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How competitive is cue competition?

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Abstract

Cue competition refers to phenomena indicating that learning about the relationship between a cue and an outcome is influenced by learning about the predictive significance of other cues that are concurrently present. In two autoshaping experiments with pigeons, we investigated the strength of competition among cues for predictive value. In each experiment, animals received an overexpectation training (A+, D+ followed by AD+). In addition, the training schedule of each experiment comprised two control conditions—one condition to evaluate the presence of overexpectation (B+ followed by BY+) and a second one to assess the strength of competition among cues (C+ followed by CZ−). Training trials were followed by a test with individual stimuli (A, B, C). Experiment 1 revealed no evidence for cue competition as responding during the test mirrored the individual cue–outcome contingencies. The test results from Experiment 2, which included an outcome additivity training, showed cue competition in form of an overexpectation effect as responding was weaker for Stimulus A than Stimulus B. However, the test results from Experiment 2 also revealed that responding to Stimulus A was stronger than to Stimulus C, which indicates that competition among cues was not as strong as predicted by some influential theories of associative learning.

Keywords

Pigeons; autoshaping; cue competition; overexpectation

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In any learning situation, the occurrence of a significant event (e.g., food, threat) is preceded by multiple cues. Humans and animals are able to use such cues for predicting upcoming outcomes. Acquiring knowledge about the relationship between a cue and an outcome is not merely a function of the co-occurrence of the two events, but can also depend on the learning histories of other cues that are concurrently present. Thus, cues can compete with each other for predictive value. The aim of this study was to investigate the strength of competition among cues.

One example for cue competition is the blocking effect where learning about the relationship between a cue and an outcome is impaired if the cue is accompanied by another stimulus that has already been established as a signal for the same outcome (e.g., Kamin, 1969). In Kamin's experiment, rats initially received fear conditioning in which a tone (Stimulus A) was repeatedly paired with footshock (A+). Then, Stimulus A was presented together with a light (Stimulus X), and this compound was also repeatedly followed by a footshock (AX+). During a final test, rats responded with less fear towards Stimulus X presented by itself than animals in a control group that received the same number of AX+ trials, but which lacked the pre-training with A+. Thus, prior learning about Stimulus A blocked learning about Stimulus X.

Another example for cue competition is the overexpectation effect, which refers to a decrease in responding towards a well-established cue due to further pairings of the stimulus with its outcome if those additional pairings occur in the presence of another well-established signal for the same outcome. Using a magazine approach procedure with rats, Rescorla (2006) initially established responding towards three individual stimuli by pairing each stimulus with food (A+, X+, Y+). Subsequently,

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two of the stimuli received further training in which they were presented as a compound that was followed by the same outcome (AX+). A final test revealed weaker responding to Stimulus X than Stimulus Y, indicating that the additional training in compound with Stimulus A caused decrements in the predictive value of Stimulus X.

Blocking, overexpectation, and other cue competition effects have been demonstrated in a variety of species ranging from honeybees (e.g., Couvillon & Bitterman, 1989) to humans (e.g., Dickinson, Shanks, & Evenden, 1984), and across different experimental procedures, including aversive (e.g., Wagner, Logan, Haberlandt, & Price, 1968), appetitive (e.g., Lattal & Nakajima, 1998), and neutral (e.g., Melchers, Üngör, & Lachnit, 2005) learning tasks. However, there have also been reliable failures to find evidence for competition among cues (e.g., Maes et al., 2016). Therefore, some authors suggested that the degree of interactions in learning across cues might vary along a continuum depending on procedural variables (e.g., Maes et al., 2016; Urcelay, 2017). The assumption of such a continuum raises the question about the strength of cue competition. This question is also relevant for the evaluation of associative learning theories as they differ in the degree of cue competition that is predicted for a given learning situation. However, the majority of experiments on cue competition were designed to detect whether or not cues compete for predictive value, but provided no means to discern different levels of cue competition.

One experimental approach for assessing the strength of cue competition was provided by Uengoer, Lotz, and Pearce (2013). Using a human predictive learning task, the authors trained participants with a blocking procedure of the form A+, AX+, where Stimulus A could be used to predict the outcome on both trial types and Stimulus X provided only redundant information. To confirm that the blocking procedure results in impaired learning about Stimulus X, participants received additional trials with BZ+, where Stimuli B and Z were equally predictive of the outcome. Further assessment of the strength of cue competition was provided by including trials that comprised a simple discrimination of the form CY+, DY−, where Stimuli C and D consistently signalled the presence and absence of the outcome, respectively, whereas Stimulus Y was uninformative. During a subsequent stage, Uengoer et al. tested responding to the individual Stimuli X, Y, and Z. Their experimental design allowed to discern three different levels of cue competition (no competition, massive competition, and moderate competition).

If there was no cue competition, then responding during the test should have mirrored the individual cue–outcome contingencies of the stimuli (e.g., Bush & Mosteller, 1951). Thus, responding should be similar across the stimuli that were consistently followed by the outcome (Z and X) with each of the responses being stronger compared with responding to Stimulus Y that was paired with the outcome only on half of its presentations (Z = X > Y).

If cues competed massively for predictive value, then Stimulus X that provided only redundant information should have elicited weaker responding compared to both Stimulus Z that was accompanied by a stimulus with equal predictive value and Stimulus Y that was uninformative for the simple discrimination (Z > Y > X)—a pattern that is predicted by a number of influential theories of associative learning (e.g., Gluck & Bower, 1988; Pearce, 1994; Pearce & Hall, 1980; Rescorla & Wagner, 1972).

The results of Uengoer et al. (2013) rather indicated a moderate form of cue competition. Their test results yielded evidence for cue competition in form of a blocking effect as responding was weaker to Stimulus X than Stimulus Z. However, the strength of cue competition was moderate rather than massive, which was indicated by stronger responding to Stimulus X than Stimulus Y (Z > X > Y; e.g., Vogel & Wagner, 2017). Corresponding evidence for moderate cue competition has been documented in humans (Jones & Zaksaite, 2018; Uengoer, Dwyer, Koenig, & Pearce, 2019), rats (Jones & Pearce, 2015; Pearce, Dopson, Haselgrove, & Esber, 2012), and pigeons (Pearce et al., 2012).

Thus, previous research indicates that cue competition operates in a moderate form. However, all the empirical evidence supporting this conclusion comes from studies employing blocking procedures. To assess whether moderate cue competition can be considered as a general principle, it is therefore necessary to extend the range of experimental procedures. If moderate effects of cue competition can be found in the context of other cue competition phenomena, this would be a challenge to some influential theories that shaped our understanding of animal learning. Therefore, we investigated the strength of cue competition in the context of overexpectation. Each of two experiments employed an autoshaping paradigm (Hearst & Jenkins, 1974), in which pigeons were trained to anticipate the availability of food (unconditioned stimulus, US) on the basis of visual cues (conditioned stimuli, CS).

Similar to the approach taken by Uengoer et al. (2013), we employed an experimental design that allowed differentiating between massive, moderate, and no cue competition. During the first learning phase, four individual stimuli were each paired with food (A+, B+, C+, D+). In the second phase, Stimuli A and D were presented together and followed by the same US (AD+), whereas conditioning of Stimulus D presented individually was continued (D+). Thus, the training schedule with Stimuli A and D constituted an overexpectation protocol that has been suggested by Rescorla (2006), who successfully demonstrated competition effects with this approach. To confirm that the overexpectation protocol decreased the predictive value of Stimulus A, the second phase also comprised trials in which Stimulus B was combined with a novel stimulus and followed by the same US (BY+). To examine the strength of cue competition, Phase 2 included additional trials in which Stimulus C appeared together with a novel stimulus,

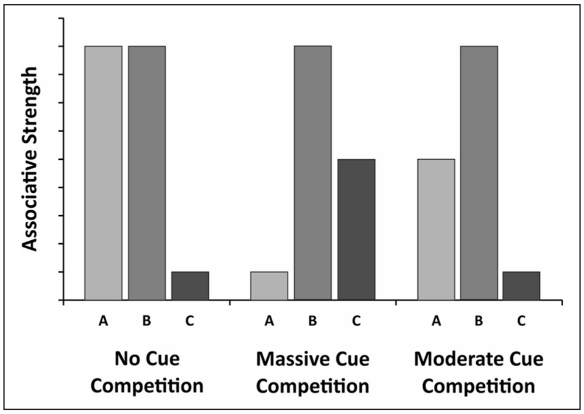

Figure 1. Predictions of associative strengths for Stimuli A, B, and C during the test phase of the experimental design according to different levels of cue competition.

and the compound was not paired with food (CZ−). In the final phase, Stimuli A, B, and C were tested individually in the absence of food to assess their associative strengths.

Figure 1 depicts different patterns of responding that can be expected for the test phase of our experimental design depending on the level of cue competition. If learning of the training schedule involves no cue competition (left-hand panel of Figure 1), responding during test should be similar across the stimuli that were consistently followed by the US (A and B) with each of the responses being stronger than the response towards Stimulus C that signalled US absence in the preceding phase ($A = B > C$; e.g., Bush & Mosteller, 1951).

If there is massive cue competition (centre panel of Figure 1), Stimulus A that was paired with the US in the presence of another well-established signal of the outcome should elicit weaker responding compared to both Stimulus B that received conditioning in the presence of a novel stimulus and Stimulus C that was not followed by the US when accompanied by a novel stimulus ($B > C > A$; e.g., Gluck & Bower, 1988; Rescorla & Wagner, 1972).

If cues compete with each other moderately for predictive value (right-hand panel of Figure 1), test responding to Stimulus A should be weaker compared to Stimulus B, but stronger compared to Stimulus C ($B > A > C$; e.g., Pearce, 1994; Vogel & Wagner, 2017).

Experiment 1

Methods

Subjects. In the first experiment, 16 pigeons (*Columba livia*) served as experimental subjects. The pigeons were obtained from local breeders and housed in an outside aviary until the start of the experiment. During the experiment, pigeons were housed in individual wire-mesh cages within a colony room that exhibited a 12-hr light–dark cycle starting at 8:00 hr in the morning. The pigeons were food-deprived and maintained between 80% and 90% of their free-feeding body weight. On training days, the birds received food only during the experimental sessions. Water was available ad libitum in their home cages. All aspects of the procedure were in compliance with the European Communities Council Directive 86/609/EEC concerning the care and use of animals for experimental purposes and were approved by the national ethics committee of the State of North Rhine-Westphalia, Germany.

Apparatus. Training was conducted in a custom-built operant chamber (40 cm × 40 cm × 45 cm; Packheiser, Güntürkün, & Pusch, 2019). The rear wall of the chamber featured a rectangular translucent response key (5-cm × 5-cm wide) located above a food hopper. An LCD (liquid crystal display) screen was mounted against the rear wall and was used for stimulus presentation at the response key location. Successfully registered key pecks were immediately followed by auditory feedback. The chamber was illuminated by two LED (light-emitting diode) stripes at the top of the chamber with an additional feeder light affixed on top of the food hopper. The chamber was situated in a sound-attenuating cubicle (75 cm × 70 cm × 90 cm) and experimental sessions were conducted with constant presentation of white noise (~80 dB) to prevent external noise from distracting the animals during the task. Hardware was controlled by a custom-written MATLAB (The Mathworks, Natick, MA, USA) code using the Biopsychology toolbox (Rose, Otto, & Dittrich, 2008).

Procedure. Visual stimuli were presented in triangular shape, either located in the top left or bottom right of a pecking key (Pearce et al., 2012). When stimuli were presented as compounds, both locations were presented simultaneously resulting in quadratic compound stimuli. Two sets of triangular stimuli served as CS, with the animals being randomly assigned to one of the stimulus sets. Figure 2 depicts examples of the stimuli used in this and the subsequent experiment (for the complete sets of stimuli and CS assignment within each set, see Supplementary Figures 1 to 4 in the Supplementary Materials).

Stimulus presentation time was 5 s. Upon termination of stimuli that were followed by the US, the food hopper was activated for a fixed period of 2 s. Stimuli associated with US absence were followed by a time window of 2 s without activation of the food hopper. Trials were separated by a fixed inter-trial interval (ITI) of 12 s. The associative value of stimuli was assessed by measuring the stereotypical pecking behaviour of the pigeons (Kasties, Starosta, Güntürkün, & Stüttgen, 2016). Thus, the number of conditioned responses, that is, pecks directed onto the visual CS, served as the dependent variable. Following a series of pre-training trials, animals received two learning phases and a test phase (Table 1).

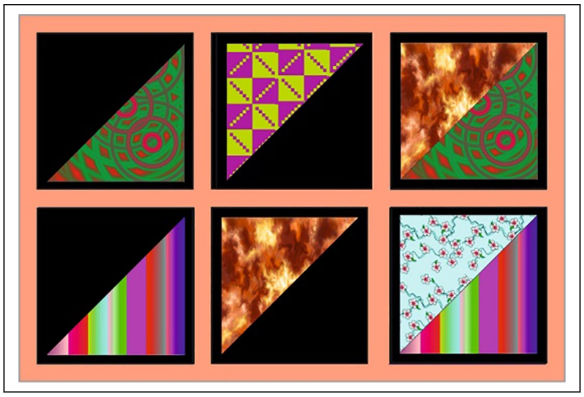

Figure 2. Examples of the triangular-shaped stimuli used in the experiments. Stimuli appeared either individually (Columns 1 and 2) or in compound (Column 3). The complete sets of stimuli and details about CS assignment are available in the Supplementary Materials (for Experiment 1, see Supplementary Figures 1 and 2; for Experiment 2, see Supplementary Figures 3 and 4).

Table 1. Design of Experiment 1.

	Target[a]	Non-Target[a]	Stimuli
Pre-training	T1+ (86) T2+ (86)	T3− (86) T4− (86)	
Phase 1	T1+ (42) T2+ (42)	T3− (42) T4− (42)	A+ (42) B+ (42) C+ (42) D+ (42)
Phase 2	T1+ (42) T2+ (42)	T3− (42) T4− (42)	AD+ (42) BY+ (42) CZ− (42) D+ (42)
Test	T1+ (84) T2+ (84)	T3− (28) T4− (28)	A− (28) B− (28) C− (28) D− (28)

Numbers in parentheses indicate the numbers of presentation of the corresponding trial types within one session. The signs "+" and "−" indicate the presence and absence of food, respectively.

[a] Target and Non-Target refer to control stimuli used for normalisation of pecking rates.

Pre-training. The pre-training phase consisted of a discrimination procedure during which the animals were presented with four stimuli that later served as control stimuli for the subsequent phases. Two of these stimuli were followed by the US (Target Stimuli T1+ and T2+). The other two triangles did not provide access to food after their presentation (Non-Target Stimuli T3− and T4−). The pre-training phase terminated once the animal pecked reliably and with a comparable number of pecks onto the two Target Stimuli and refrained from pecking onto the two Non-Target Stimuli.

Experimental phases. After successful pre-training, animals received acquisition training with Stimuli A+, B+, C+, and D+. In addition, training with the Target and Non-Target Stimuli from the preceding phase was continued during the sessions. Target and Non-Target Stimuli accompanied each experimental phase to serve both, as reference values for pecking behaviour and as fix points during the experiment as pigeons are neophobic animals (Bouchard, Goodyer, & Lefebvre, 2007) that adjust better to novel situations in the presence of familiar stimuli. Each experimental session during the first learning phase consisted of 42 presentations per stimulus resulting in 336 trials per session. Stimulus presentation was pseudo-randomised for all experimental phases.

Animals were shifted to the second learning phase if (1) at least three Phase 1 sessions were completed and (2) responding was similar across Stimuli A+ to D+ with each response being stronger compared to each of the Non-Target Stimuli. While most pigeons (11) reached the criteria after the first three sessions, four pigeons received one additional session, and one pigeon two additional sessions, to meet the criteria.

During Phase 2, some stimuli were presented together. Stimuli A and D were presented as a compound that was followed by food (AD+). Stimuli B and C were accompanied by novel Stimuli Y and Z, respectively. Presentations of the Compound BY were followed by the US (BY+), whereas Compound CZ was associated with US absence (CZ−). Presentations of the individual Stimulus D followed by the US (D+) were continued during Phase 2. Animals were shifted to the test phase if (1) at least four Phase 2 sessions were completed and (2) responding was similar across AD+, D+, and BY+ trials with each response being stronger compared to Compound CZ− and to each of the Non-Target Stimuli. Most pigeons (15) reached the criteria after four Phase 2 sessions, whereas one pigeon received one additional session for meeting the criteria. Each session of Phase 2 consisted of 42 presentations of each trial type resulting in 336 trials.

In the test phase, Stimuli A, B, C, and D were presented individually without the US. Each of the training stimuli (A, B, C, and D) and Non-Target Stimuli (T3− and T4−) was presented 28 times, whereas each of the Target Stimuli (T1+ and T2+) appeared 84 times, resulting in 336 stimulus presentations. We increased the rate of Target Stimuli to balance the number of trials with and without the US to motivate the animals to respond over the course of the test phase.

Data analysis. We used the pigeons' mean pecking rates across trials within a session as a dependent variable to measure the associative value of the stimuli. To account for the high variation in individual pecking frequency, we normalised pecking rates with respect to the Target and Non-Target Stimuli. To normalise the pecking rates, we used the following formula

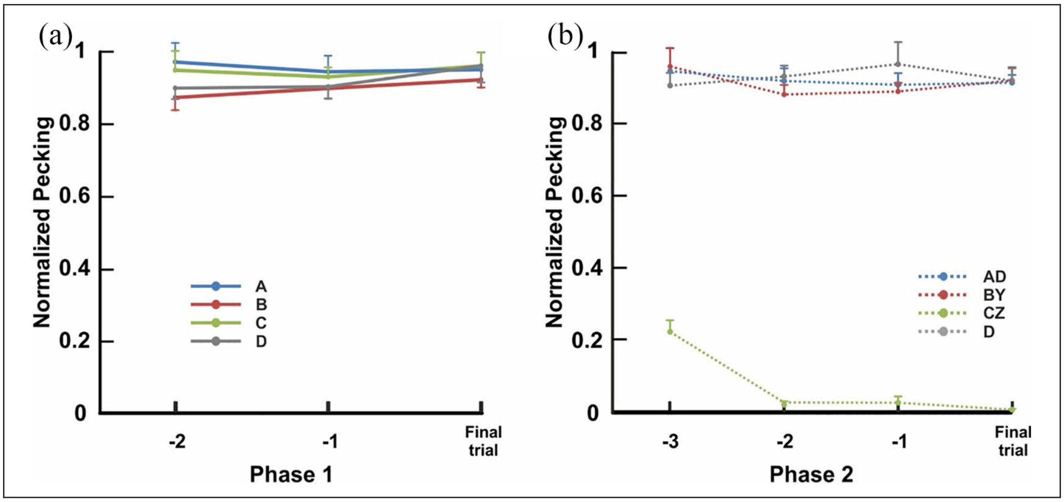

Figure 3. Pecking rates for trial types A+, B+, C+, and D+ from Phase 1 (Panel a) and for trial types AD+, BY+, CZ−, and D+ from Phase 2 (Panel b) in Experiment 1. Error bars represent SEM.

$$N(X) = \frac{R(X) - \mathit{Non\text{-}Target}}{\mathit{Target} - \mathit{Non\text{-}Target}}$$

Here, N represents the normalised mean pecking rate for a specific Stimulus X. For this normalised value, the difference between the absolute mean pecking rate R for a training stimulus and the mean pecks onto the Non-Target Stimuli was divided by the difference of the mean pecks onto the Target Stimuli and the mean pecks onto the Non-Target Stimuli. Mean pecks onto the Target Stimuli therefore served as a normalised reference of 1, whereas mean pecks on the Non-Target Stimuli served as a normalised value of 0. The data of this and the subsequent experiment have been made accessible in an online repository under the following link: https://osf.io/6ejzg/?view_only=b06e3fbc215c407a9737e7d10aa99dc8.

Results and discussion

The left-hand panel of Figure 3 illustrates responding to the Stimuli A+, B+, C+, and D+ across the last three sessions of the first learning phase. Depicted is the mean normalised pecking rate for each stimulus in each session. A two-way Stimulus (A, B, C, D) × Session (1–3) repeated measures analysis of variance (ANOVA) revealed no significant main effects of Stimulus, $F_{(3,45)} = 1.07$, $p > .250$, $\eta_p^2 = 0.06$, and Session, $F_{(2,30)} = 1.76$, $p = .189$, $\eta_p^2 = 0.10$. The Stimulus × Session interaction did not yield a significant result either ($F < 1$), indicating similar pecking behaviour across stimuli and sessions.

The right-hand panel of Figure 3 shows responding to the Trial Types AD+, BY+, D+, and CZ− across the last four sessions of the second learning phase, in terms of the mean normalised pecking rates for each trial type in each session. A stimulus (AD, BY, D, CZ) × session (1–4) repeated measures ANOVA yielded significant main effects of Stimulus, $F_{(3,45)} = 738.04$, $p < .001$, $\eta_p^2 = 0.98$, and Session, $F_{(3,45)} = 3.54$, $p < .022$, $\eta_p^2 = 0.19$. The Stimulus × Session interaction also reached significance, $F_{(9,135)} = 4.15$, $p < .001$, $\eta_p^2 = 0.25$, showing that pecking behaviour changed differentially for the stimuli across sessions. Post hoc analyses revealed that Compound CZ− received fewer pecks than each of the other trial types ($ps < .001$).

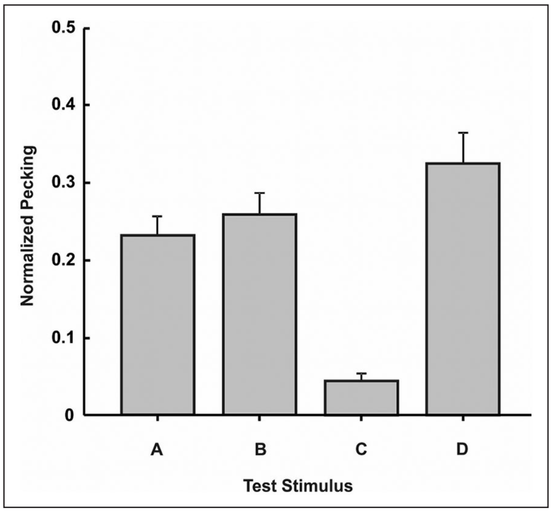

Figure 4. Pecking rates for Stimuli A, B, C, and D during the test phase of Experiment 1. Error bars represent SEM.

To assess for a summation effect, we collapsed pecking rates for each of the trial types AD+ and D+ across the first three trials in the first session of the second learning phase. A paired t test revealed no evidence for a difference between the two trial types ($t < 1$).

Figure 4 depicts responding to Stimuli A, B, C, and D presented during the test phase, in terms of the mean normalised pecking rate collapsed across all test trials for each stimulus. During testing, pecking behaviour towards the four stimuli differed significantly, $F_{(3,13)} = 32.23$, $p < .001$, $\eta_p^2 = 0.68$. Post hoc analyses using Bonferroni's correction, which focused on comparisons involving Stimuli A to C, revealed that Stimulus C received significantly fewer pecks compared to Stimulus A ($p < .001$) and Stimulus B ($p < .001$). Stimuli A and B elicited similar rates of responding, which was indicated by an inverted Bayes factor of 1.97 favouring the null hypothesis, albeit only weakly (Kass & Raftery, 1995). The inverted Bayes factor indicates that it was 1.97 times more likely for the data to have occurred under the null hypothesis. To assess for a potential difference in responding between Stimuli A and B that might have occurred at an early stage of testing, we also compared responding during the initial four test presentations of each stimulus. This comparison also revealed that there was no difference in the mean of normalised pecks between Stimulus A (0.75; SEM = 0.04) and Stimulus B (0.76; SEM = 0.03), indicated by an inverted Bayes factor of 3.88 (it was 3.88 times more likely for the data to have occurred under the null hypothesis which represents substantial evidence in favour of the null hypothesis).

The results from the test phase of Experiment 1 revealed no evidence for an overexpectation effect as responding was not modulated by whether a well-trained stimulus was paired with the US in the presence of another excitatory stimulus (Stimulus A) or in the presence of a novel stimulus (Stimulus B). Furthermore, we observed that test responding to Stimulus A was stronger than responding to Stimulus C that had signalled US presence when presented individually and US absence when compounded with a novel stimulus.

For other learning protocols, it has been demonstrated that interactions in learning across stimuli can be increased by giving a so-called outcome additivity pre-training (e.g., Beckers, De, Houwer, Pineño, & Miller, 2005; Lovibond, Been, Mitchell, Bouton, & Frohardt, 2003). In such training, subjects experience that an outcome that follows each of two individual cues (E+, F+) increases in magnitude when the two cues are presented in compound (EF++). For a second experiment, we extended the learning schedule of Experiment 1 by an outcome additivity training to increase the likelihood for interactions in learning (see Table 2).

Table 2. Design of Experiment 2.

	Target[a]	Non-Target[a]	Stimuli	Additivity training
Pre-training	T1+ (86) T2+ (86)	T3− (86) T4− (86)		
Phase 1	T1+ (30) T2+ (30)	T3− (30) T4− (30)	A+ (30) B+ (30) C+ (30) D+ (30)	E+ (30) F+ (30) EF++ (30)
Phase 2	T1+ (38) T2+ (38)	T3− (38) T4− (38)	AD+ (38) BY+ (38) CZ− (38) D+ (38)	EF++ (38)
Test	T1+ (80) T2+ (80)	T3− (20) T4− (20)	A− (20) B− (20) C− (20) D− (20)	

Numbers in parentheses indicate the numbers of presentation of the corresponding trial types within one session. The signs "+," "++," and "−" indicate trials with regular amount of food, large amount of food, and no food, respectively.

[a] Target and Non-Target refer to control stimuli used for normalisation of pecking rates.

Experiment 2

Methods

Subjects, apparatus, and procedure. We used another group of 16 pigeons as experimental subjects for the second experiment. The apparatus and procedure used in Experiment 2 were identical to those aspects from Experiment 1, unless stated otherwise. The stimuli used in Experiment 2 are depicted in Supplementary Figures 3 and 4 in the Supplementary Materials. The first learning phase comprised additional trials with individual Stimuli E+ and F+, and the Compound EF++. The amount of food following the Compound EF (++) was five times the amount of food regularly provided (+).

Animals were shifted to the second learning phase if (1) at least three Phase 1 sessions were completed, (2) responding was similar across the individual Stimuli A+ to F+ with each response being stronger compared to each of the Non-Target Stimuli, and (3) responding to Compound EF++ was at least as strong as responding to each of the Stimuli A+ to F+. While most pigeons (8) reached the criteria after the first three sessions, five pigeons received one additional session, and three pigeons two additional sessions, to meet the criteria. Each session of Phase 1 featured 30 presentations per trial type resulting in 330 trials per session.

During the second learning phase, E+ and F+ trials were no longer trained, but trials with Compound EF++ were added to the training schedule of Phase 2. Animals were shifted to the test phase if (1) at least four Phase 2 sessions were completed, (2) responding was similar across the trial types with a regular US (AD+, D+, BY+) with each response being stronger compared to Compound CZ− and to each of the Non-Target Stimuli, and (3) responding to Compound EF++ was at least as strong as responding to each of the trial types AD+, D+, and BY+. Most pigeons (14) reached the criteria after four Phase 2 sessions, whereas two pigeons received one additional session for meeting the criteria. During each Phase 2 session, 38 trials of each type were presented.

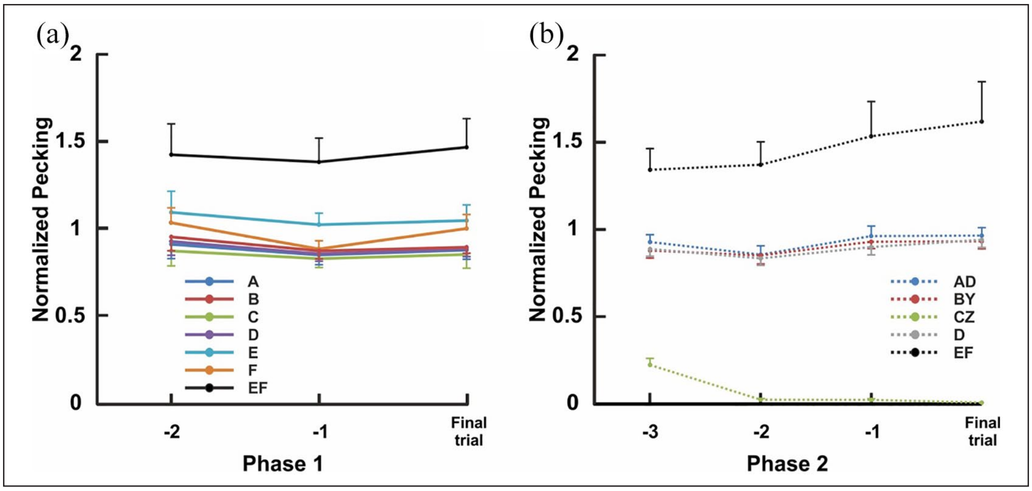

Figure 5. Pecking rates for trial types A+, B+, C+, D+, E+, F+, and EF++ from Phase 1 (Panel a) and for trial types AD+, BY+, CZ−, D+, and EF++ from Phase 2 (Panel b) in Experiment 2. Error bars represent SEM.

During the test phase, each of the training stimuli (A, B, C, and D) and Non-Target Stimuli (T3− and T4−) was presented 20 times, and each Target Stimulus (T1+ and T2+) appeared 80 times.

Results and discussion

The left-hand panel of Figure 5 depicts responding to the Stimuli A+ to F+, and the Compound EF++, across the last three sessions of the first learning phase. A Stimulus (A, B, C, D, EF) × Session (1–3) repeated measures ANOVA revealed a significant main effect of Stimulus, $F_{(6,90)} = 9.97, p < .001$, $\eta_p^2 = 0.40$, but no significant effect of Session ($F < 1$). The Stimulus × Session interaction was also not significant ($F < 1$). Bonferroni-corrected post hoc analyses showed that Compound EF++ evoked significantly more pecks compared to each of the Stimuli A+, C+, and D+ (*ps* < .05), but not compared to Stimulus B+ ($p = .068$).

The right-hand panel of Figure 5 shows responding to the trial types AD+, BY+, D+, EF++, and CZ−, across the last four sessions of the second learning phase. A Stimulus (AD, BY, D, EF, CZ) × Session (1–4) repeated measures ANOVA yielded a significant main effect of Stimulus, $F_{(4,57)} = 52.35$, $p < .001$, $\eta_p^2 = 0.77$. The main effect of Session and the Stimulus × Session interaction did not reach significance, $F_{(3,45)} = 1.89$, $p = .145$, $\eta_p^2 = 0.11$; $F_{(12,180)} = 1.66$, $p = .080$, $\eta_p^2 = 0.10$, respectively. Post hoc Bonferroni tests revealed that the Compound CZ− elicited significantly fewer pecks than each of the other trial types (*ps* < .001) and that Compound EF++ received significantly more pecks than each other trial types (*ps* < .001). For the outset of Phase 2, we found that the mean pecking rate collapsed across the first three trials in Session 1 was higher for Compound AD+ than Stimulus D+ ($t = 3.04$, $p = .008$, $d = 0.84$).

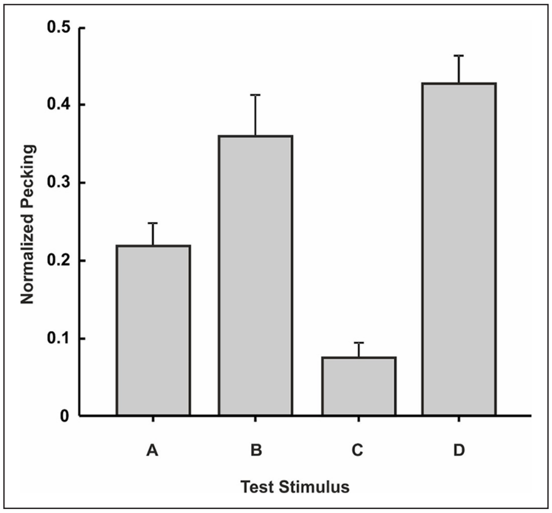

Figure 6. Pecking rates for Stimuli A, B, C, and D during the test phase of Experiment 2. Error bars represent SEM.

Figure 6 depicts responding to Stimuli A, B, C, and D presented during the test phase. A repeated measures ANOVA yielded significant differences in pecking rates towards the four stimuli, $F_{(3,13)} = 29.50$, $p < .001$, $\eta_p^2 = 0.66$. Post hoc analyses using Bonferroni's correction, which focused on Stimuli A to C, revealed that Stimulus C received fewer pecks compared to each of the Stimuli A and B (*ps* < .001). Furthermore, Stimulus A received fewer pecks than Stimulus B ($p = .012$).

As in the test of Experiment 1, we observed stronger responding to Stimulus A that had been paired with the US individually and in the presence of another excitatory stimulus than to Stimulus C that had a mixed relationship to the outcome. However, Experiment 2 revealed an effect of overexpectation. During the test, Stimulus A elicited weaker responding than Stimulus B that had been paired with the US individually and in the presence of a novel stimulus. In the next section, we discuss the theoretical implications of the present results.

General discussion

In two autoshaping experiments with pigeons, we investigated the degree to which learning about the relationship between a cue and an outcome depends on the learning histories of other cues that are concurrently present. In each experiment, animals initially received acquisition training with A+, B+, C+, and D+, followed by AD+, D+, BY+, and CZ− trials. Thus, Stimulus A was paired with the US in the presence of another well-established signal for the outcome, Stimulus B was conditioned in the presence of a novel stimulus, and Stimulus C was no longer followed by the US when accompanied by a novel stimulus. For each experiment, a final test revealed that pigeons' pecking behaviour was stronger to Stimulus A than Stimulus C, which is in accordance with the individual cue–outcome contingencies. Furthermore, the test results from Experiment 2, which included an outcome additivity training, showed an overexpectation effect as responding was weaker for Stimulus A than Stimulus B, despite the fact that the stimuli received the same number of outcome pairings. However, a corresponding finding was not evident in the first experiment (the absence of overexpectation in Experiment 1 was especially evident at the beginning of testing).

Responding during the test of Experiment 1 mirrored the individual cue–outcome contingencies of the stimuli. This pattern indicates the possibility that learning was governed by a local error term. According to a "local error correction" mechanism, the change in associative strength of a CS on a given trial depends on the difference between the maximal associative strength supported by the US and the current associative strength of the CS (e.g., Bush & Mosteller, 1951). While local error correction provides a simple explanation for the results of Experiment 1, the account fails when applied to the overexpectation effect that we observed in Experiment 2.

The pattern of responding during the test in Experiment 2 (B > A > C) indicates that stimuli competed with each other for predictive value, but that this interaction was not as massive as predicted by some theories of learning (e.g., Gluck & Bower, 1988; Rescorla & Wagner, 1972). Take, for instance, the Rescorla–Wagner theory, which assumes that changes in associative strength of a CS are governed by the difference between the maximal associative strength supported by the US and the sum of associative strengths of all CS that are present on a given trial. This "summed error correction" mechanism causes the theory to predict relatively strong and substantial interactions in learning. Figure 7 shows the predictions of the Rescorla–Wagner theory for the second phase of our experiments. As the figure illustrates, the model predicts stronger responding to Stimulus C than Stimulus A—a pattern that is opposite to the pattern that we observed in each of our experiments.

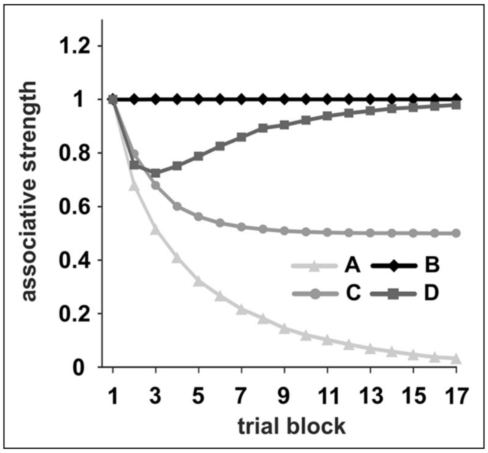

Figure 7. Changes in associative strengths predicted by the Rescorla and Wagner (1972) theory for Stimuli A, B, C, and D during the course of training in the second learning phase of the present experiments. Simulations were conducted using ALTSim (Thorwart, Schultheis, König, & Lachnit, 2009).

One way to reduce the degree of interactions among stimuli within the Rescorla and Wagner (1972) theory is to adopt a common element approach as suggested, for instance, by Vogel and Wagner (2017). This approach assumes that all stimuli used for training share a common, hypothetical element (k). Thus, a training schedule with A+, B+, C+, D+ followed by AD+, D+, BY+, CZ− would be encoded as Ak+, Bk+, Ck+, Dk+ followed by ADk+, Dk+, BYk+, CZk−. Panel a of Figure 8 depicts simulations for the second phase of Experiment 2 conducted with the Rescorla–Wagner theory applying the common element approach. As can be seen, the model predicts that the associative strength for Compound Ak is higher compared to Compound Ck, but lower compared to Compound Bk. Thus, the common element approach suggested by Vogel and Wagner accounts for the results from the test phase of Experiment 2.

The configural model of Pearce (1987, 1994) provides another theoretical framework for the results from Experiment 2. According to the theory, the stimulation provoked by a particular configuration of stimuli results in a single representation that can acquire associative strengths. The representation of a particular stimulus configuration can be partially activated by other configurations based on similarity. Panel b of Figure 8 shows the predictions of the Pearce model for the test phase of Experiment 2 (under the assumption that learning in each of the preceding phases reached asymptote). It is evident that the model correctly anticipates that Stimulus A elicited stronger responding than Stimulus C, but weaker responding than Stimulus B.

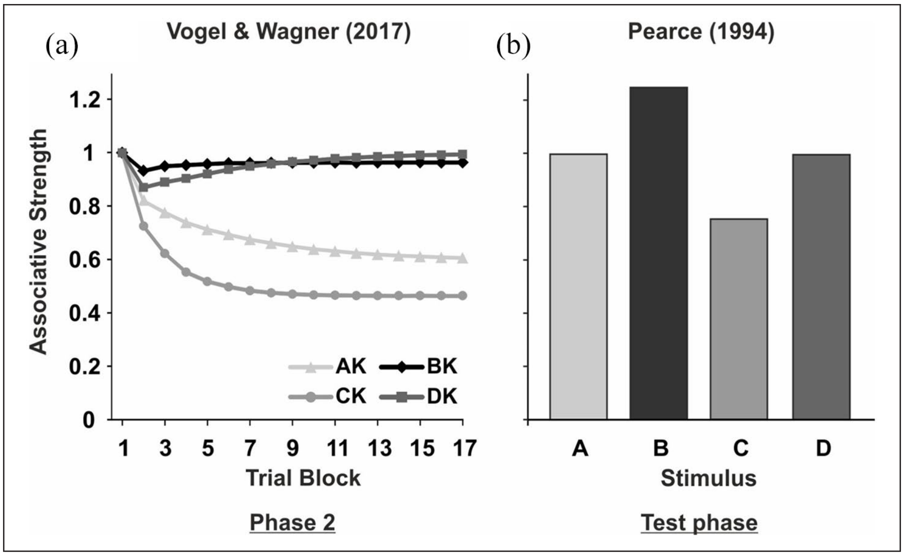

Figure 8. Panel a: Changes in associative strengths predicted by Vogel and Wagner (2017) for Stimuli A, B, C, and D during the course of training in the second learning phase of Experiment 2. Panel b: Predictions of the configural model by Pearce (1994) for Stimuli A, B, C, and D in the test phase of Experiment 2. Simulations were conducted using ALTSim (Thorwart, Schultheis, König, & Lachnit, 2009).

However, none of the learning theories discussed so far is able to account for our cross-experimental observation that Experiment 2 revealed an overexpectation effect, while cue competition was not evident in Experiment 1. An important procedural difference that may have been responsible for the diverging results is that Experiment 2, but not Experiment 1, included an outcome additivity training (E+, F+, EF++). This conclusion should be treated with caution as it relies on a cross-experimental comparison, but it is worth to consider its theoretical implications.

The impact of outcome additivity training on cue competition effects is often taken as support for the involvement of inferential reasoning processes (e.g., Beckers et al., 2005; Lovibond et al., 2003). According to an inferential reasoning account, subjects logically deduce the predictive value of an individual cue when the cue is not present in isolation but in compound with other stimuli. It is further proposed that such inferences are based on the assumption of outcome additivity: if two cues are each effective signals of an outcome, the joint occurrence of the cues should result in a stronger outcome than when only one of the cues is present. In case of the present overexpectation protocol (A+, D+ followed by AD+, D+), it can be inferred from the AD+ trials that Cue A is no longer a valid predictor of the outcome because the outcome that follows AD is as strong as the outcome following individual presentations of Cue D. An inferential reasoning account can explain the diverging results of the present experiments by assuming that outcome additivity is not a default assumption in pigeons, but that it can be established due to explicit training. This would explain the absence of overexpectation in Experiment 1 and its presence in Experiment 2.

Alternatively, the absence of overexpectation in Experiment 1 can be explained by the idea that pigeons deploy an additivity assumption by default, but that the animals were not able to assess on AD+ trials whether or not the presence of Cue A increased the outcome relative to the outcome that followed Cue D. An inference may not have been possible in Experiment 1, as the outcome used for the overexpectation protocol was at its maximal strength (there is the possibility that Cue A is an effective signal of the outcome, but its effectiveness is not observable due to outcome magnitude ceiling). In Experiment 2, the outcome used for the overexpectation protocol was explicitly trained as submaximal due to the additional EF++ trials, which made it possible to empirically verify on AD+ and D+ trials that outcome magnitude was not increased by the presence of Cue A.

As an alternative to the inferential reasoning account, Livesey and Boakes (2004) explained the impact of outcome additivity training on cue competition in terms of changes in the form of stimulus representation. According to the authors, absence of cue competition may result from the operation of strongly configural stimulus processing, in which a compound of stimuli (e.g., AD) is represented as an independent stimulus with no significant generalisation between the compound and its constituting elements (e.g., A and D). Explicit training of outcome additivity may increase the generalisation across compounds and elements, which is considered as a prerequisite for the occurrence of cue competition.

In the present experiments, configural stimulus representation may have been encouraged by aspects of our stimulus material. Triangular-shaped visual stimuli served as CS, which were arranged to yield a quadratic stimulus when presented as a compound. Considerable evidence indicates that the kind of stimuli and the way in which they are arranged can influence the nature of stimulus representation (for a review, see Melchers, Shanks, & Lachnit, 2008). Configural processing appears to be especially likely with stimuli that vary along integral dimensions (e.g., hue, saturation, and brightness of colour; Lachnit, 1988) or with stimuli that are presented spatially close together and grouped (Glautier, 2002).

Experiment 1, which provided no evidence for cue competition, yielded also no evidence of summation at the outset of the second learning phase—responding to compound AD was not stronger than responding to the individual Cue D. However, a summation effect with stronger responding to AD than D was observed in Experiment 2, which also demonstrated overexpectation. This pattern may indicate summation as a boundary condition for the occurrence of overexpectation. Alternatively, however, it is possible that the absence of summation in Experiment 1 resulted from the fact that the response level was close to ceiling prior to summation testing. This latter possibility is supported by a cross-experimental analysis using absolute numbers of pecks instead of normalised data. We found that the mean of absolute pecks calculated across Stimuli A to D from Phase 1 was higher in Experiment 1 than in Experiment 2, $t(126) = 4.94$, $p < .001$, $d = 0.87$ (see Supplementary Figure 5).

In conclusion, the present results support the notion that cue competition may be highly dependent on boundary conditions (e.g., Maes et al., 2016; Urcelay, 2017). In parallel to findings from experiments on blocking (e.g., Beckers et al., 2005; Lovibond et al., 2003), our results may indicate that explicit training of outcome additivity can also facilitate cue competition in the context of overexpectation. There are several possibilities how to explain the impact of outcome additivity training on cue competition: the training may have been effective by encouraging additivity assumptions, by providing information about outcome submaximality, or by inducing shifts in stimulus representation. A differentiation of these possibilities may be an interesting endeavour for future research. As mentioned above, however, our discussion regarding outcome additivity training was based on a cross-experimental comparison and should be treated with caution. Besides the additivity training, the present experiments differed in other procedural characteristics as the number of trial types and the number of presentations of each trial type, which may also have contributed to the diverging results between the experiments. Thus, future research will be required before it is possible to draw firm conclusions about the impact of additivity training on overexpectation.

Furthermore, this study showed that when cue competition occurred, it appeared in a moderate rather than a massive form, which is a challenging finding for some influential theories of learning (e.g., Rescorla & Wagner, 1972). This finding is consistent with conclusions drawn from previous experiments on the blocking effect (e.g., Pearce et al., 2012) and extends the range of phenomena indicating that learning does not involve a massive form of cue competition.

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Supplementary material

The supplementary material is available at qjep.sagepub.com.

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