houselight was on during the 10-sec ITI and off during the trials. Responses to the terminal stimuli were recorded in 250 msec bins.

Each pigeon experienced eight t_s values across conditions. Table 1 shows the order of training for each pigeon. All pigeons started with $t_s = 0$ (baseline), which corresponds to the standard procedure depicted in the top panel of Figure 1. Next, they all experienced $t_s = 5$ sec followed by $t_s = 1.5$ and 8.5 sec in a counterbalanced manner. After a return to baseline, they all experienced $t_s = 3.25$ s followed by $t_s = 0.75$ and 6.75 sec in a counterbalanced manner. Finally, they all experienced $t_s = 10$ sec, which means that only the S^G was shown during the terminal link of the informative option and reinforcement occurred on a random 20% of the trials.

Table 1

Order of training of each pigeon in Experiments 1 and 2

	Pigeon	**t_s (sec)**								
Experiment 1	088 230 547	0	5	8.5	1.5	0	3.25	0.75	6.75	10
	501 935 G29 958	0	5	1.5	8.5	0	3.25	6.75	0.75	10
Experiment 2	452 G37 G47	0	5	8.5	1.5	0	3.25	0.75	6.75	10
	123 709 974	0	5	1.5	8.5	0	3.25	6.75	0.75	10

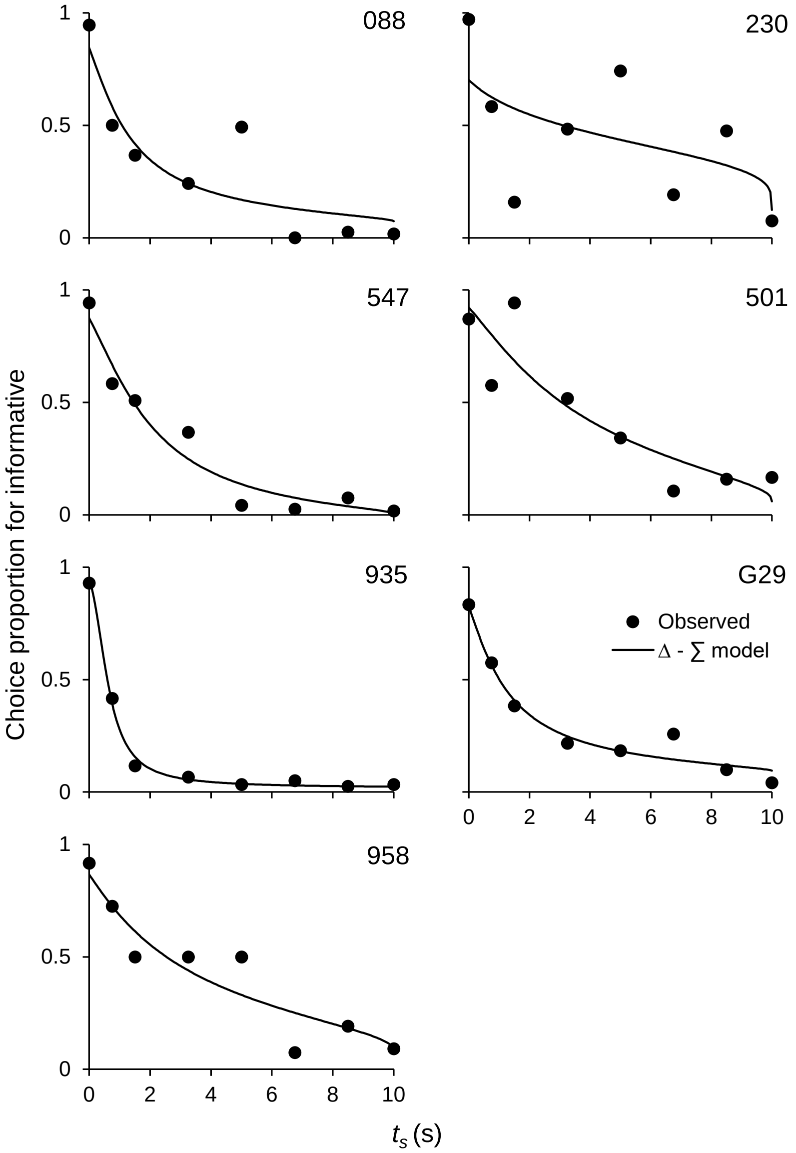
Results and Discussion

We analyzed the proportion of choices for the informative option during the last three sessions of each t_s value. We also analyzed the response rate during the terminal link duration to explore how animals adapted to the uncertainty period.

The symbols in Figure 3 show the individual proportion of choices for the informative option as a function of t_s. A preliminary paired samples *t*-test revealed that preferences in the two conditions with $t_s = 0$ did not differ significantly, $t(6) = -.603$, $p = .569$, 95% CI for the difference in mean proportions [-.169, .102], hence we averaged them into one condition for all figures and subsequent analyses, except for the rank-order correlations. Consistent with previous findings, when $t_s = 0$ sec, pigeons strongly preferred the informative, yet suboptimal option. This preference for the informative option decreased with t_s. In fact, preference showed a sharp and immediate decrease when $t_s > 0$ sec. Despite some variability between and within subjects (e.g. pigeon 230), the decreasing trend was statistically significant for every bird as revealed by Spearman's rank-order correlations, weakest correlation $r_s(7) = -.745$, $p = .021$ for pigeon 230, r_s range across pigeons: -.745 to -.946. Planned comparisons showed that averaged preference for the informative option was significantly above chance only when $t_s = 0$ s, $t(6) = 23.088$, $p < .001$, $d = 8.726$, 95% CI [.871, .960] and dropped significantly below chance when $t_s \geq 6.75$, largest $t(6) = -5.920$, $p = .001$, $d = -2.238$, 95% CI [.005, .295] when $t_s = 8.5$ s.

Figure 3

Choice proportion for the informative option in Experiment 1



Note. Individual proportion of choices for the informative option during the last three sessions of each t_s value in Experiment 1. The black dots show the observed data and the solid lines shows the best-fitting predictions of the Δ-Σ model

The solid lines in Figure 3 show the individual fits of the modified Δ-Σ hypothesis to each pigeon's preference data. To generate the predictions, we assumed that d_{TL}/d_{IL} in Equation 6 corresponded to the ratio of time under certainty to the time under uncertainty per trial and that pigeons took about 1 s to respond to the initial stimulus. Thus, for every t_s value, $d_{TL}/d_{IL} = (10 - t_s)/(1 + t_s)$. Table 2 shows the least-squares best fitting parameters and R^2 for each pigeon. The individual fits accounted well for the preference for the informative option for all but one pigeon, 230. This was somehow expected because this bird's preference was highly variable across t_s.

Table 2

Best fitting parameters and R^2 for the Δ-$\sum$ hypothesis in Experiments 1 and 2

Experiment 1					Experiment 2				
Pigeon	**c**	**β**	**α**	***R^2***	**Pigeon**	**c**	**β**	**α**	***R^2***
088	2.752	1.039	0.609	0.801	123	12.739	12.042	0.059	0.746
230	2.139	1.766	0.202	0.396	452	0.300	0.691	1.275	0.984
547	5.984	3.833	0.287	0.952	709	2.393	3.086	0.025	0.673
501	2.995	2.261	0.363	0.797	724	1.534	3.152	0.233	0.914
935	4.049	0.530	1.096	0.996	G37	0.114	0.127	1.119	0.735
G29	2.464	0.849	0.652	0.964	G47	1.239	0.000	7.100	0.905
958	2.674	1.865	0.365	0.876					

Finally, we analyzed response rate during the terminal links. Figure 4 shows the average response rate at the terminal stimuli of the informative option separately for each t_s value. One pigeon (230) was excluded from this analysis because it barely responded during the 10-s terminal link[1]. Prior to t_s (left of the vertical dotted line), pigeons showed a similar pecking rate to S^G regardless of whether that would be a reinforced trial or not. There was also an incremental trend as the programmed t_s impended, with the peak accompanying the rightward displacement of t_s across conditions. After t_s, pigeons continued pecking when S^G

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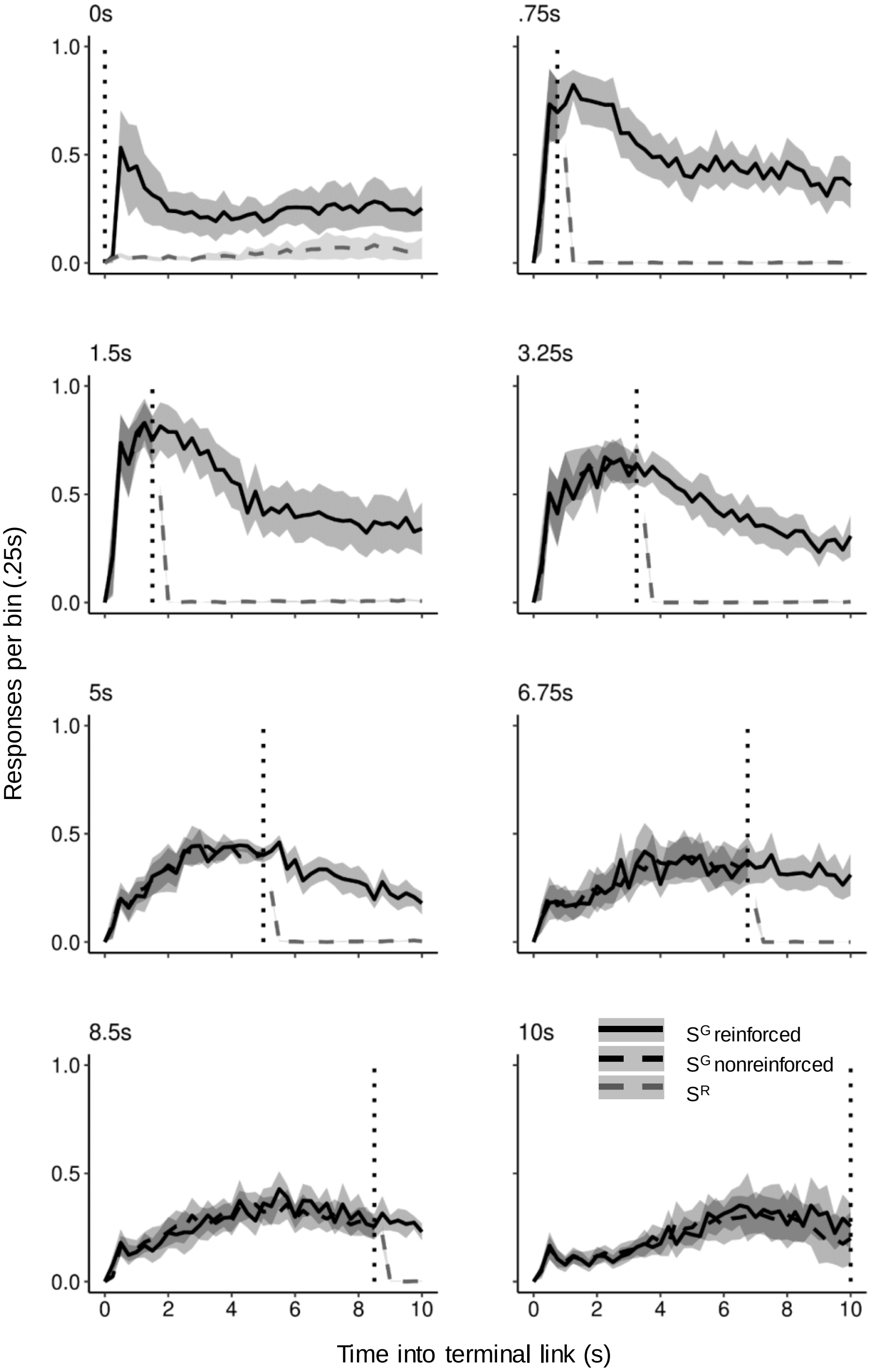
[1] For pigeon 230, the average total responses to S^G throughout the terminal link in both baselines conditions was 1.8 compared to an average of 10.3 for the rest of the pigeons.

remained, thus signaling certain reinforcement (see black-solid line to the right of the vertical dotted line) but completely ceased pecking when the stimulus changed to S^R, which signaled certain non-reinforcement (see grey-dashed line to the right of the vertical dotted line). The only exception to this trend occurred when $t_s = 0$: pigeons did peck at S^R, though infrequently. Overall, the data show that pigeons pecked at S^G but refrained from pecking at S^R. The rightward displacement of the peak-rate with t_s as well as the broadening of the rage curve suggests pigeons were sensitive to the particular t_s in effect and that they may have been timing in anticipation of the potential stimulus change. This result gives plausibility to our assumption that the functional initial- and terminal links can be construed as the time under uncertainty and the time under certainty, respectively.

Figure 4

Average response rate during the terminal stimuli of the informative option in Experiment 1



Note. The black-solid line corresponds to the rate during the S^G on reinforced trials; the black-dashed line present the rate during the S^G in non-reinforced trials; the grey-dashed line corresponds to the rate during the S^R. The vertical dotted line represents the programmed t_S. The shaded areas around each line are the Standard Error of the Mean. Data are from the last three sessions of each condition.

In summary, relative to the standard situation (i.e., $t_s = 0$), preference for the informative option declined when S^G did not predict the outcome immediately upon presentation (i.e., when $t_s > 0$). This decrease tended to follow t_s. The modified version of the Δ-∑ hypothesis with the d_{TL}/d_{IL} extra term captured well the trends of the individual findings. The response rate at the informative option terminal stimuli lends some support to the notion that the functional initial-and terminal-links may have been not the nominal stimuli, but the pigeons' state during each trial: uncertain vs. certain.

Experiment 2 - Temporarily reducing the reliability of S^R

Experiment 2 examined the effect of temporarily reducing the reliability of S^R. Every trial with the informative option started with S^R, which could change to S^G after t_s sec into the terminal link delay. As for Experiment 1, we hypothesize that the predictive value of the informative option should decline because the onset of S^R no longer signals the outcome immediately.

Method

Subjects and Apparatus

Seven pigeons kept under the same conditions as in Experiment 1 participated. The pigeons had no experience with the present task. The same operant boxes described for Experiment 1 were used. One pigeon was removed from the experiment because it acquired an idiosyncratic preference for the right key.

Procedure

Pigeons faced the modified version of the task depicted in the bottom panel of Figure 1. As in Experiment 1, the non-informative option remained unchanged. When pigeons pecked the initial link of the informative option, S^R was shown on every trial (except when t_s

= 0). On 80% of the occasions, S^R remained on for the entire 10-sec delay, after which it was turned off and the trial ended without food. On the remaining 20% of these trials, the S^R was turned off once t_s sec had elapsed, S^G was then presented for the remaining 10 - t_s sec, and the trial ended with food.

All other details, including pretraining, t_s values, and the order of training were as described for Experiment 1. Table 1 shows the order of training for each pigeon.

Results and Discussion

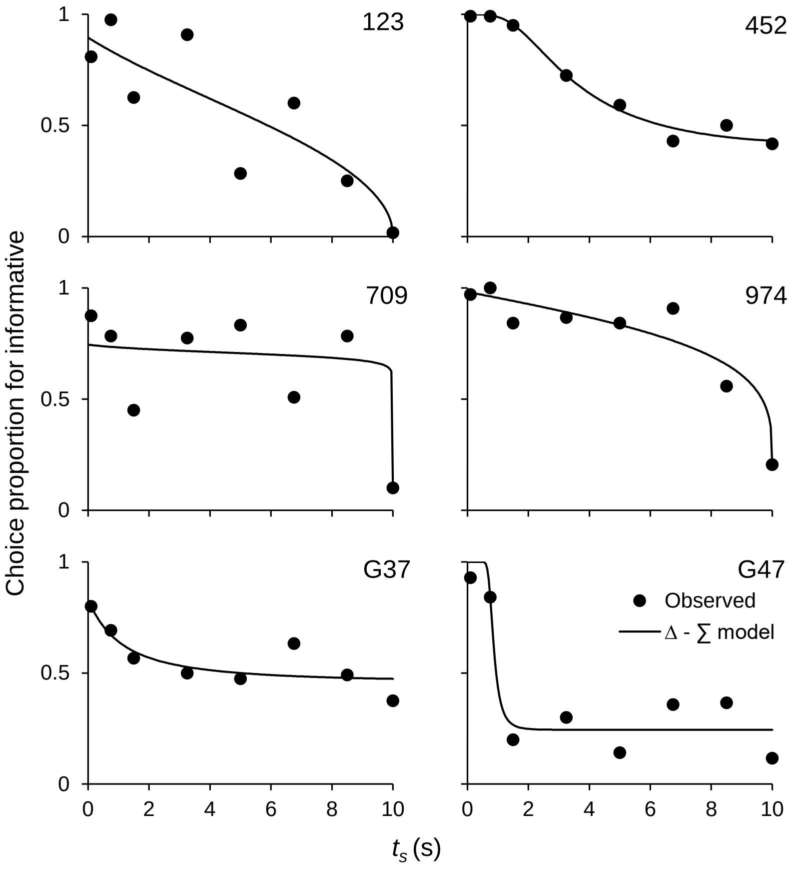
As in Experiment 1, we analyzed the proportion of choices for the informative option and response rate during the terminal link delay across the last three sessions of each condition. Preference in the two conditions with $t_s = 0$ did not differ significantly, $t(5) = -.444$, $p = .675$, 95% CI [-.057, .040] and again we averaged them for all figures and subsequent analyses, except for the rank-order correlations.

The symbols in Figure 5 show the individual proportion of choices for the informative option as a function of t_s. As in Experiment 1, when $t_s = 0$, pigeons showed a strong preference for the informative option, thus replicating the typical findings. Preference for the informative option tended to decrease with t_s, even though the effect was not as consistent as in Experiment 1. For example, the decrement showed higher variability across pigeons. Pigeons 123 and G47 reversed their preference towards the non-informative option, but in a different fashion. Pigeon 123 showed an unstable but decreasing trend, while G47 abruptly reversed preference when $t_s \geq 1.5$ sec. On the other hand, pigeons 452, G37, 709, and 974 never reversed their preference when $t_s < 10$ sec; pigeons 452 and G37 remained indifferent between the options even when $t_s = 10$ sec. Finally, pigeons 709 and 974 maintained a strong preference for the informative option even when $t_s > 5$ sec. Spearman’s rank-order correlations between preference and t_s values indicated that the trend decreasing tend was significant for five of the pigeons, weakest

significant correlation $r_s(7) = -.711$, $p = .032$; only pigeon 709 revealed was non-significant, though decreasing trend, $r_s(7) = -.620$, $p = .075$. Planned comparisons showed that averaged preference remained significantly above chance when $t_s = 0$ and 0.75 s, smaller $t(5) = 7.271$, $p < .001$, $d = 2.968$, 95% CI [.761, 1.030] and that it dropped significantly below chance only when $t_s = 10$ s, $t(5) = -4.517$, $p = .006$, $d = -1.844$, 95% CI [.037, .373].

Figure 5

Choice proportion for the informative option in Experiment 2



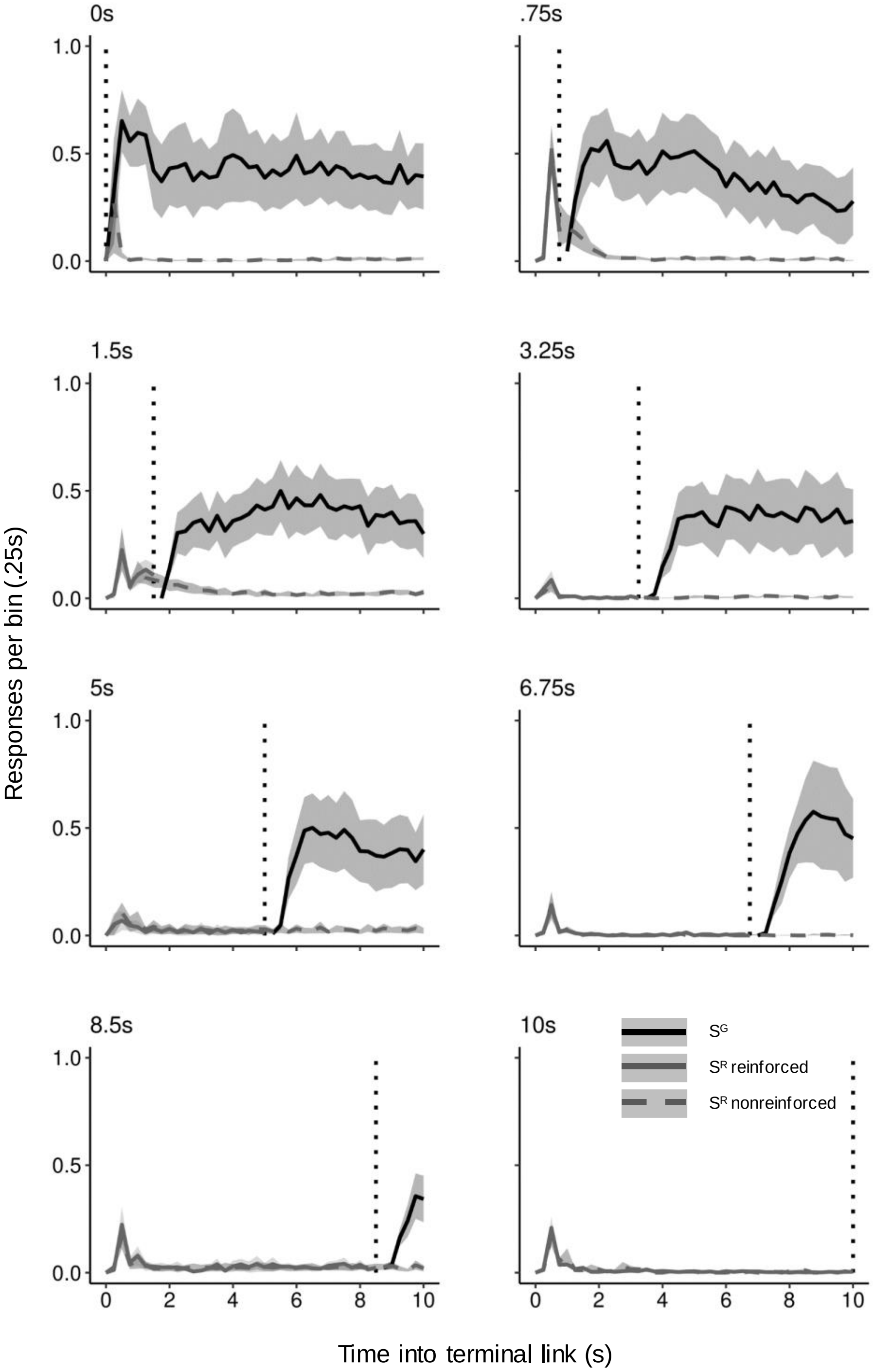
Note. Individual proportion of choices for the informative option during the last three sessions of each t_s value in Experiment 2. The black dots show the observed data and the solid lines shows the best-fitting predictions of the Δ-Σ model.

The solid lines in Figure 5 show the individual fits of the modified Δ-$\sum$ hypothesis to each pigeon's preference data. The best fitting parameters estimated by the least-squares method and R^2 for each pigeon are shown in Table 2. Despite the variability within and across pigeons, the model provided a good fit to most pigeons' preference.

Figure 6 shows the average response rate at the terminal link stimuli of the informative option separately for each t_s value. Responding was clearly modulated by the stimulus identity: Except for a few initial pecks at S^R, probably caused by response bouts aimed at the initial link, responding to S^R was mostly absent both before and after the corresponding t_s s elapsed (compare grey-solid to grey-dashed lines). When S^R switched to S^G at t_s s, the pigeons consistently pecked at S^G until the end of the trial (see black-solid line). No evidence of temporal modulation by the t_s was observed.

Figure 6

Average response rate during the terminal stimuli of the informative option in Experiment 1



Note. Average response rate during the terminal stimuli of the informative option in Experiment 2. The black-solid line corresponds to the rate during the S^G; the grey-solid line shows the rate during the S^R in reinforced trials; the grey-dashed line shows to the rate during the S^R in non-reinforced trials. The vertical dotted line represents the programmed t_S. The shaded areas around each line are the Standard Error of the Mean. Data are from the last three sessions of each condition.

In short, preference for the informative option declined with t_{s}, as predicted, but the decrease was not as pronounced as in Experiment 1. Even though the $d_{\mathrm{TL}}/d_{\mathrm{IL}}$ ratios were the same as in Experiment 1, some pigeons remained indifferent between the options when $t_s >$ 0.75 sec, reversing preference only when the informative option became completely non-informative (when t_s = 10 sec, only S^R appeared on every trial). Preference also showed greater variability both within and across pigeons. Overall, the modified Δ-∑ hypothesis was able to capture the main trends in the data.

General Discussion

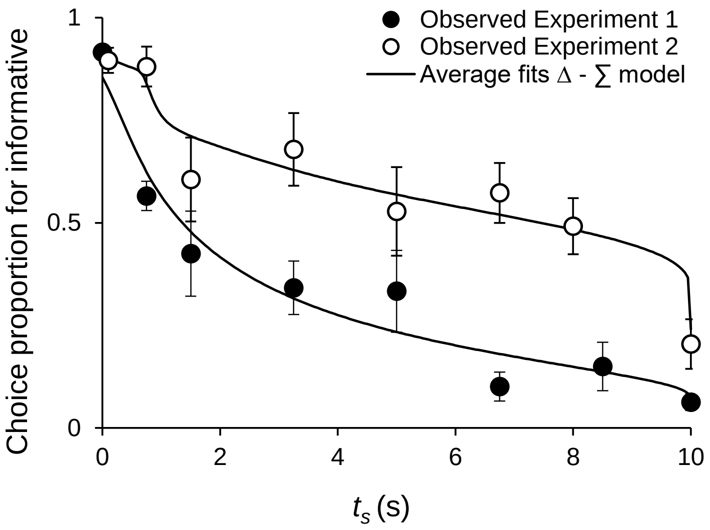
When offered a choice between an informative and a non-informative option, animals often prefer the former even when it yields less reinforcement (e.g., Fortes et al. 2016; Stagner & Zentall, 2010; Zentall & Stagner, 2011; Stagner et al., 2012; see Zentall, 2016; Vasconcelos et al., 2018 for reviews). In this study, we show that such paradoxical preferences seem to depend not only on the information conveyed by the terminal stimuli but also on when such information is conveyed. In two experiments, we showed that the informative but suboptimal option is preferred when it signals immediately whether or not food will be available, and that this preference decays the later into the terminal link delay that information is conveyed. We propose that the time under uncertainty and the time under certainty about the trial outcome play a key role in preference: Preference for the informative option increases with the latter and decreases with the former.

In Experiment 1, the nominal terminal link of the informative option always started with S^G. On 80% of the trials, after t_s s elapsed, S^G changed to S^R and the trial ended without food. On the remaining 20% of the trials, S^G remained on until the end of the trial and food ensued. Experiment 2 implemented the opposite arrangement: the terminal link started always with S^R that, on 20% of the trials, changed to S^G after t_s s and the trial ended with food; on the reaming 20% of the trials, the S^R remained on until the end of the trial which ended without food.

Our findings indicate that preference for the informative option declined as t_s increased independently of which 'terminal' stimulus was shown first (S^G in Experiment 1 and S^R in Experiment 2). Still, the effect of t_s seemed asymmetrical. Figure 7 shows how the average preference in Experiment 1 (black symbols) decreased sharply and reversed for the non-informative option, while in Experiment 2 (white symbols), the average preference decreased more smoothly and it never reversed, except when t_s = 10 sec, wherein only S^R was shown.

Figure 7

Average choice proportion for the informative option in Experiment 1 and 2



Note. Average proportion of choices for the informative option during the last three sessions of each t_s value in Experiment 1 (black symbols) and Experiment 2 (white symbols). The solid lines show the average of the best-fitting predictions of the Δ-Σ model across all pigeons. The error bars represent the standard error of the mean.

A direct between-experiment comparison is somewhat problematic given the variability observed in Experiment 2. Yet, some general points are noteworthy: First, the level of preference for the informative option when t_s = 0 sec (the typical suboptimal choice task) was comparable across experiments (M_{Exp1} = .914, SEM = .019 ; M_{Exp2} = .896, SEM = .036); second, when t_s = .75 sec, preference for the informative option abruptly dropped to indifference in Experiment 1 (M = .566, SEM = .038) while it remained strong in Experiment 2 (M = .881, SEM = .057), and; (3) when t_s = 8.5 sec, all but one pigeon (230) showed a strong preference for the non-informative option in Experiment 1(M = .150, SEM = .064) while choice remained close to indifference in Experiment 2 (M = .490, SEM = .081). A multiple regression analysis using experiment and t_s as predictors and the log-odds of preference as dependent variable returned and adjusted $R^2 \approx 1.0$. Importantly, the influence of both t_s and experiment was significant, with the log-odds of preference decreasing with increasing t_s ($\beta = -.922$) but increasing from Experiment 1 to Experiment 2 ($\beta = .388$). This confirms that preference for informative option was generally lower in Experiment 1 than in Experiment 2.

An asymmetry between the two manipulations may help us to explain these differences in preferences. Note that reinforced trials in Experiment 2, but not in Experiment 1, involved an exteroceptive stimulus change, from S^R to S^G; this implies that animals did not need to actively wait or time in the presence of S^R either before or after t_s. As such, increases in t_s may not have entailed an increase in the average time under uncertainty if the animals disengage from the task.

An analysis of the average time to reinforcement signaled by S^G may provide more evidence of the asymmetry embedded in the two versions of the task. Experiment 1, but not Experiment 2, entailed a higher cost of waiting in the presence of an ambiguous stimulus. Because, in Experiment 1, S^G continued to be the only stimulus that could be followed by food and assuming that animals always engaged with it, they paid the cost of waiting in its presence during the entire reinforced trials and a fraction (t_s) of the non-reinforced trials. Specifically, when $t_s = 0$, the onset of S^G informed that food would occur with certainty after

10 s; when $t_s > 0$, S^G informed that food would occur *on average* after longer delays (10 sec for the reinforced trial plus the time S^G was active in non-reinforced trials, all weighted by their respective probabilities). For example, when $t_s = 1.5$ sec, the average time to food once S^G was shown was 16 sec [(0.2 x 10 + 0.8 x 1.5) / .2], whereas this value climbed to 44 sec [(0.2 x 10 + 0.8 x 8.5) / .2] when $t_s = 8.5$ s. The differential patterns of response towards S^G and S^R and the time modulation of responses to S^G support this interpretation. This explains the decrease in value of the informative option with t_s and the consequent sharp decline in preference. Experiment 2, on the other hand, entailed a decrease in the average time to reinforcement signaled by S^G. Every time S^G showed up, it signaled 10 - t_s sec to food. Why these patterns generate a larger decline in preference in Experiment 1 than in Experiment 2 remains uncertain. Perhaps preference was also affected by the degree of unreliability introduced in the task. In Experiment 1, S^G became temporarily unreliable on 80% of the occasions because it was shown in every single trial and remained on past t_s only on 20% of them. Conversely, in Experiment 2, S^R became temporarily unreliable only on the 20 % of the trials where, at t_s, S^G was shown instead. Thus, even though the t_s values used in both experiments were the same, the change in reliability was larger in Experiment 1 than in Experiment 2.

Despite the difference in the preferences between Experiment 1 and 2 across the t_s value, the overall effect is that preference for the informative option decreased with t_s. Our hypothesis is that the times under uncertainty and certainty were in fact the functional initial and terminal links, respectively. The idea is encapsulated in the modified version of the Δ-$\sum$ hypothesis, where the d_{TL}/d_{IL} ratio modulates the effects of Δ. d_{IL} corresponds to the time under uncertainty and d_{TL} to the time under certainty. The modification is relevant because it incorporates the duration of states of certainty and uncertainty. In most of previous research, uncertainty has been immediately resolved in the informative option, while for the non-informative it has persisted until the end of the terminal link. Notable exceptions are a couple of experiments where the terminal link-duration on the non-informative option decreased systematically (reducing the time spent in uncertainty for that alternative). Preference for the informative option decreased with the terminal link duration on the non-informative option (Fortes et al., 2018; Zentall & Stagner, 2011). The manipulation made food closer to choice, which could have also affected preference, however these results already hinted at the effect of time spent in uncertainty. Similarly, when Vasconcelos et al. (2015) presented the terminal stimuli on the informative option at the end of the terminal link delay (right before the outcome), that is, increasing the uncertainty time for that option, starlings reversed their preference towards the non-informative option. In the present research, the overall time from choice to outcome remained constant through all conditions, preference changed only as a result of how the signaling conditions of the stimuli varied the time spend in certainty and uncertainty. Overall, the modified Δ-$\sum$ hypothesis captured well the decline in preference as the $d_{\mathrm{TL}}/d_{\mathrm{IL}}$ ratio decreased as well as the asymmetry between the experiments, with preference declining more steeply in Experiment 1 (see solid lines in Figure 7).

To conclude, the patterns of choice reported here are still another example of how suboptimal choice can be influenced by a complex set of ingredients. The predictive value of each option resulted from the signaling properties of the terminal stimuli. Systematic modifications to the temporal reliability of the stimuli on the informative option resulted in ordered changes. Preference for the informative option decreased with the ratio of time under certainty to time under uncertainty.

Chapter IV: Choice and signaled delays

Abstract

Pigeons prefer advanced information about delays to reward. In a concurrent chain procedure, pigeons chose between two alternatives leading with equal probability to a short or a long delay to food. For one of the options (*informative*), the short and long delays were reliably signaled by different stimuli (e.g. S^S for short delays, S^L for long delays). For the other option (*non-informative*), the delays were not reliably signaled by the stimuli presented (S3 and S4).

Pigeons preferred the informative over the non-informative option. More even, this preference varied with the ratio of the long to short delay. From a functional perspective, we argue this occurs because the value of information increases with more divergent delays as an animal could benefit more from avoiding known long delays. Mechanistically, we adapted the Δ-Σ hypothesis (González et al., 2020) to the current design. The adapted model suggests that preference for the informative option depends on a contrast-like process between the rate of food signaled by each stimulus. This version of the model accounted well for these results.

Introduction

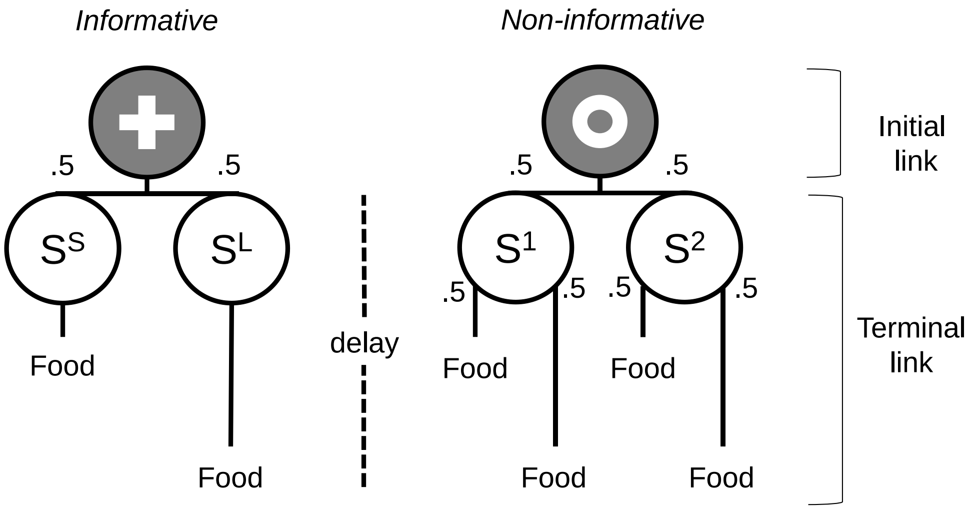
Foraging animals continuously face cues associated with different and often uncertain delays to food. In this temporally variable environment, anticipating the time to food provides an instrumental advantage to best exploit opportunities. In other words, information about *when* food will occur offers the chance to prepare for it or make better decisions about it (e.g., should I wait for it?). Therefore, we would expect animals to value alternatives with known delays to food more highly than alternatives with unknown delays.

This hypothesis has been previously studied in pigeons using the concurrent-chain procedure depicted in Figure 1. During the initial link, pigeons choose between two alternatives (cross vs. circle in the figure) that lead to mutually exclusive events in the terminal link. Both options lead to certain food, half of the trials after a short delay and the other half after a long delay. The difference between the options is that, in informative option (cross in the figure), the delays are perfectly correlated with the terminal stimuli whereas in the non-informative options (circle in the figure) the delays are not correlated with such stimuli. Briefly, in the informative option, the short and long delays occur only when a particular terminal stimulus is present, say green during the short delay (S^S) and red during the long delay (S^L). In the non-informative option, short and long delays are equally likely with each terminal stimulus, say yellow and blue (S^1 and S^2). Overall, both options yield the same rate of reinforcement, and choices have no effect on the obtained rate. Yet, pigeons prefer almost exclusively the signaled alternative (Bower et al., 1966; Frankel & Vom Saal, 1976). Even more surprising, pigeons continue to prefer the informative option when its average rate is worsened by making the long delay more frequent within this alternative (Bower et al., 1966). Similar results have been extensively reported in the behavior analysis literature as a preference for multiple schedules of reinforcement (different schedules, distinctively signaled) over mixed schedules (different schedules, undifferentiated) (Alsop &

Davison, 1986; Davison, 1972; Fantino, 1969; Hursh & Fantino, 1974; Richards, 1981).

Figure 1

Experimental task



Note. Pigeons choose between a cross (informative) and a circle (non-informative) keys during the initial link. Both options are followed either by a short or a long delay to food, each 50% of the time. In the informative option, the short and long delays are signaled by S^S and S^L, respectively. In the non-informative option, the delays are equally likely in the presence of S^1 and S2 (i.e., they are nor not signaled).

At first glance, there appears to be no functional reasons for these preferences. Even assuming that that natural selection has favored behavioral traits that maximize inclusive fitness, the reasons for these preferences remain elusive (Stephens & Krebs, 1986): why exhibit a preference when the rates of return are the same? Classical foraging theory, for instance, predicts indifference between the alternatives when the frequencies of short and long delays in each option are the same, because their long-term rate is the same (Charnov, 1976). The question of why animals show such a strong preference for information when it does not provide any improvement in energy intake or any evident instrumental leverage remains.

One possible explanation for this puzzle that has been addressed by several behavior-oriented fields is that information is reinforcing *per se*. For example, some authors propose that agents may attach *intrinsic* value to information about future outcomes independently of any instrumental purpose (Bennett et al., 2016; Eliaz & Schotter, 2007; Grant et al., 1998; Kreps & Porteus, 1978; Masatlioglu et al., 2016). Similarly, data from human studies suggest that the subjective value of non-instrumental information shares a common neural code with value for basic reward (Bromberg-Martin & Hikosaka, 2009; Kobayashi & Hsu, 2019). Although some of these explanations seem plausible, they still face the subsequent questions of why and how information became intrinsically valuable.

From an ecological perspective, one could argue that information may have instrumental value under natural circumstances, but that certain artificial conditions prevent the use of such information (Vasconcelos et al., 2015). The argument, initially applied to cues informing whether food would occur or not, hinges on the assumption that animals can use the information gathered to modulate their behavior: they can pursue a prey when facing a food-related cue or engage in a different behavior (e.g. search elsewhere) if the available cues indicate that food is not forthcoming. A similar case can be made for information about the delays to food: when facing a reliable cue about the delay to food, the animal can either accept the delay if reasonably short and wait or keep searching if it is too long. This is in fact the fundamental prediction of the marginal value theorem (Charnov, 1975; Parker & Stuart, 1976): animals should exploit a patch until the instantaneous rate gain reaches a marginal value, which is the mean rate of gain that can be achieved in all patches of the environment. The rate of reward in the non-informative option is about 1/[H(short,long)] rewards per second, where H is the harmonic mean (Bateson & Kacelnik, 1996). Thus, because only two delays are possible (short and long) the optimal policy would be for the animal to abandon the patch as soon as the delay exceed the short interval (assuming a reasonably short interval between trials). To implement such a policy the animal would have to estimate the time elapsed. In any case, it would always pay the opportunity cost equivalent to the short delay. Conversely, in the informative option, the animal can abandon the patch immediately after S^L is shown, thus avoiding most opportunity costs. Hence, the optimal decision strategy would be more profitable in the informative option because all unnecessary delays can be avoided.

Yet, when these scenarios are recreated in artificial laboratory conditions, the instrumental advantage of information is limited: the animal is forced to wait in the presence of all delays whether short or long. In other words, even though the foraging mechanisms may have been sculpted to gather and use information, the information gathered in the artificial laboratory preparation depicted in Figure 1 cannot be used —the domain of selection (the natural environment) mismatches the domain of testing (the experimental situation)— (Fortes et al., 2016; Stevens & Stephens, 2010). Since the distinction between domains is in the eye of the experimenter, we assume animals' behavior in the laboratory reflects the conditions where it evolved.

One implication of such a claim is that the putative value of the information provided by the cues depends on how different the delays are. To exemplify, imagine a forager facing an option that provides food, sometimes after a short delay, sometimes after a long one. Information about the length of the current delay ought to be more valuable when the possible delays are very dissimilar (e.g., 5 s and 20 s), than when they are similar (e.g., 10 s and 15 s) because dismissing long delays would have a greater impact on rate in the first scenario. Animals can avoid larger opportunity costs caused by long delays when the delays are more dissimilar.

To test whether preference for information about delays to reward depends on how different the possible delays are, we presented pigeons with two options, both leading to food after a short or a long delay with equal probability. The two alternatives differed only in that one had distinctive cues signaling the short and the long delays while the other had ambiguous cues (short and long delays were equally likely in their presence). Across conditions, defined as the ratio of the long to the short delay, we varied how different the delays were while keeping the overall rate of reinforcement constant across options. If the value of information about delays depends on the ratio of possible delays, we expect animals to prefer the informative option in all conditions, and this preference to vary positively with the long/short ratio.

Recently, we have advanced the Δ-Σ hypothesis (González et al., 2020) to explain preference in a procedure similar to the one depicted in Figure 1, except that the terminal stimuli of the informative option provide information about the probability of reinforcement, not delays. In such a procedure, animals prefer the informative option despite its lower rate of reward compared to the non-informative option (Fortes et al., 2016, 2017; Zentall, 2016). According to the Δ-Σ hypothesis, two higher-order drive preference in the task, Δ and ∑. ∑ corresponds to the overall probability of reinforcement of an option. The assumption is that the value of each option varies directly ∑. Δ, on the other hand, corresponds to the difference between the two reinforcement probabilities associated with the terminal stimuli of each option. Again, the assumption is that the value of each option varies directly with delta.

The issue with the task depicted in Figure 1 is that (1) ∑, the overall probability of reinforcement, equals 1.0 for both options and that (2) Δ, the difference in the probability of reinforcement with each terminal link of each option equals 0.0 for both alternatives. In other words, the options have equal ∑ and equal Δ, and thus the model predicts indifference for all conditions, independently of the long/short ratio. Thus, in case animals do prefer the informative option, we will be left with the question of how such a preference is implemented by the behaving organism. The two higher-variables proposed by the Δ-Σ model would have to be either re-defined to encompass delays or deemed insufficient to explain preference.

Method

Subjects

Seven pigeons (*Columba livia*), between 80% and 85% of their free feeding weights were used in this experiment. They were individually housed in a temperature-controlled room (around 21º C) on a 13:11 hour light/dark cycle (lights on at 8:00). Pigeons had previous experience with the suboptimal choice procedure described in (Fortes et al., 2016). Grit and water were always available in the home cage. The pigeons were cared according to the animal care guidelines of the Directorate-General for Food and Veterinary (DGAV), the Portuguese national authority for animal health, and the University of Minho. All experimental procedures were conducted in agreement with European (Directive 2010/63/EU) and Portuguese law (Ordinance 1005/92 of October 23), and were approved by DGAV (Authorization #024946).

Apparatus

Three Med Associates operant boxes for pigeons were used. The boxes were 28.5 cm high, 24 cm long, and 30 cm wide. The response panel had three centrally aligned keys; side keys were 6 cm apart from the center key. The circular keys of 2.5 cm in diameter were located 21 cm above the floor grid. The grain hopper opening (5 cm high x 6 cm wide) was located below the central key, 4 cm above the floor. When activated, the food hopper opening was illuminated with 1.1-W light. On the opposite wall, a houselight (2.8 W) was centrally located 23 cm above the floor, illuminating the entire box. Each box was enclosed in a sound-attenuating chamber, equipped with a fan to mask outside noise. A personal computer controlled all three boxes. The events were controlled, and the data recorded using ABET II software (Lafayette Instruments).

Procedure

Pretraining. Pigeons were initially trained on different Fixed Ratio (FR) schedules to eliminate any carryover from their previous experience with signaled probabilities. Each color (red, green, yellow, and blue) and symbol stimulus (cross and circle) was presented eight and four times per session, respectively. Color stimuli were shown always on the center key and the symbol stimuli were shown equi-probably on each side key. Once the FR schedule was completed, the pecked key turned off and the feeder was lifted for 3 to 5 seconds adjusted for each pigeon individually to maintain its body weight. Delivery of food was followed by a 10 s Inter-Trial Interval (ITI) with the houselight on. Each session comprised a total of 40 trials (8 with each color stimuli and 4 with each symbol). Pigeons were trained for two sessions with a FR1 schedule and for one further session with a FR5 schedule in effect on the first half of the session and a FR10 in the last half.

Experimental task. After pretraining, pigeons were trained in the procedure depicted in Figure 1. Each session comprised 96 trials: 32 choice trials and 64 forced trials. During the initial link of a choice trial, the left and right keys were illuminated with figures (Cross and Circle). A single response on either side key turned off the both keys and gave way to the corresponding terminal stimuli. The terminal delay to food in both alternatives was either short or long, 50% of the time each. When the informative option was chosen, short delays elapsed with the center key illuminated with one color stimulus (S^S) while long delays elapsed with the center key illuminated with a different color (S^L). When the non-informative option was chosen, short and long delays to food elapsed with the center key illuminated with one of two stimuli (S^1 or S^2), each on 50% of the occasions. Forced trials had the same structure as choice trials, except that only one of the alternatives was presented at trial outset. Forced trials was pseudo randomly distributed such that 16 trials with each option occurred on the left side-key and the remaining 16 on the right-side key. Choice trials were also pseudo randomly arranged such that the left vs. right location of the options was balanced. The time between the presentation of one or two options (circle and/or cross) and the peck at one of the side-keys corresponded to the latency to respond on each trial.

Each pigeon went through two baselines and three experimental conditions differing in the long and short delays. We refer to each condition using the long/short ratio. Table 1 shows the order of presentation for each pigeon. In the first and last condition (baseline 1 and baseline 2, respectively), all the delays to food were set at 12.5 sec (long/short ratio = 1.0). In the other conditions, the average delay was also 12.5 sec but the short and long delays are made progressively more dissimilar. The delays were 10and 15 sec (long/short ratio = 1.5), 7.5 and 17.5 sec (long/short ratio = 2.3), and 5 and 20 sec (long/short ratio = 4.0). All pigeons started and finished with the 1.0 ratio with the order of the remaining conditions was counterbalanced across pigeons. Each condition lasted for a minimum of 15 sessions and remained until stability was reached. Stability was assumed when: (a) there was no increasing or decreasing trend in preference during the last three sessions, and (b) the proportion of choice differed 15% or less between the highest and lowest value of the last three sessions. The figures in the initial links (cross and circle) and the color signals in the terminal links (green, red, blue, and yellow) were counterbalanced between across.

Table 1

Order of conditions for each pigeon

Pigeon	***1***	***2***	***3***	***4***	***5***
212		4.0	2.3	1.5	
283		1.5	2.3	4.0	
456		1.5	2.3	2.3	
595	1.0	2.3	1.5	4.0	1.0
860		4.0	2.3	1.5	
916		2.3	1.5	4.0	
1727		1.5	4.0	2.3	

Note. 1.0 (short=long=12.5 s), 1.5 (short=10 s; long= 15 s), 2.3 (short=7.5 s; long= 17.5 s), 4.0 (short=5 s; long= 20 s).

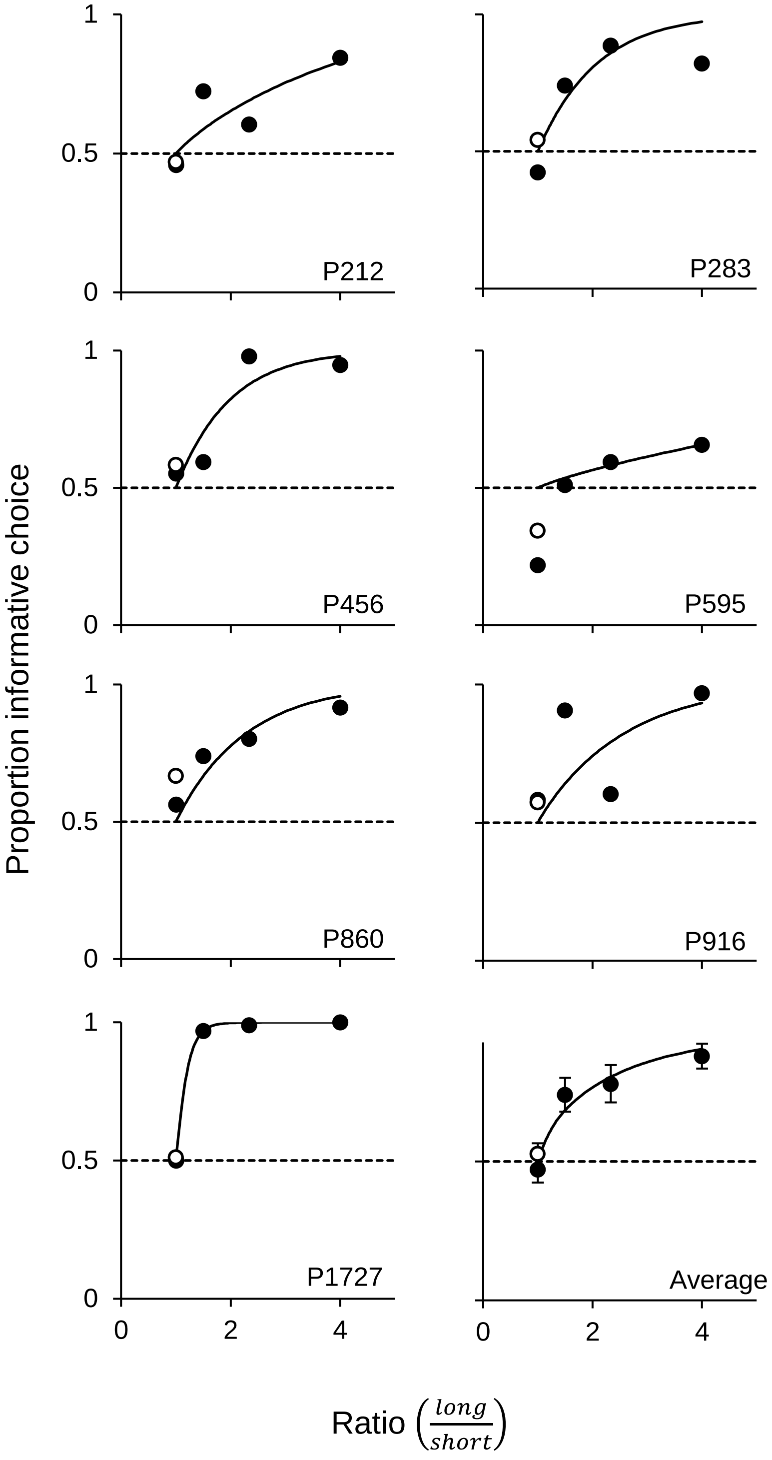
Results

Our main dependent measures were the proportion of choices for informative option,latencies to respond to each option during the last three sessions of each condition, and response rate during the four terminal stimuli. The symbols in Figure 2 show preference for the informative alternative as a function of the long/short ratio for each subject. Each circle shows the average preference across the last 3 sessions with each delay ratio. The lower right panel shows the group average. When the long/short ratio = 1.0, the average preference (±SEM) for the informative option was .47 (± .047) and .53 (± .038) in the first and second baseline conditions, respectively. With the 1.5, 2.3, and 4.0 long/short ratio the average preferences increased to .74 (± .061), .78 (± .068), and .88 (± .044), respectively. Preliminary analyses confirmed that preference did not differ significantly from chance when the long/short ratio = 1.0, larger absolute $t(6) = .695$, $p = .513$, but it surpassed significantly chance levels with the remaining long/short ratios, smallest $t(6) = 3.964$, $p = .007$, $d = 1.498$.

Despite some variability between and within pigeons, we observed an increasing trend in preference for the informative option as the long/short ratio increased. To analyze this trend, we conducted a linear regression with *ln(ratio)* as predictor and the log-odds of the average preference as dependent variable. The linear model adjusted the data well, with an adjusted $R^2 = .914$, $F(1,4) = 43.347$, $p = .007$. The beta coefficient of .967 confirmed that the log-odds of preference increased with the log of the delay ratios ($t = 6.584$, $p = .007$).

Figure 2

Choice proportion for the informative option

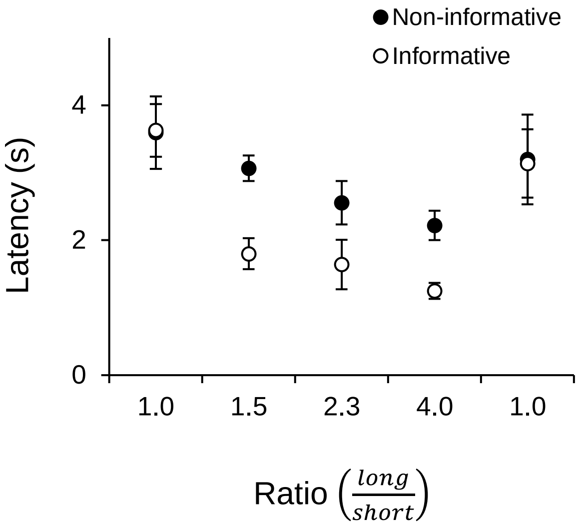


Note. Proportion of choices for the informative alternative as a function of the long/short ratio. The empty dot corresponds to Baseline 2. The error bars in the bottom right panel represent the standard error of the mean. The solid lines represent the best fitting predictions of a modified version of the Δ-∑ hypothesis.

We also measured latencies to respond during forced trials, since they are a metric of value and preference: organisms usually respond faster to preferred than to non-preferred alternatives when presented individually (Bateson & Kacelnik, 1995; Kacelnik et al., 2011; Lagorio & Hackenberg, 2012; Reboreda & Kacelnik, 1991; Shull et al., 1990; Vasconcelos et al., 2013). Here we analyzed the latencies to respond to the initial link during forced trials with each condition in search of converging evidence regarding the effect of the long/short ratio on preference. Figure 3 shows the average median latencies to respond to each option during the last 3 sessions per condition. As expected for preference data, latencies to accept each option were initially similar (delay ratio = 1.0), then they diverged as the long/short ratio increased (with longer latencies expressed to the non-informative and non-preferred option) and finally they became similar again when the long/short ratio returned to 1.0. Wilcoxon Signed-ranks tests confirmed that latencies in first condition with the long/short ratio = 1.0 did not differ across options (z = 15.00, p = .938), but it did when long/short ratio = 1.5 (z = 27.000, p = .031) and 4 (z = 28.000, p = .016). The exception was the long/short ratio = 2.3 (z = 25.000, p = .078). Finally, when long/short ratio returned to 1.0 the latencies became undifferentiated again (z = 15.00, p = .938).

Figure 3

Latencies for each option dring forced choices of each condition

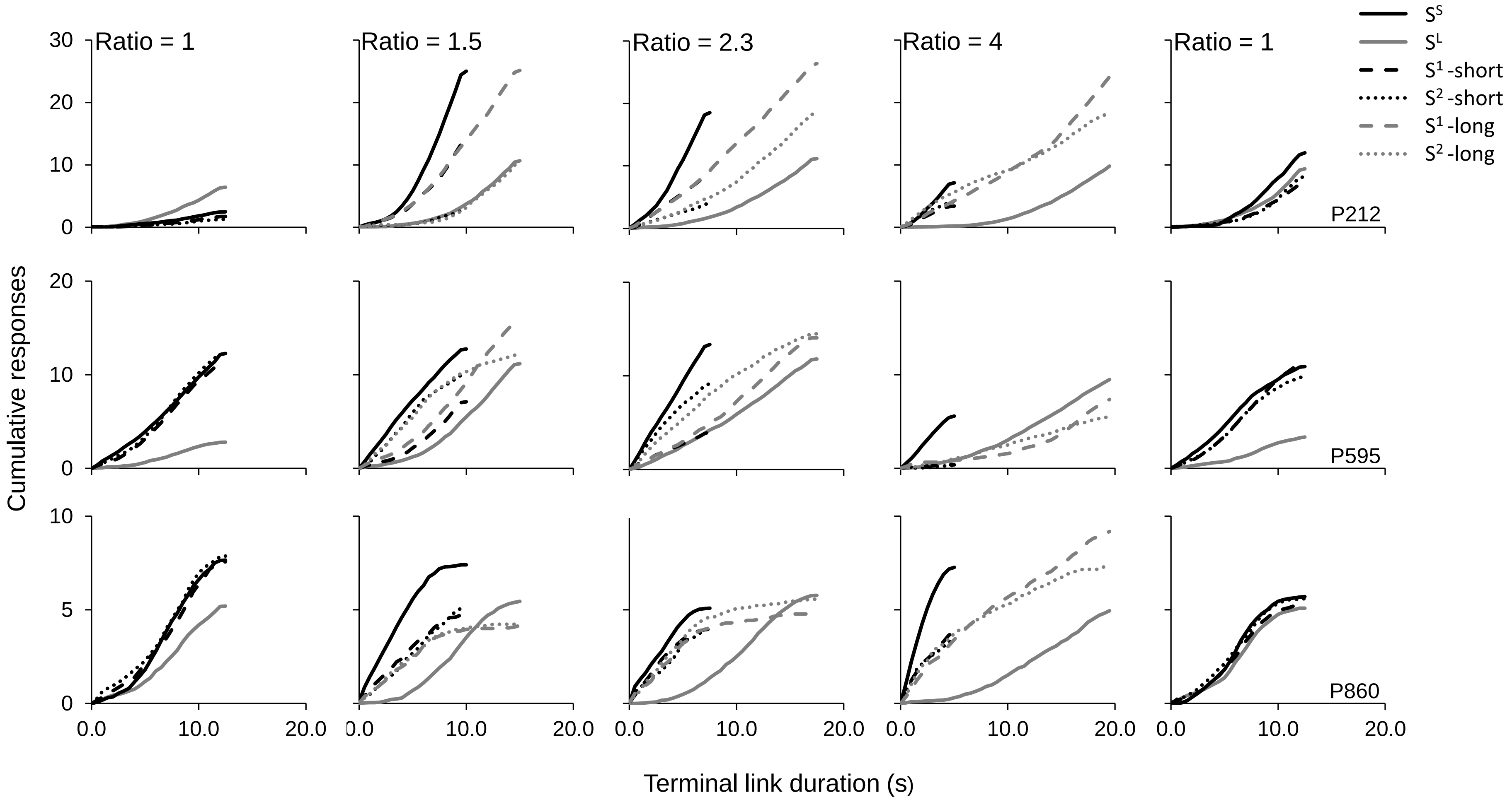


Note. Average median latencies to respond to the Informative (black symbols) and the Non-informative option (white symbols) in forced trials during the last three sessions of each condition. Error bars represent the standard error of the mean (SEM).

Lastly, we looked at the response rate during the four possible terminal stimuli (S^S, S^L, S^1 and S^2). Four of the seven pigeons did not peck to any of the stimuli during the terminal link (an average of less than 2 pecks per trial across the whole delay). Figure 4 shows the average cumulative responses during the terminal stimuli (of both forced and choice trials) for the remaining three pigeons over the last three sessions of each condition. The three pigeons developed a distinctive pattern of responding with long/short ratios > 1.0, with a higher rate of response to the S^S, than to S^L. The shape of the S^L curve resembles the typical scalloped response pattern found in fixed-interval schedules (Dews, 1978) with a low rate of responding at the beginning of the delay followed by an acceleration as reinforcement approaches. This suggests that animals were sensitive to the signaling properties of these stimuli and discriminated between delays. On the other hand, response rates to S^1 and S^2 remained undifferentiated as they should, thus confirming that pigeons had no means to identify the operating delay at least until the short delay had elapsed. Overall, these response rates were between those observed for S^S and S^L. Although in some conditions pigeons 212 and 595 showed different patterns of responses to S^1 and S^2, these differences did not last across conditions and remained consistent with the notion that they could not use the stimuli to predict the delay.

Figure 4

Cumulative responses for each terminal-link stimuli



Note. Cumulative responses at the terminal stimuli (S^S, S^L, S^1 -short, S^1 -long, S^2 -short and S^2 -long) for birds 860, 212 and 595 across conditions.

Discussion

This experiment analyzed the effect of signaling different delays to food on choice. Pigeons chose between two alternatives leading to food after an equally probable short or long delay. The alternatives differed in that, for one of them, the short and long delays were associated with distinctive cues (informative option), and for the other one, the delays were not correlated with the presented cues (non-informative option). Consistent with previous research (e.g., Bower et al., 1966; Frankel & Vom Saal, 1976), pigeons reliably preferred the informative alternative when the signaled delay were different, even though they both associated with the same rate of reinforcement. We also expected this preference to vary with the long/short ratio. A regression analysis with the *ln(ratio)* as predictor confirmed that the log-odds of the average preference for the informative option increased with *ln(ratio)*. An examination of the latencies as a measure of value supported the results: pigeons showed shorter latencies for the informative than for the non-informative option in two of the three conditions where ratio > 1.0. A look into the response patterns during terminal links suggests that the terminal stimuli helped pigeons to discriminate the delays in the informative but not in the non-informative option.

From an ecological perspective, these results support the assumption that the value of information ought to be vary directly with the improvement potentially imparted by that information—the ability to avoid long delays would be more beneficial with larger long/short ratios. Under natural circumstances, animals can use information to adjust their behavior and thus abandon patches when the rate of return falls below some threshold. In practice, when foraging, an animal could pursue prey if the available cues signal a short waiting time for food or continue searching if the available cues signal delays beyond a threshold of acceptability. In the present study, pigeons learned the contingencies associated with each stimulus, used the information so conveyed to guide preference, but did not collect the benefit of avoiding long delays: they had to endure all the waiting times in both alternatives (i.e., to pay the opportunity cost). This preference reflects the operation of mechanisms evolved to deal with the statistical properties of natural environments, not the artificial preparations of unavoidable opportunity costs. The animal behaves in the experimental preparation as if information were usable.

This notion is consistent with the logic of the ecologically-inspired model proposed by Vasconcelos and colleagues to deal with suboptimal choice (Fortes et al., 2016, 2018; Vasconcelos et al., 2015). Typically, in a suboptimal choice situation, an animal chooses between two options associated with different probabilities of reinforcement after a constant delay. The difference between the options is that for one of them (informative), distinctive stimuli signal reinforced (S+) and non-reinforced trials (S-); for the other option (non-informative), the presented stimuli do not signal the outcome. Animals prefer the informative option even if it is associated with a lower rate of reinforcement (for reviews see Vasconcelos et al., 2018; Zentall, 2016). Mathematically, the model estimates the rate of intake for an option as the probability of food over all the temporal costs. In our study, the rate of a given option is given by

$$R_i = \frac{P_{rf}}{P_{\mathrm{S}} * (d_s + h) + P_{\mathrm{L}} * (d_L + h)}$$

(Eq. 1)

where P_s is the probability of a short delay, P_L is the probability of long delays, d_s and d_L are the short and long delays, respectively, and h is the handling time, here assumed common to all alternatives. According to Equation 1, the informative and non-informative options in our experiment yielded the same rate of reward. However, if we assume that an animal can discriminate and avoid long delays (totally or partially), the rate intake for the informative option would increase. Equation 2 incorporates this idea:

$$R_{info} = \frac{P_{rf}}{P_{\mathrm{s}} * (d_s + h) + \alpha\ [P_{\mathrm{L}} *\ (d_L + h)]}$$

(Eq. 2)

The parameter α varies between 0 and 1 and determines the proportion of the long delays the animal experiences. When α = 0, the animal uses information perfectly and completely avoids this opportunity cost; when α = 1, the animal is unable to use information and waits for the long delays to elapse. Further, we assume that α corresponds to the ratio of the rates of reinforcement, which simplifies to the reciprocal of the long/short ratio with each cue:

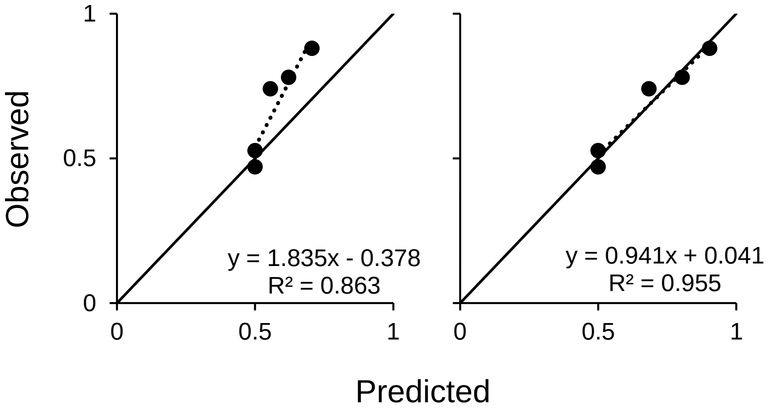
$$\alpha = \frac{1}{d_L} \div \frac{1}{d_s} = \frac{d_s}{d_L}$$

(Eq. 3)

In other words, larger long/short ratios imply smaller α. Hence, animals experience a smaller proportion of the long delays with larger long/short ratios. The model is silent about how the rate of each alternative translates into preference, but if we use Luce's ratio rule, (a/(a+b), to estimate preference, the model gives a reasonably good account of the observed data, R^2 =.863, given that the model does not include any free parameter. Figure 5 (left panel) shows the observed against the predicted preference with the RRM, although it underestimates the specific proportion, it provides a good account of the data, a notable result for a model without free parameters.

Figure 5

Predicted versus observed data according to the Vasconcelos et al. (2015) ecologically-inspired model and the modified Δ-Σ hypothesis.



Note. Symbols represent the average of the observed preferences for the informative option against the predicted preference according to the ecologically inspired model (left panel) and the Δ-Σ hypothesis (right panel). The solid line represents a perfect linear relation and the dotted line the line best fit the data estimated by the least-squares.

The foregoing discussion constitutes a normative approach to the problem. Given the usual structure of natural foraging cycles, how should animals behave if delays are signaled? Yet, the identification of a constrained optimal policy does not elucidate the contemporary behavioral processes the animal deploys to adjust behavior. To that end, we recently proposed the Δ-Σ hypothesis, a model that attempts to pinpoint the processes underlying preference in the related suboptimal-choice task (González et al., 2020). According to the model, the value of an alternative depends on two higher-order variables: (1) Delta (Δ) which is the difference between the probabilities of reinforcement associated with each stimulus within each option, and (2) Sigma (∑) which is the overall probability of reinforcement associated with each option. The value of an option is calculated according to the equation

$$V_i = (\Sigma_i)^c * e^{\beta * \Delta_i}, \qquad \text{(Eq. 4)}$$

with the scaling parameters *c* and *β* both > 0. Preference for the informative option can be estimated by Luce's ratio, a/(a+b), which simplifies to

$$P_{info} = \frac{1}{1+\left(\frac{\Sigma_{noninfo}}{\Sigma_{info}}\right)^{c} e^{-\beta\left(\Delta_{info}-\Delta_{noninfo}\right)}} \qquad \text{(Eq. 5)}$$

Yet, Equation 5 predicts indifference between the options in our task (cf. Figure 1) because the probability of reinforcement in the presence of each terminal stimulus is 1.0 (thus, both Δ_{info} and Δ_{noninfo} are zero) and ∑ is 1.0 for both options.

The Δ-∑ hypothesis assumes that the value of an option is at least partially determined by Δ, a contrast-like mechanism within the options. In the suboptimal choice task this contrast is between the probabilities of reinforcement associated with each stimulus. In our delay-based task, such contrast in indeed null but we propose that another source of contrast is present: that between the rates of reinforcement experienced with each terminal stimulus within each option. For example, in the condition with a 5 s short delay and a 20 s long delay, the Δ of rates in the informative option is .15 [(1 / 5) - (1 / 20)]; the Δ of rates in the non-informative option is 0 because the average time to food is 12.5 s in the presence of both S^1 and S^2.

We fitted this modified Δ-∑ model to the individual data in the present experiment. The solid lines in the panel of each bird in Figure 2 represent the best fit line obtained by the least-squares method. The best fitting parameters, *β* and *c*, for each pigeon are shown in Table 2; the solid line in the average panel of Figure 2 (bottom right) is the average of the individual fits. Overall, the model captures well the general increasing trends and the fit describes accurately the average preference. Figure 5 (right panel) shows the observed vs predicted preference according to the Δ-∑ hypothesis (with the average of the individual fits).

Table 2

Best fitting parameters and R^2 for the Δ-∑ hypothesis

Pigeon	**c**	**β**	***R^2***
212	1.0	23.732	0.657
283		25.694	0.810
456		4.323	0.815
595		20.748	0.795
860		17.553	0.980
916		102.725	0.299
1727		10.536	1.000

The best fitted parameter *c* remains constant because $\sum_{\text{noninfo}}/\sum_{\text{info}}$ always equals 1 (the probability of food was the same in both options), hence any *c* value would yield 1. This means that the ∑ played no role in the variation of preference with changes in the long/short ratio. . *β*, on the other hand, did affect the patterns observed as it should. It modulated the weight of the only intervening variable, Δ_{info}-Δ_{noninfo}.

To conclude, in this experiment we showed that the preference for informative over non-informative options extend naturally to a situation where information is about delays, not probabilities of reinforcement. We found that preference for signaled delays varied with the ratio between the long and short delays within alternatives. From a normative standpoint, this preference and trend may occur because animals use evolved mechanisms designed to deal with usable information: animals can use information to maximize the rate of food intake by avoiding, for example, relatively delayed opportunities (in comparison with the background). Although this strategy cannot be implemented in the experimental condition, we believe it reflects the conditions in which it evolved and where most, if not all, information is instrumental. As a normative model, the ecologically-inspired model is not directed at predicting specific preferences of behaving organisms but at understanding the selective pressures shaping behavior and deriving optimal policies imposed by those pressures. To predict preference, we modified the Δ-$\sum$ hypothesis to accommodate another sort of contrast: that between rates of reward. The modified version accounted well for data. Together, these models provide a complementary approach to the proximate and ultimate causes of preference for signaled delays.

Chapter V: Conclusion

In the present dissertation, we studied the effect of signaled outcomes on choice. Previous research has shown that animals prefer informative over non-informative options whether they disambiguate trials with food from those without food (for reviews, see Cunningham & Shahan, 2018; McDevitt et al., 2016; Vasconcelos et al., 2018; 2016) or short from long delays to food (Alsop & Davison, 1986; Bower et al., 1966; Davison, 1972; Fantino, 1969; Frankel & Vom Saal, 1976; Hursh & Fantino, 1974; Richards, 1981). Three studies helped us deepen our knowledge about the causes of such preference. Together, the studies suggest that the *predictive value* of the terminal stimuli plays a key role in the emergence of this preference for informative options.

The first study revolved around the suboptimal choice procedure (Zentall, 2011). In this task, animals choose between two initial keys associated with probabilistic reinforcement after a delay. The task has two crucial features: (1) choosing one of the options (*informative*) leads to different terminal stimuli signaling reinforced and non-reinforced trials; while choosing the other option (*non-informative*) leads to stimuli that do not signal whether the trial will be reinforced or not; and (2) reinforced trials are less frequent in the informative option thus yielding a lower rate of reinforcement in the long run. Two versions of the task have coexisted in the literature. In one of them (the standard procedure), the non-informative option involves the presentation of one of two possible terminal stimuli; in the other version (the original procedure), the non-informative option involves the presentation of the same stimulus on every trial. Although frequently referred to as equivalent, a formal test with the same delays and probabilities was pending.

The results from the first study confirmed that both procedures are functionally interchangeable. These findings are theoretically important for two process-based approaches to suboptimal choice. On the one hand, the recently presented Delta-Sigma (Δ-∑) hypothesis (González, 2020) needs an ancillary assumption to deal with the original procedure. The model proposes that preference results from a contrast-like process between the probabilities of reinforcement associated with the two terminal stimuli within each option, Δ, and the overall probability of reinforcement associated with each option, Σ; but when only one terminal stimulus exists (i.e., the non-informative option in the original procedure), Δ cannot be computed. González and colleagues presupposed that the presence of a single stimulus translates into a Δ of zero. The findings of our first study support the assumption. Similarly, the results supported the assumption made by the temporal-information hypothesis (Cunnigham & Shahan, 2018) that an option with two terminal stimuli associated with the same probability of reinforcement is functionally equivalent to an option with a single terminal stimulus with the same probability of reinforcement. The findings are also methodologically significant because they provide a solid ground for the comparison of studies using one or the other procedure; also, they rule out confounding variables such as the number of conditioned reinforcers and a possible preference for stimulus variability.

The equivalence between procedures was also suggested by the latency data. The times to respond in the standard and original procedures were similar: shorter latencies for the informative option (the preferred one) than for the non-informative option and similar latencies towards both options non-informative options in the hybrid procedure (where no preference was observed)

The latency data also provided an ideal opportunity to test the Sequential Choice Model (Kacelnik et al., 2011; Shapiro et al., 2008). This general approach to choice suggests natural selection shaped mechanisms to cope with sequential (one option at a time) rather than simultaneous choices (two or more options simultaneously) because the latter are rare in nature. The model proposes that, in the exceptional event that two or more options are found simultaneously, independent sequential mechanisms for each option are triggered with the fastest one being expressed as a choice. This lead to two predictions: (1) we should be able to predict simultaneous choices from sequential latencies, and; (2) latencies to make simultaneous latencies should be shorter than latencies to accept sequential options because the independent processes would be competing. Our results provided strong evidence supporting both predictions.

The second study explored how delaying the moment at which the informative option disambiguates the outcome affects choice. In Experiment 1, when the informative option was chosen, the same terminal stimulus was presented but it only signaled forthcoming reward if it remained active after a fixed time into the delay to outcome (t_s, switching time). If the stimulus changed to a different one at t_s sec, the new stimulus signaled that food would not be available at the end of the delay. In Experiment 2, the complementary manipulation was in effect: When the informative option was chosen, a terminal stimulus was presented; if it remained active after t_s sec, it signaled no food would be available at the end of the delay; when it changed to a different stimulus at t_s, that new stimulus signaled food would be the delivered at the end of the trial.

The results showed that preference for the informative option decreased with t_s in both experiments. However, the decrement was sharper when the stimulus-change at t_s sec signaled no-food (Experiment 1) than when it signaled food (Experiment 2). The cause of such difference remains uncertain, but we proposed some non-exclusive hypothesis: (1) In Experiment 1 a reinforced trial was signaled only if the terminal stimulus remained active after t_s, making information time-dependent, hence harder to track than in Experiment 2, where a reinforced trial was signaled by a exteroceptive stimulus change; (2) pigeons might have been timing the average time to food in the presence of the only stimulus that immediately preceded food increasing the opportunity cost in Experiment 1 but not in Experiment 2; (3) In Experiment 1 the stimulus for food became unreliable 80% of the trials (compared to baseline), in experiment 2 the stimulus for no-food became unreliable only 20% of the trials, thus the change in reliability compared to standard procedure was greater in Experiment 1 than in Experiment 2.

Regardless of the difference, the overall conclusion was that the predictive value of the informative option was reduced in both experiments because uncertainty about the trial outcome did not vanish once the terminal link was initiated but persisted up to t_s sec into the terminal link. A modification to the aforementioned Δ-∑ hypothesis including a role for the time spent under certainty and uncertainty about the trial outcome accounted well for our findings.

From an ecological perspective, reliable and immediate information about future outcomes can be used by animals to behave adaptively under natural circumstances: if a cue signals food, they can pursue that option, if it signals no food they can keep searching (Fortes et al., 2016, 2018; Vasconcelos et al., 2015). Delaying the moment when the possible outcomes are disambiguated reduces this advantage and consequently the option’s value.

Finally, the third study expanded the scope of this dissertation to the preference for information about the delays to reward. In a similar choice procedure, pigeons choose between two options. One was informative in the sense that distinctive stimuli signaled whether food would be presented after a short or a long delay; the other option was non -informative because the presented stimuli did not disambiguate whether the current delay to food was the short or the long one. Both options yielded the same rate of reinforcement, but pigeons preferred the informative option. Moreover, this preference increased as the ratio of the long to the short delay increased. We concluded that the predictive value of the informative option depended on the potential advantage it provides. In nature, an animal benefits more from disambiguated delays when it can avoid relatively long delays; the greater the ratio, the higher the cost of engaging with options associated with long delays.

To account for this preference, we again modified the Δ-∑ hypothesis. The original model proposes that Δ depends on the difference between probabilities of reinforcement; yet in our third study all probabilities equaled 1.0, hence, $\Delta = 0.0$. Nonetheless, the manipulation did include another source of contrast: that between rates of reinforcement (i.e., for the same amount of food, shorter delays lead to higher rates of reinforcement). Therefore, we assumed the Δ operated on rates, not probabilities. This modification provided a good account of the data and constitutes a parsimonious adjustment of the model.

To summarize, the three studies in this dissertation examined choice between options with asymmetrical information. Previous research has systematically found a preference for informative options both when they yield a lower rate of reinforcement than the alternatives and when the rate is the same. At first glance, this behavior appears as a maladaptation. Why prefer less to more food? A closer inspection reveals that under natural circumstances this preference may prove adaptive. The comparison of the protocols in the first study showed that the valuation of information appears to underlie the preference for signaled outcomes. The manipulations of the second and third study, where the putative advantages were systematically changed, showed that animals' choices followed these changes. In experiment 3, pigeons showed a stronger preference for the informative option as the information provided a greater advantage. These overall findings suggest that animals appear to track any available information provided in a manner that is sensitive to the putative advantage it conveys.

We believe that our two-sided approach, both mechanistic and functional, takes us closer to answer, in the words of Niko Tinbergen, the "*what is this good for?*" and the "*how does it work?*" questions (Tinbergen, 1963). These are different but interlinked questions that will undoubtedly broaden our understanding of behavior.

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