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Differences in Paradoxical Choice Between Pigeons (*Columba livia*) and Rats (*Rattus norvegicus*): The Problem of Cue Trackability

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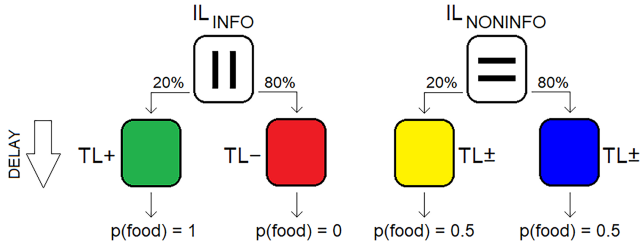
Organisms are believed to attempt to maximize their net energy intake while foraging. The paradoxical choice task shows that they may instead prefer to obtain information rather than primary reward when the outcome is uncertain. That is, they prefer stimuli that consistently predict food or no food (informative option), to stimuli that inconsistently predict both food and no food in larger amounts (noninformative option). This task also seems to indicate that some species (like pigeons, *Columba livia*, and starlings, *Sturnus vulgaris*) are more prone to choose the informative option, while other species (like rats, *Rattus norvegicus*, and humans, *Homo sapiens*) tend to favor reward procurement through the noninformative option. There is empirical evidence for and against this view. However, an analysis of the literature suggests that species differences in paradoxical choice might be less pronounced than often believed. We argue that pigeons and rats are usually not tested under conditions that are motivationally equivalent for both species—in particular, the opportunities to track consistent stimulus–food pairings are less often met in the rat studies than in the pigeon studies.

Keywords: suboptimal choice, motivation, tracking behavior, information seeking, uncertainty

Classical theories in behavioral psychology and behavioral ecology rely on the assumption that organisms forage on food items in a way that maximizes their net energy intake (Charnov, 1976; Herrnstein, 1961; Stephens & Krebs, 1986). When given a choice between two (or more) food options, and in the absence of aversive factors, they are therefore predicted to favor the most profitable alternative. However, in some circumstances, organisms may spend time and effort in doing activities with uncertain consequences while free food is available in larger amounts (e.g., Inglis et al., 1997) or pay a cost to obtain information that has no effect on the final outcome (e.g., FitzGibbon et al., 2020). These findings depart from traditional views on foraging while revealing an important fact: There are situations in which looking for information is more useful than focusing on primary reward.

The paradoxical choice task provides similar evidence that behavior is sometimes "suboptimal" in terms of reward rate (Kendall, 1974; Spetch et al., 1990; Zentall, 2016). In this task, the animal must select one of two initial-link (IL) stimuli. Choosing one IL stimulus has the immediate effect of revealing a terminal-link (TL) stimulus, which consistently indicates whether the trial will end with food delivery (TL+) or no food delivery (TL−) with a 100% probability a few seconds later (Figure 1, left). The delay to food is typically 10 s but is sometimes extended up to 50 s. In general, the TL stimulus followed by food is less frequent than that followed by no food. In our illustration in Figure 1, the green color always predicts food and occurs in 20% of the trials, while the red color always predicts no food and occurs in 80% of the trials. An IL stimulus leading to consistent TL stimuli provides information and will be referred to as IL_{info} stimulus. Choosing the other IL stimulus reveals one of two TL stimuli (yellow or blue color) that are both inconsistently followed by food or no food (TL±) with a 50% probability following the same delay (Figure 1, right). In this case, the IL stimulus provides no information and will be denoted $IL_{noninfo}$ stimulus.

Figure 1
Paradoxical (Suboptimal) Choice Task



Note. After providing a single response (lever press or key peck) at an IL stimulus (IL_{info} or $IL_{noninfo}$), what follows is independent of any additional responses. A choice trial starts with the two IL stimuli presented. IL = initial link; info = information; noninfo = no information; TL = terminal link. See the online article for the color version of this figure.

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The fact that the animals from all species tested may come to prefer the IL_{info} stimulus (here offering a 20% chance of food) to the $IL_{noninfo}$ stimulus (50% chance of food) suggests that their choice does not strictly depend on the reward rates involved. This paradoxical preference may result from the information provided following choice and has also been interpreted in terms of the reinforcing value of the TL stimuli—that is, 100% for a TL+ stimulus and only 50% for a TL± stimulus (but see Case & Zentall, 2018).

Pigeons (*Columba livia*) and starlings (*Sturnus vulgaris*) are known to be highly suboptimal, preferring the IL_{info} stimulus despite enormous deficits in the reward amounts to be collected via this option. Pigeons maintain their preference even if they could receive 35 times more food via the $IL_{noninfo}$ stimulus (Fortes et al., 2016), and starlings remain suboptimal with only a 5% chance that the TL+ stimulus occurs (Vasconcelos et al., 2015). By contrast, other species like rats (*Rattus norvegicus*) seem to show this preference for a more restricted set of parametric values. For example, several studies indicate that TL durations of 30 s are necessary (and sometimes even not sufficient) to induce paradoxical choice in rats (Alba et al., 2021; Cunningham & Shahan, 2019, 2020), while pigeons also express this preference for durations as short as 10 s (e.g., Zentall, 2016).

Explaining the pigeon–rat differences requires considering species-specific differences in the ability of organisms to learn and express motivated behaviors about the stimuli presented. This relates to the question of the adequacy between what an organism has to do and what natural selection allows this organism to learn (Timberlake, 1993, 1994). However, this also relates to the conditions to be satisfied to allow the organism to become motivated by a stimulus whose pairing with food is unguaranteed. In this article, we argue that pigeons and rats are usually not tested under conditions that are motivationally equivalent for both species—specifically, they are tested under conditions that are unfavorable to rats. Briefly, we defend the assertion that organisms exposed to the paradoxical choice task track the alternative where consistent cue–food pairings (TL+ and TL−) can be found (Anselme, 2022, 2023). Under reward uncertainty, organisms are assumed to track the information (degree of consistency) between stimuli and outcomes, that is, to try to determine where, when, and how to find cues that predict as consistently as possible the presence of rewards. For example, hoarding behavior (i.e., storing food outside of one's body for later use) is a typical case of consistency tracking: In prevision of upcoming difficult times, the hoarder looks for locations (contexts) where to cache food—that is, where to establish consistent associations between specific signals (spatial cues or others) and some food items (rewards). This operation will considerably reduce the time and effort required to seek food when environmental unpredictability comes to increase. In other words, the animal will predominantly track the selected locations (contexts) where the cues consistently predictive of food can be found, and will only focus on those cues once detected at a smaller scale (no need to develop incentive salience for and hence remember the cues explicitly, which may have disappeared or be surrounded by other appetitive cues). Perhaps in line with this, both coal tits (*Periparus ater*) and humans (*Homo sapiens*) seem to use contextual familiarity, not the recollection of specific cues, to retrieving cache contents (Smulders et al., 2023).

As noted above, consistency tracking relates to the concept of information, which has mostly been defined as entropy or uncertainty reduction (Atlan, 1972; Balsam & Gallistel, 2009; Friston, 2010; Shannon, 1948). In the paradoxical choice task, information denotes a consistent association between two events that are not guaranteed in advance, that is, a TL+ stimulus predictive of food or a TL− stimulus predictive of no food. Hence, a stimulus giving access to consistent associations will have high significance in the environment. Any cue (from context) whose presence disambiguates the meaning of another cue (acting as a conditional stimulus [CS]) relative to the presence or absence of an outcome is called an occasion setter (Holland, 1992). In a natural setting, occasion setters are crucial to reveal where associative consistency is, so they should play an important role in behavioral orientation and decision. In the paradoxical choice task, the IL_{info} stimulus may play the role of an occasion setter because it indicates the option ("context") that contains information, in the form of consistent cue–reward pairings. In contrast, the $IL_{noninfo}$ stimulus provides no information and hence does not act as an occasion setter.

Consistency tracking operates at the IL level and should be distinguished from stimulus tracking, which operates at the TL level and relates to incentive salience attribution to the TL stimuli—a core psychological process leading an animal to approach and interact with a cue repeatedly associated with food delivery (see Berridge, 2007). Indeed, we will see that choice in this task does not always predict the number of responses to the TL stimuli, suggesting that the whole process requires more than incentive salience (Alba et al., 2021; González-Torres et al., 2020; Martínez et al., 2017; Trujano & Orduña, 2015). Also, we argue that the pigeon–rat differences in paradoxical choice do not denote differential sensitivity to the task between the two species, but rather that the trackability of the TL stimuli–food pairings at the IL level is often reduced in rats compared to pigeons. We propose several experimental tests of this idea, with predictions not made by traditional theories of paradoxical choice.

Several Interpretations of the Pigeon–Rat Differences

A major challenge for theories of paradoxical choice is to explain why the same probabilistic or temporal arrangements of IL and TL stimuli may generate distinct responses in pigeons and rats (or other species; see Table 1). According to the theory of positive contrast (Stagner & Zentall, 2010), organisms prefer the IL_{info} alternative because they expect less at the IL level (e.g., 20% chance of food) than what occurs in a successful trial at the TL level (100% chance of food when the TL+ pops up). In the opposite, a lower contrast (sometimes no contrast) exists with the $IL_{noninfo}$ alternative (in the example, 20% vs. 50%), which is therefore not preferred. Alternatively, the signal-for-good-news or SiGN theory (Dunn et al., 2024; McDevitt et al., 2016) attributes preference for the IL_{info} alternative to the reinforcing value of the onset of the TL+ in this alternative (which improves local context, as a TL− might occur), compared to the TL± (or even a fully predictable TL+, see further) in the other alternative (which does not improve local context). Both theories may sound similar, the former insisting on the importance of probability contrast for paradoxical choice, while the latter puts forward the reinforcing value of delay reduction once the individual knows what is coming. However, for example, only the SiGN theory predicts the well-established evidence that a longer TL duration promotes paradoxical choice.

Theories based on the probabilistic contrast that exists between what is expected at the IL level and what occurs at the TL level

Table 1
Representative Pigeon and Rat Studies of Paradoxical Choice With a Specification of the Parametric Values and Behavioral Effects Mostly Discussed in This Article

Study	Species	IL stimuli		TL stimuli	
		Type	Choice	Type	Duration
González and Blaisdell (2021)	*C. livia*	Key lights	Info	Key lights	30 s
González-Torres et al. (2020)	*C. livia*	Treadles	Non-Info	Ambient lights	10 s
McDevitt et al. (2019)	*C. livia*	Circle cues	Info (only if outcome signaled)	Key lights	10 s
Smith and Zentall (2016)	*C. livia*	Cross versus circle cues	Info	Key lights	10 s
Alba et al. (2021)	*R. norvegicus*	Nosepokes	Non-Info	Levers	10–30–50 s
Chow et al. (2017)	*R. norvegicus*	Nosepokes	Info	Lever (TL+) Blackout (TL−)	10 s
Cunningham and Shahan (2019)	*R. norvegicus*	Levers	Info	Light–tone (TL+) Blackout (TL−)	10–50 s
Jackson et al. (2020)	*R. norvegicus*	Colors	Non-Info	Scents	Almost instant[a]

Note. IL = initial link; TL = terminal link.
[a] The TL stimulus (scent) was located aside the food cup.

(Stagner & Zentall, 2010), as well as between the alternatives (González et al., 2020), do not align with observed interspecific differences. They are not designed to tell us why pigeons and rats or dogs (*Canis lupus*) or humans do not react the same way to identical reward probabilities (e.g., Jackson et al., 2020; McDevitt et al., 2019). Similarly, theories based on temporal information (Cunningham & Shahan, 2018; McDevitt et al., 2016) are not typically designed to capture why distinct animal species may show differential sensitivity to identical stimulus durations (e.g., Jackson et al., 2020; McDevitt et al., 2019). There are hypotheses attempting to explain why organisms often prefer the IL_{info} alternative with longer TL durations (see further), but it is unknown why pigeons and starlings exhibit a preference for an informative option with 10-s TL stimuli (A. P. Smith & Zentall, 2016; Vasconcelos et al., 2015), while rats and humans often favor this option for TL stimuli of at minimum 30 s (Cunningham & Shahan, 2019; Lalli et al., 2000; but see Chow et al., 2017). (Of note, contrary to rats, humans have systematically failed to show paradoxical preference; e.g., Bodily et al., 2023.)

Are rats more sensitive to the conditioned inhibitory effects of the TL− stimulus than pigeons, causing avoidance of the IL_{info} alternative to the benefit of the $IL_{noninfo}$ alternative (e.g., Martínez et al., 2017)? The hypothesis of interspecific differences in the sensitivity to conditioned inhibition has been discussed by several authors (Daniels & Sanabria, 2018; Martínez et al., 2017). However, pigeons are also sensitive to conditioned inhibition in this task, though it is difficult to tease out issues of inhibition as a primary cause versus as a marker of some other cause of paradoxical preference (González & Blaisdell, 2021, 2023). And, in rats and pigeons, a TL+ stimulus reinforces responses more than a TL− stimulus inhibits responses (Ajuwon et al., 2023; McDevitt et al., 1997; Stagner et al., 2015). Table 2 summarizes the main theories and predictions related to the pigeon–rat differences in paradoxical choice.

A temporal-information model proposed by Daniels and Sanabria (2018) provides a formalism to understand the pigeon–rat differences. The model relies on the assumption that the value of an alternative depends on that of its TL stimuli and on an associability parameter whose value decreases in proportion to the certainty of the TL stimulus-reinforcer relationship. According to this model, pigeons would prefer an informative option to a noninformative option because of a faster decay of associability for the TL− stimulus (predictive of no reinforcement) than for the TL+ stimulus (predictive of reinforcement). By contrast, rats would make the opposite choice because no loss of associability occurs for these two stimuli. The model's formalism implements the apparent evidence that the conditioned inhibitory property of the TL− stimulus dissipates over training and comes to play little role in choice with pigeons (Fortes et al., 2016; Laude et al., 2014; McDevitt et al., 1997), while it seems to exert a strong, persistent influence in rats (Alba et al., 2021; Martínez et al., 2017; Trujano & Orduña, 2015). However, associability or conditioned inhibition is mostly inferred from empirical data rather than measured. In pigeons, a TL+ stimulus generates more responses than a TL− stimulus, and a compound TL+ TL− (summation test) produces a low level of responses, suggesting that the TL− stimulus acquires its inhibitory properties over the course of training (González & Blaisdell, 2021; but see Laude et al., 2014). Given that pigeons typically prefer the option that contains the TL− stimulus (IL_{info} alternative), it is perhaps more accurate to say that they are sensitive to conditioned inhibition at the TL level but that this phenomenon does not determine their choice at the IL level (but see González & Blaisdell, 2023, for an empirically-supported argument that inhibition does play a causal role on IL choice preference). As shown further, pigeons seem to prefer information, even if about bad news (TL−), to the absence of information (TLs ± in the $IL_{noninfo}$ alternative). We will argue that this is also true of rats.

In another vein, and in line with Timberlake's (1993) behavior systems theory, Zentall et al. (2019) suggested that the pigeon–rat differences may relate to the ecological significance of the stimuli involved. Briefly, Timberlake's theory suggests that organisms have various innate behavior systems (for feeding, reproduction, and so forth), that are adapted to meet consistent ecological needs. There is a certain amount of species-specificity in behavior systems along with more general properties with more phylogenetic breadth. Behavior systems theory posits that an unconditional stimulus or US (e.g., food) activates a behavior system (feeding system) relevant to that US. Pavlovian conditioning superimposes a conditional stimulus (CS, such as a light or a lever) on the behavioral system activated by the US, so that the CS can elicit components of that system through a CS–US association. For example, rats can barely be conditioned to a light-malaise association (Miller & Domjan, 1981) because light

Table 2
Summary of the Main Theories of Paradoxical Choice and Their Interpretation of the Pigeon–Rat Differences at the Time of Choice

Authors	Cause of paradoxical choice	Cause of the pigeon–rat differences
Zentall and coll.	Stagner and Zentall (2010) Reinforcing effect of the positive contrast between initial expectation (IL) and TL+ occurrence	Zentall et al. (2019) Both species attribute incentive salience to distinct stimuli because they possess different behavior systems
Orduña and coll.	Martínez et al. (2017) Low sensitivity to conditioned inhibition induced by the TL−	Trujano and Orduña (2015) Conditioned inhibition induced by the TL− is stronger in rats than in pigeons
Spetch and coll.	McDevitt et al. (2016) Reinforcing effect of TL duration when good news (TL+) occurs in a context of likely bad news (TL−)	No prediction
Sanabria and coll.	Daniels and Sanabria (2018) Slower associability decay process of attentional allocation for the IL_{info} than the $IL_{noninfo}$ option	Daniels and Sanabria (2018) Conditioned inhibition (associability decay) induced by the TL− is stronger (slower) in rats than in pigeons
Shahan and coll.	Cunningham and Shahan (2018) More temporal information is conveyed by the IL_{info} than the $IL_{noninfo}$ option	Cunningham and Shahan (2018) Rats are less sensitive to the ratio between the delay to TL to the delay to food at the choice point than pigeons
Vasconcelos and coll.	González et al. (2020) Reinforcing effect of the positive contrast between initial expectation (IL) and TL+ occurrence, weighed by food probability of each option	No prediction

Note. coll. = colleagues; IL = initial link; TL = terminal link.

never causes a malaise in a natural setting; they are not evolutionary designed to associate these two events. Another example is that of racoons (*Procyon lotor*) trained to place wooden coins in a container for reward (Breland & Breland, 1961). The racoons quickly failed to do this simple instrumental task, preferring to rub the coins against each other and causing a kind of unwanted reward omission. The reason for such a misbehavior is the higher evolutionary relevance of washing behavior elicited by food compared to the trained action—a phenomenon called "instinctive drift."

A long CS–US time interval activates an early portion of the behavior system, leading to a general search strategy and to relatively random locomotion (exploration: Travel, chase, etc.; Timberlake, 1993). A short CS–US time interval, however, elicits a focal search strategy, consisting of approaching the CS and displaying consummatory behaviors toward the US (exploitation: Capture, bite, etc.) or even to the CS (autoshaping). According to Zentall et al. (2019), general search should occur with stimuli associated with a low incentive salience, while focal search should occur with stimuli associated with a higher incentive salience. They argued that pigeons and rats simply differ in the type of stimuli leading to incentive salience attribution. Pigeons attribute a high incentive salience to key lights, which should favor focal search and hence a preference for the informative option—because the TL+ is temporally proximal to guaranteed food delivery. By contrast, rats attribute a low incentive salience to key lights (Chow et al., 2017), which should induce general search and hence a preference for the noninformative option. However, this analysis does not explain why rats exposed to TL stimuli with a high incentive salience, such as levers (Trujano & Orduña, 2015) and scents (Jackson et al., 2020), also often prefer the noninformative option. It is arguable that the temporal proximity of a TL stimulus (CS) to food reward (US) favors incentive salience and focal search. Indeed, the TL stimuli induce responses in proportion to the probability of their association with food such that TL+ > TL± > TL− (e.g., González & Blaisdell, 2021; Martínez et al., 2017). However, there is strong evidence that choice at the IL level can be dissociated from response strength at the TL level both in rats (Alba et al., 2021; Martínez et al., 2017; Trujano & Orduña, 2015) and pigeons (González-Torres et al., 2020). Thus, the relevance of connecting preference in this task to incentive salience can be questioned.

The Consistency Tracking Hypothesis

We argue that two distinct processes operate when organisms are exposed to the paradoxical choice task. The first process is *stimulus tracking*: At the TL level, organisms track the revealed stimulus through incentive salience and focal search—as discussed above. Given that the TL stimulus is temporally proximal to the reward, the motivational salience of the TL stimulus is a direct function of reward probability: A TL+ stimulus is predictive of food and will be tracked, while a TL− stimulus is not and will be avoided. At this stage, organisms are engaged in reward exploitation. The second process is called consistency tracking: At the IL level (at the time of choice), organisms track the consistency of the TL stimulus–reward pairings rather than the TL stimulus or the reward amount (Anselme, 2022, 2023). This process refers to the ability to discriminate and prefer the alternative in which consistent stimulus–food pairings can be found (IL_{info}), before the stimuli are revealed and despite a low probability of food delivery. Consistency tracking is assumed to be a component of a general search or exploratory strategy because the IL stimuli are temporally more distal to reward and associated with some uncertainty that can be resolved in advance (at the TL level) by means of appropriate choice—for details, see the introduction. Under the assumption that the evolutionary function of general search is to resolve uncertainty through consistency tracking (in opposition to focal search, which favors the approach to and interaction with a stimulus), the IL_{info} alternative is the appropriate choice to achieve this goal. Accordingly, the IL stimuli are not much attributed to incentive salience, a process that does not appear to control choice behavior (Alba et al., 2021; Martínez et al., 2017; Trujano & Orduña, 2015). In other words, an IL_{info} stimulus is chosen as a higher-level means allowing organisms to track the consistent TL

stimulus–food pairings (TL+ and TL−); it is not tracked for any inherent acquired/motivational value like a TL stimulus can be.

Compelling evidence for the consistency tracking hypothesis can be found in multiple studies with pigeons (and starlings), although other interpretations may also work (e.g., McDevitt et al., 2016). For example, A. P. Smith and Zentall (2016) tested pigeons in the paradoxical choice task for 30 sessions, with the consistency of TL stimuli–reward pairings in both alternatives (Experiment 1, signaled 50% vs. signaled 100%), in the right alternative only (Experiment 2, unsignaled 50% vs. signaled 100%), and in the left alternative only (Experiment 3, signaled 50% vs. unsignaled 50%). The pigeons' preferences were compatible with the view that they tracked the consistency of the TL stimuli–food pairings, independently of the food amounts received. Thereby, in Experiment 1, both alternatives were consistent and the pigeons showed indifference across the 30 sessions, although one alternative provided much more food than the other. In Experiment 3, the consistent alternative came to be preferred (around Session 15) to the inconsistent one despite providing identical food amounts. The consistency of a TL stimulus–food pairing can also be changed over training and this manipulation has interesting consequences. In pigeons that showed a preference for the informative option, extinguishing the reinforcing value of one of the two TL± stimuli in the $IL_{noninfo}$ alternative or partially reinforcing the TL− stimulus in the IL_{info} alternative induces a preference for the initially noninformative option (González & Blaisdell, 2023). In the first situation, the $IL_{noninfo}$ alternative gains in informational content (one TL± stimulus becomes a TL− stimulus), while in the second situation, the IL_{info} alternative loses some informational content (the TL− stimulus becomes a TL± stimulus). In either case, the initial $IL_{noninfo}$ alternative therefore increases in consistency and hence becomes more attractive, despite being the poorest option in terms of reward rate. At first glance, this reasoning seems unapplicable to rats, which prefer the $IL_{noninfo}$ alternative in most studies. As shown below, the consistency tracking hypothesis shows that the pigeon–rat differences may rely on the type of TL stimuli used, and provides a way to test this prediction.

Stimulus tracking and consistency tracking are therefore different, although complementary processes. Their difference lies in their motivational origin. Stimulus tracking obeys the principle of incentive salience attribution to a cue (Berridge, 2007). After repeated pairings of a CS with a US, the CS becomes a source of incentive salience if the US transfers its motivational properties to the paired CS (US → CS)—a phenomenon that occurs in parallel to the predictive learning of their association (CS → US). The incentive salience of a CS associated with high food amounts or with a high probability of food should therefore be high, leading to fast approach and handling of the CS—that is, more successful pairings simply mean fewer opportunities to miss and hence inhibit the motivational transfer from the US to the CS. Stimulus tracking allows a cue that has been detected or expected to be approached and handled, increasing an organism's fitness value. However, consistency tracking motivates organisms differently: It increases with the inconsistency (uncertainty) of a CS–US pairing. Associative inconsistency prolongs uncertainty about the outcome, which motivates organisms to look for quick disambiguation (Anselme, 2023). To reduce ambiguity (or uncertainty) duration, organisms should not be focused on the CS or the US (stimulus tracking) but rather on the attempt to find consistent pairings at the TL level (for examples unrelated to the paradoxical choice task, see Anselme, 2021; Anselme & Güntürkün, 2019). In the wild, consistency tracking increases fitness because it speeds up the learning of the causal structure of an uncertain environment, leading to better decisions in the future and to reduce ambiguity duration in that environment (Anselme, 2023).

A corollary to this view is that organisms should choose the $IL_{noninfo}$ stimulus when they lack opportunities to produce consistency tracking (at the IL level) with the stimuli used at the TL level. It is suggested that consistency tracking or preference for the IL_{info} stimulus only occurs (a) if the TL+ stimulus and/or (perhaps to a lesser extent) the TL− stimulus have trackable features and (b) if the TL+ stimulus has features that differ from those of the TL− stimulus. In the absence of one of these two conditions or both, the TL–food consistency is not trackable at the IL level and organisms should focus on reward procurement (they should preferentially choose the $IL_{noninfo}$ alternative). Whether a TL− stimulus can be as significant as a TL+ stimulus under traditional testing is quite unlikely, as explained in section 4. We aim to show that, compared to most pigeon studies and for several reasons, the TL+ and/or TL− stimuli often used in rat studies are inappropriate to generate trackable consistent pairings with reward. A TL stimulus that satisfies both conditions should have several properties, defined and exemplified in the next subsections.

TL Stimuli Must Be Discrete and Spatially Localizable

A CS can be attributed to incentive salience if discrete, localizable, and, in a sense, manipulable. For example, some rats approach a retractable lever predictive of food delivery because this lever is occasionally made available for a short duration in one location and favors physical interaction (sniffs, nibbles, presses). By contrast, a nonmanipulable CS like a tone, a light, or a food port is poorly attractive to rats—even if it is localized, associated with food, and discriminated from other cues (Beckmann & Chow, 2015; Chow et al., 2017; Cleland & Davey, 1983; Meyer et al., 2014). Pigeons mostly show the reverse tendency, at least with respect to levers and localized lights: They are prone to peck at illuminated response keys but do not easily interact with levers—contrary to rats, the pigeon's visual system is excellent and of primary importance to detect food items based on their color and contrast with the background (Hodos, 1993). If incentive salience (focal search) is closely related to the expression of consummatory behaviors, it is hardly surprising that stimulus manipulability is important to motivate approach and physical contact—similarly to what happens with TL stimuli in the paradoxical choice task (e.g., González & Blaisdell, 2021; Trujano & Orduña, 2015).

What does this tell us about choice behavior at the IL level? According to the consistency tracking hypothesis, incentive salience takes place at the TL level, not the IL level. Thus, stimulus manipulability at the TL level should not be important to make a choice at the IL level. Nevertheless, the TL stimulus must be discrete and localizable to be tracked—to induce a decision—at the IL level. The violation of these two properties may explain a preference for the $IL_{noninfo}$ alternative, as illustrated below.

Let's see what happens in a situation in which consistency behind the IL stimuli has a low or perhaps no trackability. González-Torres et al. (2020) exposed pigeons to a traditional paradoxical choice task, although they used atypical IL and TL stimuli. The IL stimuli were two treadles (or levers, located on two opposite panels) that

had to be pressed to initiate choice, and the TL stimuli were ambient lights of distinct colors, presented for 10 s before food was delivered (or not). The selected treadle remained available during exposure to the associated ambient light, and the pressing responses to the treadle were recorded. Although the pigeons could discriminate the TL stimuli (the number of pecks during their presentation was a function of the probability to receive food), most individuals preferred the $IL_{noninfo}$ alternative. However, the same pigeons came to prefer the IL_{info} alternative when key lights instead of ambient lights were used as TL stimuli—and also key lights instead of treadles as IL stimuli. For the authors, the $IL_{noninfo}$ choice was an effect of the treadle more than the ambient lights because stimulus tracking (also called "sign-tracking") can occur when the secondary reinforcer is an ambient stimulus. However, we saw above that stimulus tracking does not happen in rats, at least with tones (Cleland & Davey, 1983; Meyer et al., 2014), despite these animals being particularly good in this task with levers. The reason we mentioned is that a tone cannot be handled, and hence is not or is poorly attributed to incentive salience (but, in pigeons, see Patterson & Winokur, 1973). However, we also specified that manipulability of a TL stimulus should not play a role at the IL level, where choice is made, although the TL stimulus should be discrete and localizable to orient choice. A tone is discrete and more likely to be localizable than ambient light, because it emerges from a loudspeaker. In nature, the localizability of sounds in general allows organisms to use them as predictors of potential food (prey) or danger (predator), offering them the opportunity to track consistent sound–food pairings—like what we assume typically happens for TL–food associations at the IL level in the paradoxical choice task. Accordingly, rats can track pairings involving tones in the paradoxical choice task (e.g., Alba et al., 2021; Cunningham & Shahan, 2019).

By contrast, ambient lights cannot be localized and hence are in no way predictive of food in any context. So, natural selection was unable to shape organisms to track ambient lights. In terms of the conditions for paradoxical preference defined earlier, ambient lights satisfy condition 2 (because they are contrasted with different colors) but not condition 1 (because diffuse cues cannot be tracked). In the study by González-Torres et al. (2020), however, the treadles may explain why the pigeons seemed to respond more to a TL+ than a TL− ambient light, while preferring the $IL_{noninfo}$ alternative. Once a treadle (IL stimulus) was selected and its associated ambient light (TL stimulus) was being shown, the pigeons actually responded to the ambient light via the treadle, which remained available and was the unique local stimulus with which an interaction was possible. So, their behavior was influenced by the ambient light (the pigeons responded more when a TL+ light rather than a TL− light was turned on), but this influence was indirect/facilitatory because they only responded to the IL stimulus (which was both the choice stimulus and a poor TL stimulus). So, the treadle may have played a role in motivating a response in association with an ambient light, but the light acted as a facilitatory cue whose consistency was not tracked—causing a preference for the $IL_{noninfo}$ alternative.

TL+ and TL− Stimuli Must Be Sensorily Distinguishable

In pigeons, key lights involve a dominant sensory modality (vision) and they are sensorily distinguishable (of different colors) at the TL level, resulting in a preference for the IL_{info} alternative. In rats, many studies have used levers as TL stimuli in both alternatives, and these studies show that rats prefer the $IL_{noninfo}$ alternative. Levers can be touched, an important sensory modality for rats, but they cannot properly be sensorily distinguished because they are visually and tactually very similar, if not identical. Of course, they are discriminable at the TL level because they are localized events (e.g., left vs. right on a wall). As noted earlier, the substantial work by Orduña and his colleagues demonstrated that the levers are discriminable, at the TL level, because they generate a number of responses that varies according to the probability of food that follows (e.g., Alba et al., 2021; López et al., 2018; Martínez et al., 2017). However, this property alone is possibly not sufficient to generate consistency tracking at the IL level. In experiments with multiple levers (e.g., Alba et al., 2021; Martínez et al., 2017), there is a lack of stimulus-dependent distinguishability, such as visual features (e.g., red vs. green color), touch sensations (e.g., smooth vs. gained surface), or auditory perceptions (quiet vs. loud sound). Lever location alone is stimulus-independent because it is a function of the animal's orientation relative to the stimulus. Two levers might therefore be difficult to distinguish at the time of choice—that is, before one of them is inserted. Although overly speculative, such a view provides a post hoc explanation for when paradoxical choice is or is not observed in rats. Martínez et al. (2017) used levers for the IL_{info} and the $IL_{noninfo}$ alternatives. A red and a blue light served as TL+ and TL− stimuli, respectively, for the IL_{info} option and also as TL± stimuli for the $IL_{noninfo}$ option. Although rats are poorly receptive to lights, we argue that the use of the same lights for both options may have induced even more confusion, and rats favored food over information. Of note, this is not to say that incentive salience comes to control choice in the absence of consistency tracking at the IL level. It just means that animals will favor the most profitable option ($IL_{noninfo}$), irrespective of the upcoming TL stimuli, with incentive salience operating only at the TL level once a lever-light compound is revealed.

We suggest that the opportunity to track consistent TL stimuli–food pairings is less likely when the TL stimuli involved are too similar. Current findings support this view that stimulus-dependent sensory qualities are a crucial determinant of preference at the IL level. For example, in Experiment 1 with rats, Alba et al. (2021) found optimal choice with levers only and TL durations of 10, 30, and 50 s. By contrast, Chow et al. (2017) used TL durations of only 10 s with rats and found a suboptimal choice with a lever as TL+ and blackout as TL−. In Experiment 2, Alba et al. (2021) used TL durations of 50 s and found suboptimal preference when the TL+ was a light-tone compound and the TL− a blackout (like Cunningham & Shahan, 2019), but optimal preference when the TL+ was a light (a stimulus to which rats seem poorly receptive). In short, with levers, condition 1 for paradoxical choice is satisfied (the TL+ and TL− lever can physically be tracked) but condition 2 is not (the TL stimuli used are sensorily too similar, especially the TL+ and TL−). Not satisfying condition 2 yields some confusion that may prevent consistency tracking and force the organisms to focus on reward maximization. This should particularly be true when the TL+ and TL− stimuli are identical because they are also both consistent in their association with food (TL+ → food; TL− → no food), so even more difficult to distinguish at the IL level: The TL+ stimulus may partially be associated with the absence of food, and conversely with respect to the TL− stimulus—undermining the feeling of consistency in the IL_{info} alternative.

Such an interpretation requires further development through concrete examples. Daniels and Sanabria (2018) reported that paradoxical

choice in rats seems to occur only if the TL+ and TL− stimuli are associated with distinct sensory modalities (see above, e.g., Alba et al., 2021; Chow et al., 2017; Cunningham & Shahan, 2019). However, the experimental results available do not demonstrate that two distinct sensory modalities are required; they only demonstrate that using sensorily too similar stimuli as TLs in the IL_{info} alternative causes a preference for the $IL_{noninfo}$ alternative. Ojeda et al. (2018) used four different 10-s sounds with rats (TL+: pure tone of 78 dB; TL−: buzzing sound of 74 dB; TL ± 1: white noise of 74 dB; TL ± 2: clicking sound of 74 dB). They found that rats may prefer the IL_{info} alternative, provided that it only causes moderate losses (e.g., 40% reward probability against an $IL_{noninfo}$ alternative offering 50% reward probability). However, when the IL_{info} alternative offers a 20% reward probability, like in most studies with pigeons, rats switch their preference toward the $IL_{noninfo}$ alternative. The limited tolerance of rats to losses in this study might be the consequence of the lower consistency trackability of a sound–reward pairing relative to a lever–food pairing at the IL level. Sounds may be localizable events, especially in a Skinner box, but possibly less than a lever and a 10-s duration is typically not sufficient to motivate consistency tracking (e.g., Cunningham & Shahan, 2019). Beyond that, Ojeda et al.'s (2018) study indicates that paradoxical choice may exist in rats with TL+ and TL− stimuli from the same sensory modality. In a recent study, González et al. (2024) tested rats with different sounds and a larger difference in reward rates between the IL_{info} (20% chance) and the $IL_{noninfo}$ (50% chance) alternatives, as well as longer TL durations (60 s). A relatively equivalent number of rats strongly favored the IL_{info} and the $IL_{noninfo}$ alternatives (7 vs. 10 in male and 8 vs. 12 in female). In similar configurations, some studies report suboptimal preference (Cunningham & Shahan, 2019, 2020), while other studies report clear-cut preference for the $IL_{noninfo}$ alternative (e.g., Alba et al., 2021). Although rats may respond differently from pigeons in this task for ecological reasons, a comparison with the studies mentioned above indicates that increasing the trackability of TL stimuli (using different sounds instead of similar levers, and perhaps a longer exposure to consistent TL stimuli) may improve rats' preference for information. It must be noted that, among the few studies conducted with rodent and nonrodent mammals, some of them failed to show true paradoxical choice with TL+ and TL− stimuli from the same sensory modality (Jackson et al., 2020; McDevitt et al., 2019; Molet et al., 2012). However, the use of lights of different colors (T. R. Smith et al., 2017) or of different shapes as TL stimuli (Bromberg-Martin & Hikosaka, 2009) induces paradoxical choice in rhesus monkeys (*Macaca mulatta*).

If a tone–food pairing is less trackable than a lever–food pairing at the IL level, this may explain why paradoxical choice seems to require longer durations of the TL stimuli when a tone rather than lever is used as TL+ with rats. Indeed, several studies report paradoxical choice with tones whose presentation lasts between 30 and 50 s, but not with tones of shorter durations (Alba et al., 2021; Cunningham & Shahan, 2019, 2020). In comparison, a TL+ lever of 10 s is sufficient to generate a paradoxical choice (Chow et al., 2017)—provided that the TL− stimulus is not a lever. The positive effect of a longer TL duration on preference for the IL_{info} alternative, for any kind of stimulus, has been well documented (Cunningham & Shahan, 2019; Lalli et al., 2000; Spetch et al., 1990, 1994). It can also be explained. In particular, the SiGN hypothesis suggests that, contrary to the TL ± stimuli, the TL+ stimulus acts as a conditional reinforcer because its onset provides the good news that food will be delivered (McDevitt et al., 2016). Thus, a longer TL+ stimulus has increased conditioned reinforcing effects, compared to those of the TL ± stimuli. The consistency tracking hypothesis interprets the effects of a longer TL duration differently but in a perfectly compatible way. This hypothesis posits that, under reward uncertainty, organisms try to find consistent associations to reduce ambiguity duration. So, they prefer the IL_{info} when the duration of the TL stimuli increases, because a longer exposure to TL+ and TL− decreases the cost of having to wait for disambiguation, a decrease that should be reinforcing. Contrary to the SiGN hypothesis, this view predicts that a TL− stimulus (information) should somehow be preferred to a TL ± stimulus (no information) because, despite being bad news, it resolves uncertainty by providing a reliable signal of what is coming next—a view indirectly or partially supported by several recent findings (Ajuwon et al., 2023; González & Blaisdell, 2021, 2023; Sears et al., 2022). In accordance with earlier developments, it is not surprising that long TL stimuli do not induce paradoxical choice when the stimuli are all levers or all lights with rats (Alba et al., 2021; Trujano & Orduña, 2015), which are sensorily too similar, and not even belonging to a relevant sensory modality for foraging behavior in the case of lights. However, a tone presented as TL+, but not as TL−, is both physically localizable and sensorily distinguishable and causes paradoxical choice when its duration is long enough.

TL Stimuli Must Be Compatible With the Animal's Ecology

We have argued that a preference for the IL_{info} alternative requires a TL+ and/or TL− stimulus that is physically localizable and sensorily distinguishable from the TL− stimulus. A third condition is necessary: The stimulus must be learnable and able to motivate a response to it. As already noted, this only occurs with the appropriate superimposition of a conditioning process on a preexisting behavior system shaped by natural selection (Timberlake, 1993, 1994). The failure to condition to events or the propensity to return to innate action patterns is traditionally interpreted in relation to learning—some associations cannot be easily established, or lead to the development of interfering responses—but might also result from a very weak CS–US association or from the inability of a US to transfer its motivational salience to a specific CS. In these cases, the CS–US association fails to directly affect behavior even if learned (Blaisdell et al., 1999; Holland, 1990). It is not the place to discuss this question, but these limitations can be related to unmatching between a conditioning task and an organism's ecology.

On this basis, it becomes obvious why key lights are more effective as secondary reinforcers for food in pigeons (as vision-oriented foragers) than in rats (which mostly use their senses of touch and smell to forage). In the paradoxical choice task, this means that, if a light–food pairing does not support conditioning (whether because it cannot be learned or because light cannot be incentivized relative to food), nothing can be tracked at the IL level. In other words, tracking the consistency of light–food pairings through the IL_{info} stimulus is more unlikely with rats, as opposed to pigeons. For example, rhesus monkeys show IL_{info} preference with flashing lights as TL stimuli because vision is a relevant sensory modality in primates for foraging (Bromberg-Martin & Hikosaka, 2009; T. R. Smith et al., 2017), and hence those stimuli are compatible with their ecology. Incompatibilities between conditioning and a behavior system related to an animal's ecology mean that condition 1 is not satisfied.

Tracking the consistency of TL lights is easier for pigeons than rats, but rats should be sensitive to scents in the process of showing paradoxical choice. However, one study used TL scents in rats and dogs and found a preference for the $IL_{noninfo}$ stimulus in both species—yet, both species are well known for their developed sense of smell (Jackson et al., 2020). Several factors may explain this unexpected result. First, the scents used represent a potential problem (rats: essential oils including patchouli, orange, frankincense, and helichrysum; dogs: cassia, peppermint, eucalyptus, and geranium). It is likely that rats and dogs can learn an association between any scent and food, but it can be questioned whether any scent is able to stimulate motivation for food similarly. As human beings, we could certainly learn that the smell of a flower or the smell of ammoniac are predictive of food, but our appetite is more likely to be stimulable through conditioning by the flower scent than by the ammoniac scent. Indeed, novel flavors in water cause lower weight gain than drinking unflavored water, suggesting that scents and flavors can unconditionally act as an indicator that food has been eaten and thus reduce appetite for longer, even when there was no caloric change (Seitz et al., 2020). In Jackson et al.'s (2020) experiments, we do not know how rats and dogs were receptive to those scents (mostly from nonedible plants and with sometimes full-bodied fragrances, such as peppermint and eucalyptus). Of note, Seitz et al. (2020) used the scent of peppermint tea but the nondiluted essential oils used in Jackson et al.'s study were probably of much higher concentrations in comparison. In case of repulsion for one or several of those scents, the food amount to be delivered by means of the $IL_{noninfo}$ stimulus could be favored to the detriment of consistency tracking via the IL_{info} stimulus. Second, the authors mentioned that, for rats and dogs in their procedure, the TL stimuli (information) in the IL_{info} alternative occurred in the same location where the food would be found. This was not the case for pigeons, which showed a paradoxical choice. This may have reduced the predictive value of the TL stimulus and discouraged consistency tracking at the IL level. All these reasons are speculative, and deeper investigation is necessary to determine whether any of them is correct or if other factors explain the relative avoidance of the IL_{info} stimulus by rats and dogs. However, they point to the importance of motivation at both the IL and TL levels to develop paradoxical choices.

Paradoxical Choice With Consistent Associations in Both Options

Most studies of paradoxical choice contrast a consistent (informative) and an inconsistent (noninformative) option. However, several other studies use two consistent options and yet show paradoxical preference (Belke & Spetch, 1994; Case & Zentall, 2018; Dunn & Spetch, 1990; Gipson et al., 2009; Kendall, 1974; McDevitt et al., 1997; Prokasy, 1956; Spetch et al., 1990): The animal is given a choice between a signaled 50% option in which the cues consistently predict food or no food (e.g., if green → food, if red → no food) and a 100% option in which a cue consistently predicts food (e.g., blue → food). Preferring the former to the latter option, instead of developing indifference, is incompatible with the consistency tracking hypothesis—which cannot therefore be a complete account of paradoxical choice.

Nevertheless, the consistency tracking hypothesis might explain why, in this configuration, no preference is shown for many training sessions. A. P. Smith and Zentall (2016) obtained indifference between both options across 30 sessions and Case and Zentall (2018) reported an emerging preference for the signaled 50% option only after 25 sessions. Kendall (1974) found paradoxical choice within 15 sessions in most of his pigeons, but they were trained with TL durations shorter in the suboptimal option than in the optimal option. Because of delay aversion (e.g., Mazur & Biondi, 2009), this may have directly contributed to their preference for the suboptimal option after all TL durations were equalized. Beyond this fact, the consistency tracking hypothesis cannot account for the slow emergence of paradoxical choice with consistent associations in both options, and other interpretations have been provided (e.g., Dunn et al., 2024; Laude et al., 2014; Stagner & Zentall, 2010). Nevertheless, paradoxical preference might somehow relate to the informational content of the signaled 50% option relative to the 100% option. As often argued since Shannon's (1948) seminal work, information only exists in the presence of uncertainty (Balsam & Gallistel, 2009; Friston, 2010). The opportunity to obtain a signal that disambiguates the outcome in the 50% option abolishes uncertainty, carrying some information, while there is nothing to disambiguate in the 100% option. Of course, this information is noninstrumental; it cannot be used in any way to change the outcome. However, noninstrumental information is sought in various tasks, even when a cost has to be paid for it (e.g., Bennett et al., 2016; Rodriguez Cabrero et al., 2019). The primacy of information, whether instrumental or not, may suggest the existence of an innate mechanism leading organisms to obtain information independently of its consequences—such as a reduction in the food amount received. One possibility for the slow development of paradoxical choice with two consistent options is that, in this configuration, pigeons need more time to learn where the informative option is and to become motivated by the reliability of its cues over the sessions. More research is necessary to clarify this question, and a confirmation of this interpretation would enrich the consistency tracking hypothesis.

Original Predictions of the Consistency Tracking Hypothesis

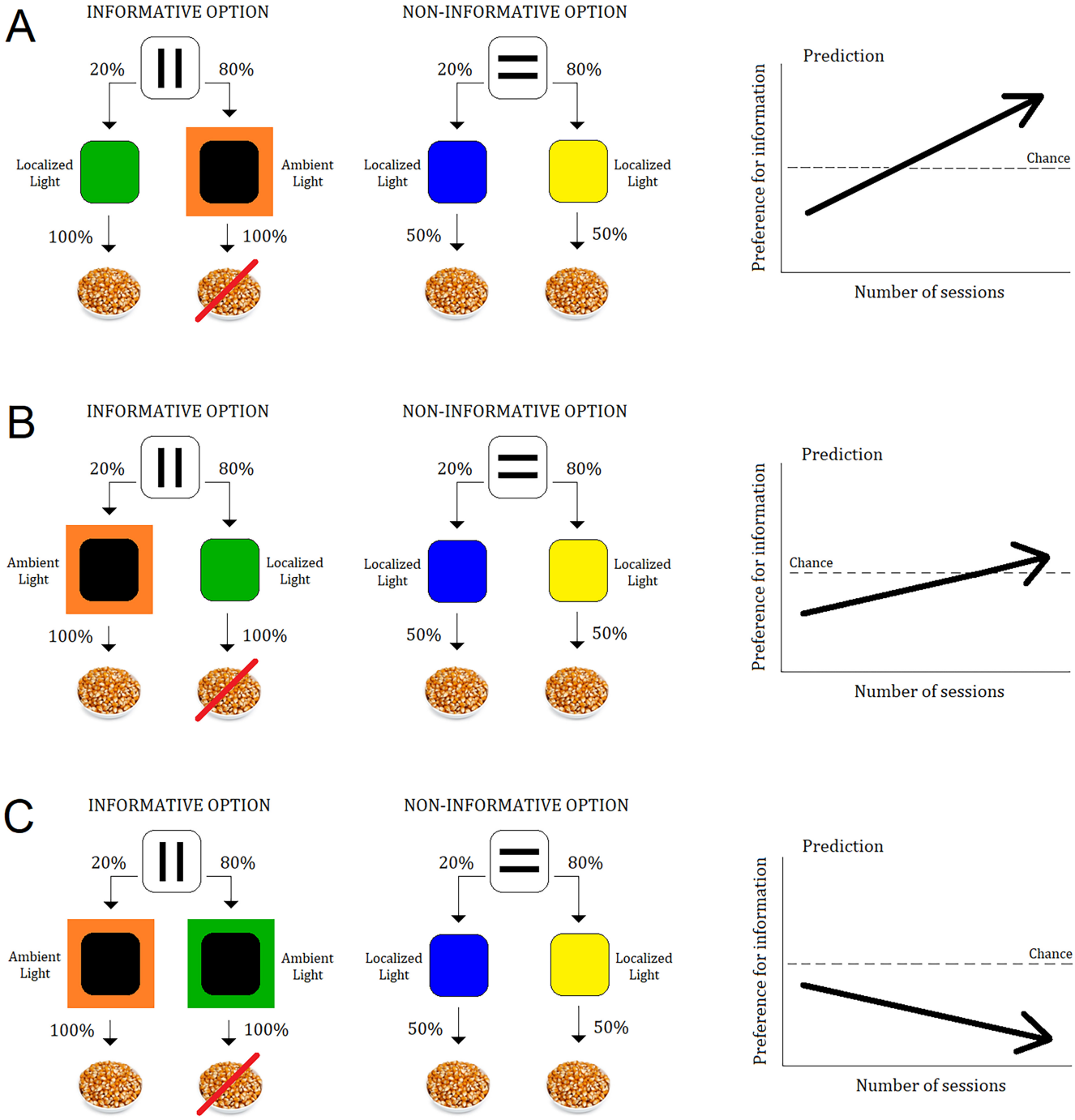
In this article, we suggested in accordance with empirical work (e.g., González & Blaisdell, 2021; Trujano & Orduña, 2015) that TL stimuli can be tracked through incentive salience attribution, once revealed to an animal—the attribution (measured as a response rate to a TL stimulus) being proportional to the probability that the stimulus is followed by food delivery. We also suggested, however, that IL stimuli are poorly attributed to incentive salience and determine choice based on the trackability of the TL stimuli–food pairings (see Anselme, 2022, 2023). Such a theoretical distinction is supported by the fact that animals may respond more to the TL+ stimulus while preferring the $IL_{noninfo}$ alternative, which contains only TL± stimuli (e.g., Alba et al., 2021; González-Torres et al., 2020). A consequence of our view is that the alternative with a TL+ stimulus will be chosen at the IL level only if the TL+ stimulus has properties that make its pairing with food trackable and distinguishable from the TL− stimulus, in addition to having a good fit to the animal's ecology and foraging behavior system.

The consistency tracking hypothesis makes predictions that are similar to those of other theories, even if the interpretations provided may differ, and are compatible with existing results. For example, it

predicts that using a localizable TL+ stimulus (key light for pigeons or lever for rats) and a nonlocalizable TL− stimulus (ambient light or blackout) should generate a paradoxical choice, as reported in several studies (Figure 2A; Chow et al., 2017; Cunningham & Shahan, 2019). However, the consistency tracking hypothesis also makes predictions relevant to the question discussed in this article

Figure 2

Predictions of the Consistency Tracking Hypothesis With Respect to Paradoxical Choice



Note. (A) Traditional configuration of stimuli known to induce a preference for the IL_{info} alternative in pigeons and rats. The TL+ stimulus is a localized key light and the TL− a nonlocalized ambient light. (B) Inversion of the TL+ and the TL− light conditions compared to the previous configuration is predicted to strongly reduce and perhaps abolish paradoxical choice. (C) The use of nonlocalizable ambient lights as TL+ and TL− stimuli should quickly and maximally favor the $IL_{noninfo}$ alternative. IL = initial link; info = information; noninfo = no information; TL = terminal link. See the online article for the color version of this figure.

and is not derivable from traditional theories. Thereby, the reverse situation with a nonlocalizable TL+ and a localizable TL− should strongly reduce preference for the IL_{info} alternative, and perhaps even cause preference for the $IL_{noninfo}$ alternative (Figure 2B). This is because, in the natural setting in which animals evolved, the consistency of a localizable TL+ stimulus is more likely to be tracked than that of a localizable TL− stimulus (McDevitt et al., 1997; Stagner et al., 2015): A TL+ stimulus (reliable predictor of food) is rare and tracking its associative consistency with food is always beneficial to survival, whereas a TL− stimulus (reliable predictor of no food) is very common—most environmental cues are not food predictors—and should therefore be learned as such but mostly ignored. Beyond the fact of offering better knowledge of the environment, why should a stimulus predictive of nonreward (TL−) be avidly tracked/sought? The trackability of its consistency is therefore unimportant. For example, introducing a 5-s delay between choice and the onset of the TL+ stimulus strongly reduces preference for the IL_{info} alternative, but only little change occurs when the 5-s delay precedes the TL− stimulus (McDevitt et al., 1997). In other words, even if the consistent absence of food provides useful information, organisms mainly search for its presence and will therefore be more prone to select the IL_{info} alternative when the TL+ stimulus rather than the TL− is trackable. A nonlocalizable TL+ makes it nontrackable and should therefore dampen the individual's willingness to select the IL_{info} alternative, despite reducing uncertainty.

Accordingly, in a recent study with rats, Ajuwon et al. (2023) found that a silent TL+ stimulus with an audible TL− stimulus delayed the development of a preference for the IL_{info} alternative and caused greater response variability, compared to an audible TL+ stimulus with a silent TL− stimulus. However, over the course of training, preference for the IL_{info} alternative increased and became equivalent in both situations. The authors suggested that this difference might result from a combination of two processes. First, the initial absence of preference with a silent TL+ stimulus is compatible with a conditioned reinforcement account, which predicts that no conditioning is possible in the absence of an explicit cue. Second, the late expression of a preference with the silent TL+ stimulus is compatible with the information hypothesis that the audible TL− stimulus is informative and stimulates responding, though to a lesser extent than the audible TL+ stimulus does. Although this explanation is plausible, we would like to note that silence is a nontrackable stimulus at the TL level, making the consistency of the silence–food pairing impossible to track at the IL level. Our experiment, described in Figure 2B, can disentangle both explanations. If a silent TL+ does not allow for conditioned reinforcement, an ambient light used as a TL+ is an explicit, conditional stimulus. It should therefore not induce any retardation in preference for the IL_{info} alternative in pigeons, relative to a key light, in case conditioned reinforcement is involved. By contrast, we predict that, because it is nonlocalizable, an ambient light is a nontrackable stimulus and should reduce or perhaps abolish preference for the IL_{info} alternative—irrespective of its explicit, conditional nature. Finally, a situation that should precipitate preference for the $IL_{noninfo}$ alternative would be to use nontrackable pairings for the TL+ and the TL− stimuli (Figure 2C). In this case, the consistency of the TL stimuli–food pairings become nontrackable at the IL level, leading organisms to favor food procurement in the $IL_{noninfo}$ alternative—despite the explicit, conditional nature of both cues in the IL_{info} alternative.

A related prediction would be that if we used two IL_{info} options, but for one IL_{info} stimulus the TL+ and TL− were difficult to discriminate from each other (e.g., light orange vs. dark orange), while for the other IL_{info} stimulus, the TL+ and TL− were easy to discriminate (e.g., blue vs. yellow), pigeons should have a preference for the IL_{info} stimulus that is associated with blue and yellow TL stimuli.

Mesolimbic dopamine plays a crucial role in the attribution of incentive salience to cues (Berridge, 2007), and we saw that incentive salience controls the reactivity to TL stimuli in pigeons (González & Blaisdell, 2021; González-Torres et al., 2020) and in rats (e.g., Martínez et al., 2017; Trujano & Orduña, 2015). The consistency tracking hypothesis predicts that dopamine-induced incentive salience has much less significance, if any, at the IL level. The question of how dopamine influences paradoxical choice has not really been investigated, apart from one study in which the basic conditions of the task were changed (A. P. Smith et al., 2018).

TL stimuli get their incentive properties from a transfer of the incentive value of their associated reward, and this process seems to relate to the uncertainty of cue timing. Indeed, Schultz and his team showed that dopamine signaling in the ventral tegmental area—a midbrain nucleus—migrates from the time of delivery of reward to the time of delivery of the CS that predicts reward (for a review, see Schultz, 1998). That is, when the delivery of a reward is surprising (unexpected), dopamine fires to that unexpected but important event. After CS–US learning, however, dopamine no longer fires when the reward occurs because the reward was expected. Instead, dopamine fires to the onset of the CS, because the CS is unexpected (unpredicted) at the time of its onset. This phenomenon can be interpreted in terms of learning (Schultz, 1998) as well as in terms of motivation (Anselme, 2013; Berridge, 2012). This makes the prediction that, if one were to measure dopamine firing in the ventral tegmental area at the beginning of acquisition of a paradoxical choice procedure, and again at the end of training when the task is well learned, we might predict a dopamine response to the food reward early in training, which then migrates to occur during the TL stimuli later in training. If the IL stimuli are just CSs more distal to reward delivery than TL stimuli are, dopamine signaling should eventually migrate to occur during the IL stimuli where it stays (because the onset of IL stimuli is usually always somewhat unpredictable). By contrast, if the IL stimuli do not promote incentive salience, as our hypothesis suggests, their onset should not be associated with intense dopamine signaling. However, TL stimuli (especially the TL+ stimulus) should continue to induce dopamine release late in training because their probability of occurrence is held relatively low.

Conclusion

Several theories account for various aspects of the paradoxical choice task, but they do not explain (or do not fully explain) the differences in preference between species—mainly pigeons and rats. If innate differential sensitivity to conditioned inhibition induced by the TL− stimulus was the exclusive process at stake, why paradoxical preference has been found in all the species tested would be hard to explain. Here, we have argued that sensitivity to conditioned inhibition is only part of the whole story and that the ability to become motivated to track the consistency of TL–food associations at the time of choice is crucial in this task. We described the conditions required for consistency tracking and showed that the TL stimuli are less often appropriate in rat studies than in pigeon studies.

Although partly speculative, our view generates a set of testable predictions that cannot be made by the other theories of paradoxical choice. If confirmed, our view would suggest that animals do not process IL and TL stimuli by means of the same psychological mechanisms and that interspecific differences in this task are less significant than often believed.

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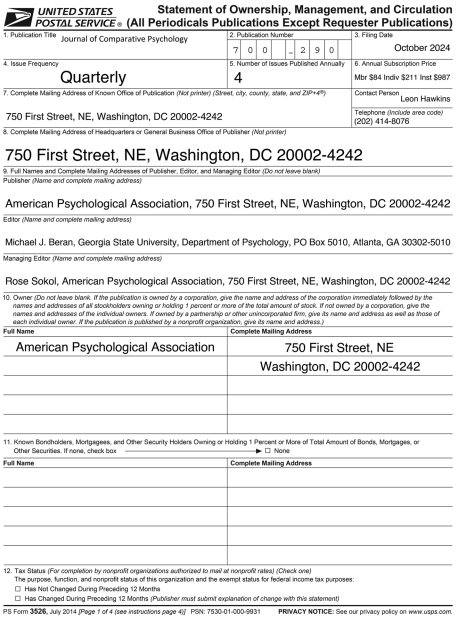

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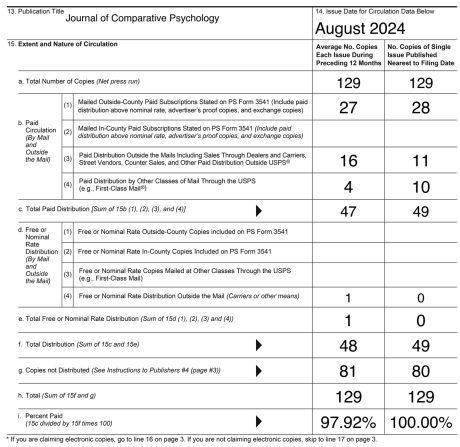

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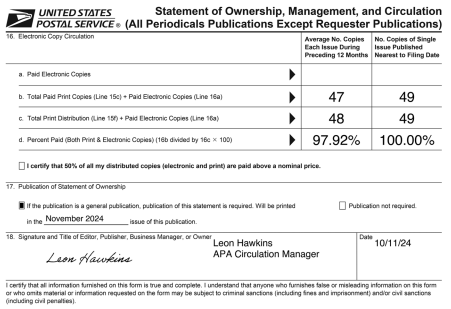

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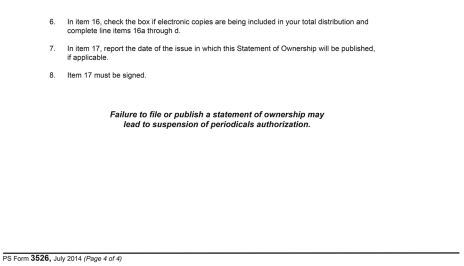

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