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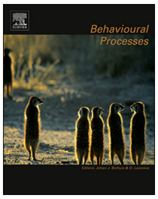

Differences in rats and pigeons suboptimal choice may depend on where those stimuli are in their behavior system

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ABSTRACT

Timberlake (1993) proposed that much learning research can be better understood in the context of *behavior systems theory*. Learning theories generally have not considered how procedures may interact with evolutionarily prepared foraging contexts, thereby leading to anomalous conclusions. An example of such a conclusion is the apparent species difference when given a choice between a lower percentage of signaled reinforcement (20%) and higher percentage of unsignaled reinforcement (50%). Pigeons generally show a preference for the suboptimal alternative. Rats, however, often choose optimally. Orduña et al. have suggested that rats choose optimally because they show conditioned inhibition to signals for nonreinforcement, whereas pigeons do not. We suggest, however, that such fundamental species differences are unlikely. Rather, differences in the search mode elicited by the stimuli, together with some generalization between the signals for reinforcement and nonreinforcement are more likely to account for the species differences in suboptimal choice. When we used a retractable lever as the signal for reinforcement and a light stimulus as the signal for nonreinforcement, the rats showed suboptimal choice, not unlike that of pigeons. In this case, how the conditioned stimuli conform to the animals' behavior systems natural predispositions appears to affect how the animals react to those stimuli. Thus, when the search modes are matched between species and there is no generalization between the two signals, similar behavior can be found. Timberlake's contribution of behavior systems provides an evolutionary context in which species differences in sensory, response, and motivational differences can be separated from learning differences.

1. Introduction

Certain learning theories (e.g., Hull, 1943) assume that responding can be manipulated by means of contingencies with largely unstated regard for context and organismic variables. Timberlake (1993), however, argued for a more organismic approach and put behavior change into the broader context of *behavior systems*, and the degree to which the reinforced behavior is consistent with the natural behavior of the organism (see also Bolles, 1970; Domjan and Galef, 1983). According to Timberlake, learning evolved initially to support experience-based alterations of already-functioning systems that allowed closer tracking of survival-related aspects of the environment. Thus, learning occurs and can be effectively studied within the context of a functional system (Timberlake and Lucas, 1989).

Such an approach suggests that brief predictive stimuli should tend to control behavior associated with proximate (or focal) search such as chase, approach, and capture, whereas longer stimuli should tend to control more general search processes such as travel, exploration, and investigation (Timberlake, 1993). Furthermore, if the animal interprets the stimulus as relating to a general search behavior it may elicit foraging behavior different from its focal search behavior (closer to chase and capture of prey).

According to Timberlake (1993), early laboratory researchers who developed learning apparatus and procedures may have incorporated some aspects of ecology and regulatory approaches in their procedures (e.g., pecking by pigeons and maze running by rats) but their theories generally did not include those ecological concepts and their procedures rarely noted the ecology that gave rise to the studied behaviors. Timberlake's message suggests that when species appear to show qualitatively different behaviors in response to similar procedures, one should probably look to differences in the natural ecology of the species, rather than conclude that the underlying learning mechanisms are different.

Following Timberlake's suggestion, we have applied a behavior systems approach to recent discrepancies in the reporting of economically suboptimal choice preferences between pigeons and rats. Rather

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than assuming that the two species differ in whether they show suboptimal choice or not, we have proposed that differences found between pigeons and rats may have originated from species-specific ecological differences in the conditions conducive to obtaining the effect.

To explain how we came to consider a behavior systems approach to the differences in findings between rats and pigeons we should first describe the procedures that gave rise to the differences in behavior observed.

2. The suboptimal choice task with pigeons

It is assumed that animals have evolved to gain the most benefit (energy) for the lowest cost to maximize their fitness (Stephens and Krebs, 1986). We have found, however, that under certain conditions animals deviate considerably from maximizing their rate of reinforcement (they choose suboptimally). There are several versions of this procedure that have been studied with pigeons (see Belke and Spetch, 1994; McDevitt et al., 2016; Spetch et al., 1990, 1994). The most striking example is one in which pigeons are given a choice between two alternatives, one that rewards them 20% of the time the other that rewards them 50% of the time (Stagner and Zentall, 2010). When given a choice between such discrepant probabilities, if the 20% reinforcement alternative is unsignaled, pigeons readily choose the 50% alternative maximizing energy intake. In the suboptimal choice task, however, if the 20% alternative is chosen, it results in a reward-associated stimulus 20% of the time, always followed by reinforcement, whereas 80% of the time it results in a different stimulus that is never followed by reinforcement (see Fig. 1). When outcome-correlated cues are used, choice preferences shift and pigeons show a strong preference for the 20% reinforcement alternative (see Fig. 2; Stagner and Zentall, 2010).

Follow-up research demonstrated that this preference does not result from the uncertainty of reinforcement associated with the optimal alternative (Zentall and Stagner, 2011). Apparently, although the signal for reinforcement (a win) associated with suboptimal alternative becomes a strong conditioned reinforcer, the signal for the absence of reinforcement (a loss) does not appear to become an effective conditioned inhibitor (Fortes et al., 2016; Laude et al., 2014; Stagner et al., 2011).

Earlier research using a somewhat different procedure may help to clarify the mechanism involved in this suboptimal choice. The procedure involved the choice between one alternative that always yielded a signal for 100% reinforcement and a suboptimal alternative that 50% of the time yielded a signal for 100% reinforcement but 50% of the time yielded a signal for the absence of reinforcement (see Fig. 3). The results with this procedure have been somewhat mixed, although they generally reported a preference for suboptimal choice (Belke and Spetch, 1994; McDevitt et al., 2016; Spetch et al., 1990, 1994).

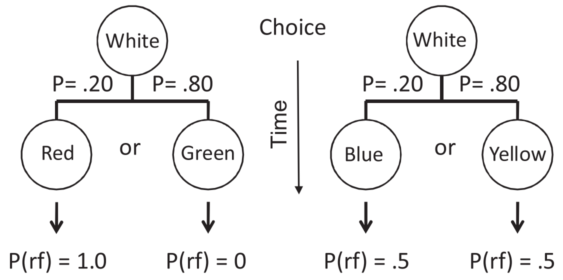

Fig. 1. Training: Choice trials: one alternative, associated with 20% reinforcement, led to a signal (Red) for reinforcement on 20% of the trials and a signal (Green) for the absence of reinforcement on 80% of the trials (overall 20% reinforcement). The other alternative led to either of two signals, both of which led to a signal for 50% reinforcement (overall 50% reinforcement). After Stagner and Zentall (2010).

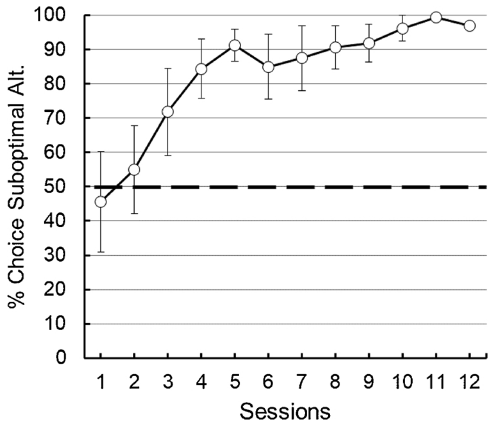

Fig. 2. Choice of the 20% signaled reinforcement over 50% unsignaled reinforcement by pigeons. After Stagner and Zentall (2010).

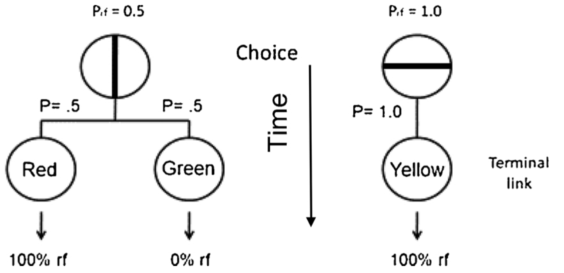

Fig. 3. Training: Choice trials: one alternative, associated with 50% reinforcement, led to a signal for reinforcement on 50% of the trials (red) and a signal for the absence of reinforcement on 50% of the trials (green); overall 50% reinforcement. The other alternative always led to a signal for 100% reinforcement (yellow). After Smith and Zentall (2016).

The conclusion appears to be that pigeons choose the suboptimal alternative primarily based on the *value* of the conditioned reinforcer that follows choice (Smith and Zentall, 2016; Stagner et al., 2012; Zentall et al., 2015) rather than on the probability of reinforcement associated with the two alternatives at the time of choice. Thus, if pigeons are given a choice between 50% signaled reinforcement and 100% reinforcement, both signals are associated with 100% reinforcement and indifference has been found (Smith and Zentall, 2016; see Fig. 4).

Several theories have been proposed to account for why pigeons choose suboptimally. Based on the results with the 20% signaled versus 50% unsignaled alternative (Fig. 1) it has been proposed that signals

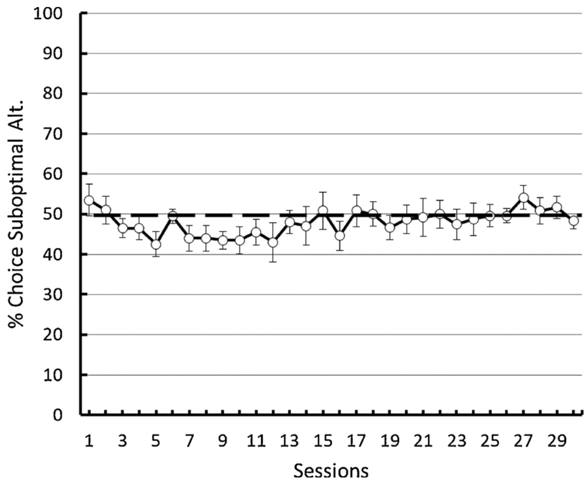

Fig. 4. Choice of 50% signaled reinforcement over 100% reinforcement by pigeons. After Smith and Zentall (2016).

following choice of the suboptimal alternative provide information, whereas those that follow the optimal alternative do not (Blanchard et al., 2015; Vasconcelos et al., 2015). Similarly, Cunningham and Shahan (2018) suggest that the cue for reinforcement following suboptimal choice signals reinforcement sooner than the cues following optimal choice. Positive contrast (or what McDevitt et al., 2016 call signals for good news) between the expected value of the suboptimal alternative at the time of choice and upon the appearance of the signal for reinforcement that follows has also been proposed (Smith and Zentall, 2016; Stagner and Zentall, 2010). This hypothesis has been supported by the results of research that has found a reliable preference for the suboptimal alternative with continued training (Case and Zentall, 2018).

If the probability of reinforcement associated with the conditioned reinforcers that follow choice do not play a major role in choice, it suggests that stimuli that predict the absence of reinforcement (conditioned inhibitors) do not inhibit choice of the suboptimal alternative. Stimuli associated with the absence of reinforcement may not affect pigeons choice because in nature, such stimuli may simply encourage the animal to look elsewhere and perhaps encounter a stimulus that predicts reinforcement. In the present procedure, however, pigeons cannot reject such stimuli to increase the probability of encountering a conditioned reinforcer. According to behavior systems theory, a stimulus associated with the absence of reinforcement should interfere with focal search (Tinsley et al., 2002) but may not affect choice on later trials. Furthermore, in nature, approaching a conditioned reinforcer (e.g., a tree signaling ripe fruit) would tend to increase the probability of finding more ripe fruit. In the suboptimal choice procedure, however, choice of the suboptimal alternative does not increase the probability of reinforcement because the probability of reinforcement does not change with repeated choice of the suboptimal alternative.

3. The suboptimal choice task with rats

Initial studies with rats using a design similar to that used by Stagner and Zentall (2010; see Fig. 1) found that rats tended to choose optimally (Roper and Baldwin, 2004; Trujano and Orduña, 2015). In these studies, a choice response to one of two levers resulted in the presentation of diffuse stimuli (i.e., spatially- and color-differentiated lights or tones of differential frequency) either correlated or uncorrelated with reinforcement. The researchers hypothesized that, unlike pigeons, which appear to disregard the frequent losses associated with choosing the suboptimal alternative, rats are sensitive to the signals for a loss (Martínez et al., 2017; Trujano et al., 2016; Trujano and Orduña, 2015).

Evidence that rats are sensitive to loss signals (conditioned inhibitors) was shown by means of a conditioned summation test (Rescorla, 1969) in which choice of the suboptimal alternative resulted in both the cue for reward and the cue for omission presented simultaneously (Trujano et al., 2016). The results of the conditioned summation test showed that presenting the loss signal together with the signal for a win attenuated responding. This result led to the hypothesis that pigeons and rats may differentially weigh risky choice outcomes when they are preceded by outcome-correlated cues. Although a species difference in the susceptibility to suboptimal choice is a possible conclusion, one should first examine the possibility that differences in the stimulus conditions under which the two species were tested may have been responsible for the differences in findings.

Chow et al. (2017) hypothesized that the light or tone used as a win signal in previous research may not have been effective conditioned reinforcers or they lacked sufficient *incentive salience* (Robinson and Berridge, 2008). Incentive salience refers to the tendency to attribute greater value signals of reward relative to their purely predictive value. Individuals display incentive salience to a stimulus by showing relatively greater amounts of approach and contact with the stimulus (sign tracking; Hearst and Jenkins, 1974), while a lack of incentive salience is associated with relatively greater amounts of approach and contact with the location of reward delivery (goal tracking; Boakes, 1977). For example, pigeons often display sign tracking to lights (Brown and Jenkins, 1968), stimuli commonly used in suboptimal choice research. Conversely, rats tend to show goal tracking to reward-predictive lights and tones (Beckmann and Chow, 2015; Boakes, 1977), whereas they tend to exhibit sign tracking to retractable levers used as signals for reward (Beckmann and Chow, 2015). For this reason, Chow et al. (2017) used the appearance of a lever as the win signal and found significantly greater suboptimal choice than with a light as the win signal (see Fig. 5). Therefore, the attribution of incentive salience to reward-paired stimuli appears to be an important factor in promoting various forms of suboptimal decision making (Morrison et al., 2015).

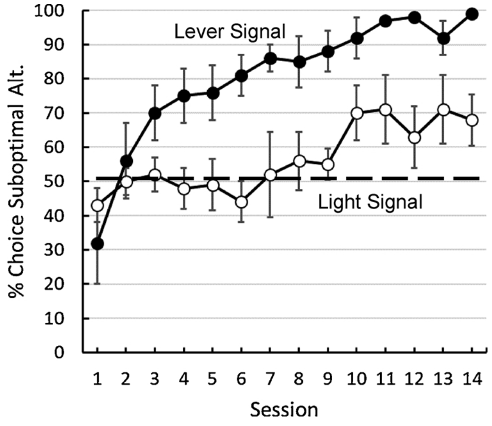

Fig. 5. Choice of 20% signaled reinforcement over 50% unsignaled reinforcement by rats. After Chow et al. (2017).

Inspired by a behavior systems perspective, we hypothesize that visual cues represent different levels of search for rats and pigeons. The feeding sequence in the rat typically begins with responding related to general search characterized by attention to novelty and search for cues such as lights or tones that predict the location or timing of food. This level may be characterized by approach-and-investigate behaviors. By our hypothesis, for rats, lights and tones would likely activate a general search but the appearance of the retractable lever would be more likely to activate behavior more specific to the capture of prey (focal search). We propose that for the pigeon, visual stimuli very likely directly trigger focal search characterized by the capture of prey. Thus, for both species, stimuli that are associated with focal search would be capable of developing incentive salience, whereas other stimuli (e.g., lights and tones for rats) may activate general search. How diffuse the stimulus is (e.g., tones and some lights) and the duration of the stimulus are likely to affect the particular search mode, as well.

4. Incentive salience: between-subject vs. between-stimulus effects

An important finding from Chow et al. (2017) is that individual differences in sign tracking *rate* were not predictive of suboptimal choice (see also Smith et al., 2018; Martínez et al., 2017); this is important as incentive salience often refers to differences between individuals' propensity to display sign versus goal tracking behavior (e.g., Berridge and Robinson, 2016). However, findings with suboptimal choice procedures corroborate previous research suggesting that different stimuli also affect the degree of sign tracking behavior (Beckmann and Chow, 2015; Chow and Beckmann, 2018; Chow et al., 2017; Meyer et al., 2014; Singer et al., 2016). For example, all rats demonstrate sign tracking when the appearance of a lever signals a win (Chow and Beckmann, 2018; Martínez et al., 2017; Smith et al., 2018). Importantly, using a retractable lever as a cue can generate suboptimal choice (Chow et al., 2017; Smith et al., 2018 c.f. Martínez et al., 2017), whereas lights tend to produce goal tracking and do not generate suboptimal choice (Chow et al., 2017; Trujano and Orduña, 2015).

In the context of behavior systems theory, the finding that lights (which tend to elicit goal tracking in rats) do not predispose rats towards suboptimal preferences to the degree that levers (that elicit sign tracking; Chow et al., 2017) does raise the possibility that the lever is tapping into a different search strategy from the rat's behavioral repertoire. Thus, the lever may serve as a better conditioned reinforcer for the rat because it is a moving object that makes a noise and because it relies more on the tactile information conducive to rats' tendencies to handle and manipulate their food during consumption. Alternatively, a light might serve as a better conditioned reinforcer to a pigeon, as the pigeon relies heavily on vision for finding and consuming food. Furthermore, the sign tracking that is elicited in both species by the different stimuli (i.e., pecking towards lights for pigeons and grabbing, sniffing, and nibbling levers for rats) may reflect the tendency of that stimulus to be consistent with the species' consummatory behavior. Thus, incentive salience may be an expression of a behavior mode engaged by specific stimulus-outcome relations. The stimulus that serves as a better conditioned reinforcer for both species elicits sign tracking behavior that might reflect the ability of that stimulus to elicit the appropriate consummatory behavior.

It is relatively easy to demonstrate that pigeons will choose suboptimally when the discriminative stimuli resulting from the choice are visual cues that produce sign tracking. If the above analysis is correct, however, it should be relatively difficult to demonstrate suboptimal choice when the discriminative stimuli are auditory cues, stimuli not generally associated with proximal reinforcement.

5. Incentive salience: necessary but may not be sufficient

To further assess the role of sensitivity to losses, Martínez et al. (2017) used four different levers spatially located on the left and right of the front and back of the experimental chamber. Their results showed that, despite the use of a lever as a win signal, the rats preferred the optimal alternative when the appearance of a different lever signaled a loss.

One explanation for the discrepant results between Martínez et al. (2017) and Smith et al. (2018) may be that the lever stimuli used by Martínez et al. (2017) for both the win and loss events produced some generalization between those win and loss signals. Indeed, Fortes et al. (2016) showed that when a loss signal is made to weakly predict reward (e.g., less than 10% of the time), pigeons' suboptimal preference sharply declined.

6. Concluding remarks

Following Timberlake's approach, we have taken into account several factors, beyond simple procedural and training differences that may help decipher discrepancies between species in their suboptimal preferences, including the stimulus-specificity of incentive salience attribution. Intuitively, it is reasonable to conclude that conditions conducive to suboptimal preference for one species should also be sufficient for another; however, the ability of different stimuli to serve as more or less effective conditioned reinforcers across species suggests otherwise. Indeed, behavior systems theory would suggest that different stimuli become associated with different aspects of reward-related behavior that are determined by both the reward itself and species-specific foraging behavior (Timberlake, 1994). Therefore, the question is not '*do rats choose suboptimally,*' but rather '*under what conditions are rats predisposed to respond suboptimally,*' and '*why might these differences exist?*' In other words, it is important to define the boundary conditions for the suboptimal choice effect across species. As it stands, the existing literature appears to suggest that suboptimal choice relies largely on having a stimulus that sufficiently taps into species-specific, reward-related behavior that competes with cooccurring, economically advantageous operant contingencies (Beckmann and Chow, 2015; Cunningham and Shahan, 2018; Dayan et al., 2006).

Beyond pigeons and rats, the list of species demonstrating suboptimal choice has already grown to include starlings (Vasconcelos et al., 2015; Fortes et al., 2016), rhesus macaques (Blanchard et al., 2015; Bromberg-Martin and Hikosaka, 2009; Smith et al., 2017) and humans (Iigaya et al., 2016; Lalli et al., 2000). Thus, understanding the boundary conditions for the effect across species will become increasingly important in establishing the common behavior mechanisms underlying decision-making. Timberlake's behavior systems theory may aid future studies directed toward such a goal.

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