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Absolute and relational control of a sequential auditory discrimination by pigeons (*Columba livia*)

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Abstract

Recent evidence indicates that pigeons can readily learn visual discriminations based on both absolute and relational stimulus factors. To examine how these two types of control function in their non-dominant auditory modality, we tested four pigeons in a go/no-go sequential auditory discrimination in which both absolute and relational cues were redundantly available. In this task, sequences of *different* sounds created from one set of pitches were reinforced, while *different* sequences created from another set of pitches and any *same* sequences made from either set of pitches were not. Across three experiments, we independently varied the relative discriminability of the absolute and relational components. The pigeons were consistently and primarily controlled by the absolute fundamental pitch of our notes in all of the experiments, although this was influenced by the range and arrangement of the pitches used in each set. A majority of the pigeons also demonstrated relational control when this component was made more salient. The more robust control exhibited by absolute factors is consistent with the comparative hypothesis that birds in general may have a well-developed aptitude for processing absolute pitch in many auditory settings. The relational control is consistent with our recent evidence of same/different auditory learning by pigeons.

Keywords: Pigeons; Audition; Absolute control; Relational control; Stimulus control

Recent years have seen an upsurge in interest directed at understanding how animals use stimulus relations of different types to guide their behavior. The capacity to recognize regularities among two or more stimuli is a critical component of analogical reasoning and intelligence and can serve the important function of letting animals predict future events based on previously experienced relations. Whereas the study of matching relations received much early attention (Berryman et al., 1965; Carter and Werner, 1978; Cumming et al., 1965; Holmes, 1979), over the last decade the focus has shifted more to investigations of *same/different* (S/D) relations. In a S/D task, the animal has to respond *same* when all stimuli on a trial are identical and *different* if one or more of the stimuli are different from the others. The degree to which this learned behavior transfers to novel *same* and *different* relations is generally taken as evidence of concept formation (Cook and Wasserman, 2006). Using variations of this basic S/D task, it has been found that birds (pigeons, parrots), monkeys (rhesus monkeys, baboons), apes (chimpanzees), and cetaceans (dolphins) are capable of learning S/D concepts across a wide variety of simultaneously and successively presented visual elements (Bovet and Vauclair, 2000; Cook et al., 1997, 2003; Fagot et al., 2001; Mercado et al., 2000; Pepperberg, 1987; Thompson et al., 1997; Wright et al., 1984; Young and Wasserman, 2001). Studies of S/D relations in the auditory modality have received far less attention, with dolphins, monkeys, budgerigars, zebra finches, and pigeons all showing the capacity to learn S/D discrimination or concepts in this modality, too (Cook and Brooks, in press; Dooling et al., 1987; Herman et al., 1994; Lohr and Dooling, 1998; Wright, 1998; Wright et al., 1990).

Outside of the study of basic psychophysics, investigations of auditory processing in pigeons have been limited, especially with regards to advanced cognitive capacities. The current investigations grew out of our recent research examining auditory S/D learning (Cook and Brooks, in press). They used a go/no-go task in which pigeons were taught to discriminate sequences of 12 different pitches, timbres, or complex stimuli (a *different* sequence) from sequences in which one of these values (randomly selected each trial) was repeated (a *same* sequence). After

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learning these discriminations, their pigeons showed good transfer to sequences composed from novel values of pitch, timbre, and complex sounds. This transfer suggested for the first time that pigeons could detect and use general S/D relations in a domain other than their primary visual modality.

The current experiments extended these observations by examining how these relational components in auditory sequences might compete and interact with the item-specific, or absolute, components during the development of stimulus control. As discussed, relational factors are those invariants in a situation derived by the comparison of two or more stimuli and their relations (e.g., same/different, identity, larger or smaller, order, etc.). In these experiments, it was the relation of *same* and *different* among the sounds in a sequence that was of primary concern. Absolute factors are those discriminative properties concerned with item-specific information about each individual stimulus (e.g., pitch, timbre, size, color, etc.) and do not entail any comparison among stimuli. In these experiments, it was the absolute property of each note's specific frequency or pitch within a sequence that was of primary concern. While S/D studies are designed to make relational information the exclusive and salient guide to the reinforcement contingences, in the current experiments we used an altered procedure where the pigeons had the option to use either the relational S/D information, the absolute frequency or pitch information, or both types of information to solve this auditory discrimination. With this comparison, we could then judge the relative saliency of these types of information and how they interact in service of better understanding the mechanisms of auditory stimulus control.

Over and above its earlier history and debate primarily in the domain of transposition (Riley, 1968; Spence, 1937), the interaction of absolute and relational aspects of stimulus control has become of increasing interest because of the recent evidence that pigeons are sensitive to both types of information in different settings. The growing evidence of S/D learning across a number of different contexts and procedures have strongly pointed to the possibility that this type of relational information is readily available to them (Blaisdell and Cook, 2005; Cook, 2002; Cook et al., 1997, 2003; Katz and Wright, 2006; Wasserman et al., 1997, 2002; Young and Wasserman, 2001). On the other hand, there is also considerable evidence that pigeons can also process and memorize large amounts of specific and detailed information during learning. They can easily memorize large numbers of specific pictures using absolute information (Chase and Heinemann, 2001; Cook et al., 2005; Fagot and Cook, 2006; Fersen and Delius, 1989; Greene, 1983; Vaughan and Greene, 1984). For instance, Cook et al. (2005) found that pigeons can memorize between 800 and 1000 different pictures (apparently the upper limit; see Fagot and Cook, 2006). In conditional discrimination settings, they often learn item-specific rules or configurations when tested with only limited numbers of stimuli (Carter and Werner, 1978; Wright, 1997). It is the tension created in organisms between the competing needs to memorize absolute particulars and specific details while still extracting generalized invariant relations that is at the heart of understanding discrimination learning and the subsequent development of intelligence (Cook and Smith, 2006; Cook and Wasserman, 2006; Wright, 1997).

Among the questions raised by this general topic is whether there are comparative differences in how absolute and relational information is processed or employed by different species. In the auditory domain, the latter comparative issue has been of particular interest to Weisman et al. (2004). Weisman et al. proposed that birds and mammals may differ substantially in their ability to use absolute information within the auditory domain, especially with regards to their capacity to process absolute pitch. They suggested that songbirds, and perhaps birds in general, are very attuned to absolute pitch, while mammals have a less developed sense of absolute pitch and, in the case of humans, may rely more on relational information when processing auditory information. Consistent with this hypothesis are a number of experiments showing that zebra finches, white-throated sparrows, budgerigars, and pigeons are very good to excellent at learning to make discriminations based on absolute pitch, whereas humans and rats tested in identical procedures are generally poorer, especially with more demanding discrimations (Friedrich et al., 2007; Weisman et al., 2004). Regarding the use of relational information, birds have been shown to be sensitive to this information in some settings but not in others. Several songbird species, for example, use relational information in song perception and production (Hurly et al., 1990; Weisman et al., 1990). However, starlings, zebra finches, and pigeons have been shown to be constrained in their transfer of discriminations based on relational rising and falling pitch sequences in part because of their memorization of the absolute values of training stimuli (Cynx, 1995; Page et al., 1989). Clearly the relationship between absolute and relational information in auditory processing is a complex issue, and understanding the interaction of these factors is critical to a complete theory of discrimination learning and stimulus control.

To investigate the relative importance of absolute and relational properties for pigeons in learning to discriminate auditory sequences, we adapted a procedure utilized by Wasserman et al. (2002). In this procedure, four conditions are compared that permit the identification of control by absolute and relational factors in multi-item discriminations. Using this procedure, they found in tests using simultaneous mixed arrays of visual icon stimuli that both relational and absolute properties could simultaneously control their pigeons' behavior. Their study, as well as subsequent research comparing both types of control, suggested that absolute factors tended to exert greater control than relational cues when the number of icons in the displays was reduced. The subsequent research also found that absolute factors exerted control later in the learning of the discrimination than relational factors (Gibson and Wasserman, 2003, 2004).

In our adaptation, each condition consisted of a sequence of auditory stimuli that contained a combination of both relevant absolute (pitches selected exclusively from octave A versus octave B) and relational (*same* versus *different* sequences of pitches) information. The AD condition (*different* sequences composed of pitches from octave A) was designated as the S+ sequence. The three remaining conditions were designated as the S− sequences, and each overlapped to varying degrees with the S+ condition. In the BD condition (*different* sequences composed of pitches from octave B), the relational information was the same as the S+ sequence but differed in its absolute properties. In the AS condition (*same* sequences composed of pitches from octave A), the relational information was different from the S+ sequence but shared its absolute properties. In the BS condition (*same* sequences composed of pitches from octave B), both types of information differ from the values of the S+ condition. Any similarities in performance between the AD condition and the other conditions can then be attributed to the common component of the conditions, whereas any differences can be attributed to the unshared component.

By comparing subsequent pecking behavior among these conditions, the degree of absolute and relational control can then be determined. Three patterns are particularly informative. If the S+ condition is superior to the three S− conditions, then it would indicate that both relational and absolute information control performance (AD > BD = AS = BS or AD > BD = AS > BS). If only absolute factors are governing performance, then those conditions containing differences in pitch should separate themselves (AD = AS > BD = BS). Finally, if only relational factors are governing performance, then those conditions containing differences in *same* and *different* relations should separate themselves (AD = BD > AS = BS).

In the following experiments, we tested four pigeons in a series of experiments using this shared cue procedure with sequences of auditory stimuli. Over three experiments, we varied the relative discriminability of the absolute and relational components in the discrimination to better understand how these factors contributed to the development and maintenance of stimulus control within the auditory modality.

1. Experiment 1

Experiment 1 examined the above questions using sets of stimuli selected from two different octaves (see keyboard legend in Fig. 2 for details). Four birds were tested for 50 sessions using the four conditions outlined above to see how the absolute and relational components of the discrimination emerged to control behavior. This question was examined not only across sessions, but also using our trial-wise technique of profiling peck rates within sequences.

2. Methods

2.1. Animals

Four male pigeons (*Columba livia*) were tested. Two were experimentally naive (#B2 and #B3; each 1 year old), and the other two had served in experiments involving the discrimination of humans versus baboon faces and an equivalence-based visual S/D discrimination (#B1 and #L4; each 6 years old). All were maintained at 80–85% of their free-feeding weights in a 12:12 LD colony room and given free access to grit and water.

2.2. Apparatus

Testing was conducted in a flat-black Plexiglas chamber (42.5 cm wide × 44 cm deep × 39.5 cm high). All events were controlled by a computer with sound card (SoundMax Integrated audio card; Analog Devices). The visual stimuli were presented on a color monitor visible through a 25.5 cm × 21.5 cm opening in the chamber's front panel. Pecks were detected by an infrared touch screen (EloTouch) that formed this window. The auditory stimuli were simultaneously presented from two multimedia speakers (HK-195, Harmon-Kardon; frequency range = 90 Hz to 20 kHz) located towards the front of each side of the chamber. The speakers were played through plastic grills in the side of the chamber consisting of a 90 cm × 120 cm grid of 5 mm holes. A houselight in the chamber's ceiling was illuminated at all times, except during timeouts. Mixed grain was delivered by a food hopper centrally located below the viewing window.

2.3. Stimuli

Auditory stimuli were software-generated synthesized waveforms (Sonar Version 4, Cakewalk, Boston, MA). These 16-bit files were sampled at 44,100 samples/s. The stimuli were 12 pitches from the fourth and fifth octaves and created using an alto saxophone timbre. The timbre was synthesized by combining the distinct harmonic and partial frequencies to the fundamental frequency of each pitch to simulate the harmonic spectral signature of the instrument (which also enlarged the total frequency spectrum by several kHz beyond the fundamental pitch). Six notes were used to create each stimulus set. One set consisted of the D4, E4, F4, G4, A4, and B4 notes of the fourth octave (293–494 Hz), and the other set consisted of the D5, E5, F5, G5, A5, and B5 notes of the fifth octave (587–988 Hz). For birds #B1 and #L4, set A stimuli consisted of notes from the fourth octave and set B stimuli from the fifth octave, and for birds #B2 and #B3, set A stimuli consisted of notes from the fifth octave and set B stimuli from the fourth octave. WAV files of these sounds were presented at 76–82 dB as measured from the bird's typical position in chamber (Radio Shack sound pressure meter; Weighting A, fast response).

2.4. Procedure

Each trial started with a peck to a centrally located 2.5 cm white circular warning signal. This was replaced by a 6.7 cm purple square, to which the birds directed pecks during sound presentations. Twelve auditory stimuli were then presented in succession, each for 1.5 s and separated by an inter-stimulus interval (ISI) of 0.05 s. Four separate kinds of sequences were tested. The AD condition consisted of all six stimuli of set A, each played once in a random order and then repeated in this sequence a second time, creating a *different* sequence of exclusively set A pitches. The BD condition consisted of all six stimuli of set B played once in a random order and then repeated a second time, creating a *different* sequence of exclusively set B pitches. The AS condition consisted of one pitch, randomly selected each time from set A, repeated twelve times to form a *same* sequence composed of pitches from set A. The BS condition consisted of one pitch, randomly selected each time from set B, repeated twelve times to form a *same* sequence composed of pitches from set B. Pecks during AD sequences were rewarded with 2.8 s access to grain on a variable interval schedule (VI-8). Pecks to any of the other three sequences were not reinforced and resulted in a 10 s timeout following the completion of the sequence.

Experiment 1 consisted of 50 sessions of testing. Each session consisted of 72 trials: 36 trials of AD sequences (S+) and 12 trials each of the BD, AS, and BS sequences (S−). To get uncontaminated measures of responding to AD sequences, six randomly determined AD trials per session were conducted as unreinforced *probe* trials. These probe trials eliminated reinforcement as a source of stimulus control and accurately estimated true response rates without any interference related to food consumption.

3. Results

Shown in Fig. 1 are the mean acquisition results for Experiment 1 across sessions. Because the discrimination of the four conditions increased during the latter items comprising each 12-item sequence (see results in Fig. 2), the mean peck rate shown in Fig. 1 is averaged over the last three items of each sequence. As can be seen, the absolute properties of the discrimination dominated the relational properties, as the set A conditions (AD and AS) had a stronger separation from the set B conditions (BD and BS) over the 50 sessions than the differences associated with a division of these conditions along *different* (AD and BD) and *same* (AS and BS) properties. Despite this general pattern, we did see individual differences among the pigeons that merited a more fine-grain analysis to understand what happened.

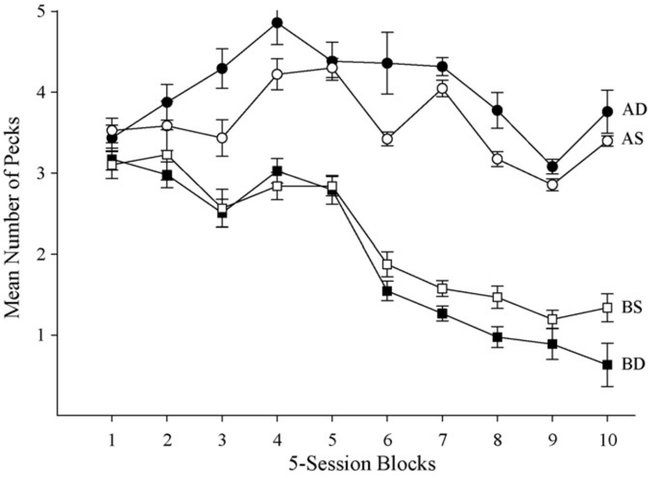

Fig. 1. Mean number of pecks over the last three serial position intervals across five-session blocks for the four conditions tested during training in Experiment 1. The error bars represent the standard error of the mean.

Shown in Fig. 2 are the overall mean and individual results collected during the last 15 sessions of training, during which discrimination was at its best. Each panel shows mean peck rate during each item of the 12 sounds comprising a sequence or trial. We have found this type of trial-wise profile to be revealing in our recent experiments (Cook and Brooks, in press; Cook et al., 2003; Cook and Roberts, 2007). Examining the averaged results of all four birds confirms the pattern seen across sessions, with absolute information seemingly more salient than relational information. Overall, there was a larger separation of peck rate based on absolute properties than those associated with relational properties. In addition, there were differences in how quickly each type of control emerged in the sequence. Based on

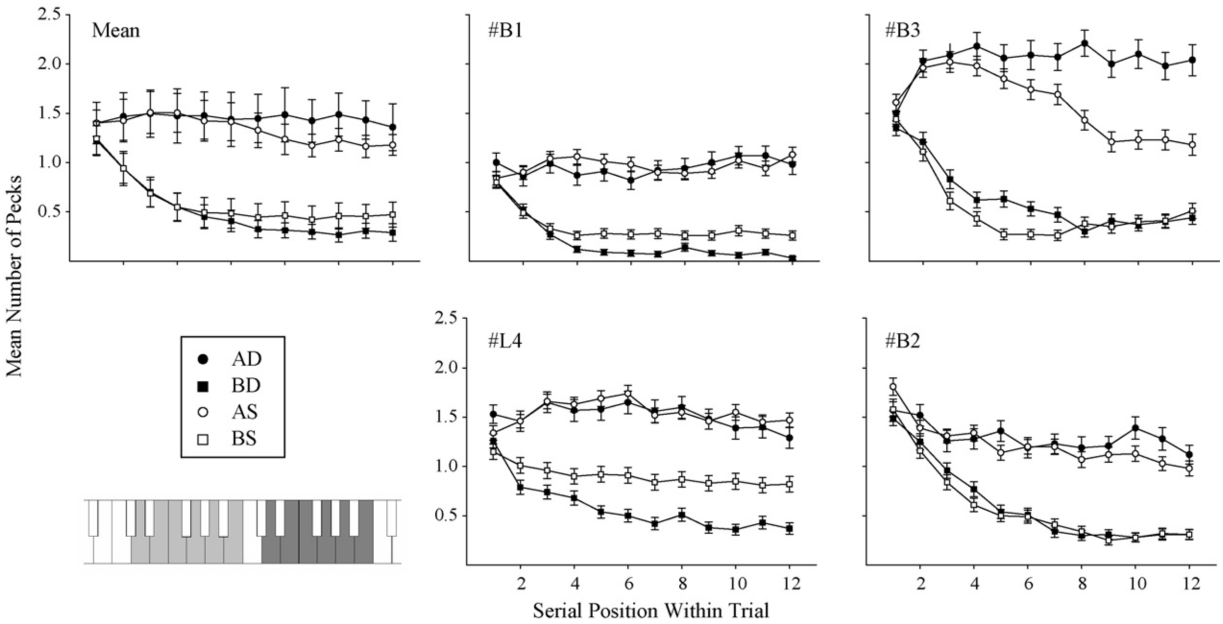

Fig. 2. These graphs show peck rate for all four conditions tested during training in Experiment 1 across 12 items serially presented within a trial for the last 15 sessions for all four birds and for each bird individually. The error bars represent the standard error of the mean. The keyboard depicts the relations of the stimuli within each stimulus set tested in Experiment 1, with one set consisting of six notes from the fourth octave, and the other set consisting of six notes from the fifth octave.

a criterion of a 15% difference in peck rate between conditions, the set A conditions separated from the set B conditions as early as the first item of a sequence as the pigeons quickly detected the octave range of each sequence. Only between the third to sixth item of the sequence did the *same* and *different* properties of the conditions begin to exert any type of control as the AD and AS or BD and BS started to separate.

Examination of the four remaining panels reveals that each bird showed strong control by absolute properties but differed individually in the degree and type of control exhibited by the relational aspects of the discrimination. To examine these issues, we conducted a series of two-way repeated measures (absolute [set A versus set B] × relational [*same* versus *different*]) ANOVAs on the mean peck rate combined over the last three items of each sequence for the last 15 sessions of testing for each bird to evaluate performance. An alpha level of $p < .05$ was used to judge all statistical significance. All four pigeons exhibited a significant difference in peck rate as a main effect of each sequence's absolute properties, #B1–$F(1, 2) = 2253.3$; #B2–$F(1, 2) = 151.3$; #B3–$F(1, 2) = 864.9$; #L4–$F(1, 2) = 1134.2$. Regarding the relational main effect, three of four birds showed significant differences according to this division, #B2–$F(1, 2) = 39.4$; #B3–$F(1, 2) = 658.2$; #L4–$F(1, 2) = 65.7$; this was not significant for #B1, $F(1, 2) = 6.3$, $p = .13$. Finally, the interaction of these two factors showed significant asymmetries in the degree of control exhibited among the four conditions for three of the four birds, #B2–$F(1, 2) = 25.7$; #B3–$F(1, 2) = 245.3$; #L4–$F(1, 2) = 163.9$; this almost reached significance for #B1, $F(1, 2) = 17.7$, $p = .052$.

This analysis revealed that the pattern among the conditions was different between the pigeons. Birds #B2 and #B3 showed consistently more pecks to the AD condition than to the AS condition, while exhibiting no differences in peck rate among the BD and BS conditions. This pattern is consistent with our pre-experimental hypotheses that these birds were processing the relational and absolute aspects of the sequence. Birds #B1 and #L4 demonstrated a different pattern with little or no difference in peck rate between AD and AS conditions but a clearly lower rate of responding to BD sequences than to BS sequences. This pattern did not fit our pre-experimental expectations for relational control, as we had anticipated that the BD condition would receive more pecks than the BS condition because of its shared *different* component with the AD S+ condition.

3.1. Discussion

Experiment 1 revealed that both absolute and relational components could simultaneously control the sequential auditory discrimination tested here. The absolute component of the discrimination was consistently the stronger or more salient of these two properties. For all birds, the difference in peck rate related to absolute control was larger than that observed for any relational control. This was true across sessions and also within a trial. In the latter, evidence of absolute control consistently emerged sooner within a sequence than did relational control, which tended to emerge only after a number of items had been presented in a sequence.

Presumably, the factor controlling the discrimination of the absolute properties is related to the range of pitches in each set's octave. Given the range of frequency values tested and their spectral arrangement, the birds only had to divide a fairly wide range of pitch, something they are known to be able to do (Cook and Roberts, 2007; Friedrich et al., 2007). One important caveat to keep in mind is that these are not pure tones but have a total spectral content that mimics the sound of a saxophone. Thus, while the fundamental frequency was the primary feature changed across the stimuli, subtle differences in the total frequency content of each note could have played a role. Bearing this in mind, the general pattern is consistent with Weisman et al's (2004) suggestion that absolute pitch is not only important to songbirds but to birds in general.

Although the results were more mixed, evidence indicative of spontaneous control by the relational *same* and *different* properties of the sequences was present. Two of the birds (#B2 and #B3) showed a significant pattern that was exactly what we predicted for this type of relational control. Although absolute pitch range was still important, these two birds provide good evidence for the presence of relational control. In these two cases, the AD condition supported the highest peck rate and reliably separated from the AS condition, followed by the BD and BS conditions. The latter two conditions showed some separation over the initial items of a sequence, but generally converged towards the end of a sequence. One possibility is that a floor effect may be muting any differential relational responding during the latter phases of the sequence. Another possibility is that the birds might be showing some contextual responding to the *same* and *different* properties based on the absolute octave of each. For the set A conditions, the relational component can be of further help by allowing the pigeons to discriminate between positive (AD) and negative conditions (AS). For the set B conditions, the absolute factor may already tell the pigeon all it needs to know as both the BD and BS are negative conditions. Thus, the salience of some absolute cues may block the development of relational control.

The other two birds (#B1 and #L4) showed similar patterns to each other that revealed, apart from reliance on absolute factors, a separation based on relational factors as well (although this pattern was statistically significant for just one of them). In these two birds, the BD condition surprisingly supported lower peck rates than did the BS condition, while the AD and AS conditions were roughly equivalent. We had expected that the shared *different* properties of the BD and positive AD condition would have instead elevated peck rates to the former condition, whereas we projected the BS condition would be the lowest as it shared no properties with the positive condition. Thus, this pattern surprised us.

We considered two accounts of this outcome. The first account suggested that relational factors did come to control performance in these conditions, but only within the context of the absolute range of values comprising each set. Thus, much as suggested above, the pigeons learned different things depending upon the different octaves of each sequence. While this contextual account is possible, it provides no basis for why the BD condition would be consistently lower. Unlike with the first two birds, where the shared features and reinforcement contingencies within each set seemed to naturally account for their difference, this fails here. Wasserman et al. (2002) suggested that difference is more discriminable than sameness, but this has not been our previous experience with visual S/D discriminations, where sameness is typically the easier condition. A second account suggests that relational factors might not be involved, but that the difference is more a byproduct of averaging. Altogether, there are six examples of the BS condition, in which a different set B stimulus is used to create a *same* sequence. In contrast, the BD condition uses all six stimuli each time (although in a random order each time). If some B pitches are better identified as negative than others, then their regular presence in the BD sequences might promote better and more consistent response suppression. In turn, the averaging of performance for the different pitches would tend to elevate the combined measure of the BS condition. When we examined performance in the BS condition, some pitches did support better performance than others. This certainly suggests that this latter account might be feasible. Because of these complications, however, we are reluctant to attribute the discriminative behavior of these latter two pigeons to relational control.

4. Experiment 2

If absolute and relational factors compete for control when both are present, then changes in their relative salience should result in an inverse relation between the two factors. Thus, Experiment 2 examined the consequences of increasing the difficulty of the absolute discrimination relative to the relational component. In the first experiment, the total range of absolute discrimination was spread out across two octaves. Clearly, this type of range discrimination was relatively easy for the pigeons. In the second experiment, the difficulty of the absolute discrimination was increased by altering the arrangement of the pitches and compressing the total range of both sets to a single octave. Thus, the six pitches forming each set were alternated, for the most part, within this octave (see keyboard legend in Fig. 4). This tonal compression and alternating arrangement made the absolute discrimination much harder, as the pigeons needed to discriminate adjacent tones with fundamental frequencies that were separated by 6%. Prior auditory research with pigeons had suggested this difference was right at or just above their difference threshold for frequency discriminations over this range (Delius and Tarpy, 1974; Price et al., 1967; Sinnott et al., 1980). By making the absolute discrimination much harder, we hoped the pigeons would come to rely on the relational component of the discrimination to a greater extent.

5. Methods

5.1. Animals and apparatus

The same pigeons and apparatus used in Experiment 1 were used in Experiment 2.

5.2. Procedure

The procedure was identical to Experiment 1, except for changes in the pitches assigned to set A and set B. Six notes again comprised each stimulus set. One set remained identical in composition from Experiment 1, with the pitch values for the second set juxtaposed in the half-steps between these values. Because of the half-step relation between pitches E and F in the first set, two values in the second set was also placed adjacent to each other in order to match this half-step relation. Two pigeons were tested from the range of the fourth octave, and two were tested with a range of pitches from the fifth octave. For pigeons #B2 and #B3, set A stimuli were composed of the D4, E4, F4, G4, A4, and B4 notes of the fourth octave (293–494 Hz), and set B stimuli were composed of the C4, Db4, Eb4, F#4, G#4, and Bb4 notes of the fourth octave (262–466 Hz). For subjects #B1 and #L4, set A stimuli were composed of the D5, E5, F5, G5, A5, and B5 notes of the fifth octave (587–988 Hz), and set B stimuli were composed of the C5, Db5, Eb5, F#5, G#5, and Bb5 notes of the fifth octave (524–932 Hz). All four conditions (AD+, AS−, BD−, and BS−) were again tested for 50 sessions with the same number of trials per condition.

6. Results

Shown in Fig. 3 are the mean acquisition results over the 50 sessions of Experiment 2 as measured by peck rate over the last three items for each 12-item sequence. As anticipated, the discrimination was now much harder for the pigeons, and the differences in peck rates among the conditions were much smaller than observed in Experiment 1.

The results for the individual pigeons shown in Fig. 4 are consistent with this general summary. Each panel again shows mean peck rate during each of the 12 items comprising a sequence within a trial for all four pigeons and for mean performance over the last 15 sessions of testing. We again conducted a series of two-way repeated measures (absolute [set A versus set

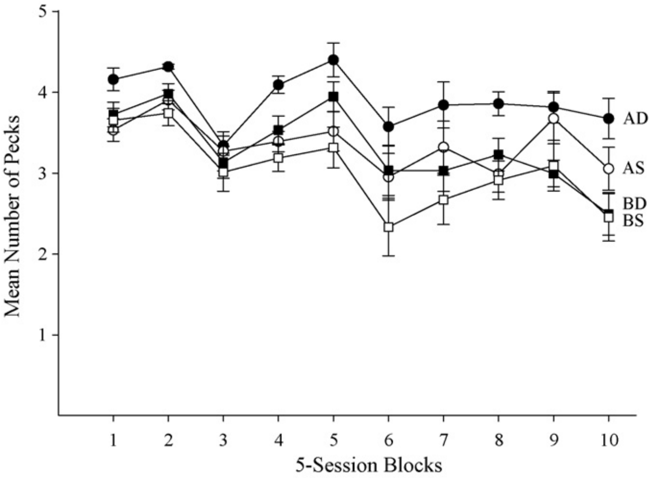

Fig. 3. Mean number of pecks over the last three serial position intervals across five-session blocks for the four conditions tested during training in Experiment 2. The error bars represent the standard error of the mean.

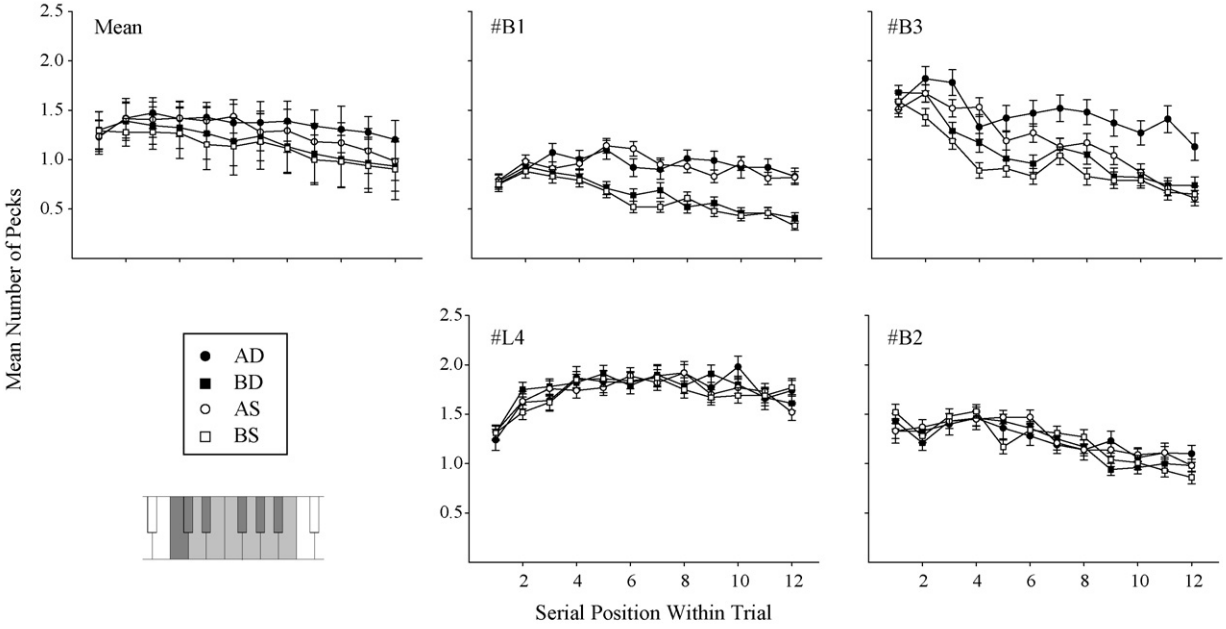

Fig. 4. These graphs show peck rate for all four conditions tested during training in Experiment 2 across 12 items serially presented within a trial for the last 15 sessions for all four birds and for each bird individually. The error bars represent the standard error of the mean. The keyboard depicts the relations of the stimuli within each stimulus set tested in Experiment 2, with one set consisting of six notes from either the fourth or fifth octaves (depending upon bird), and the other set consisting of six alternate notes from within the same octave.

B] × relational [*same* versus *different*]) ANOVAs on the mean peck rate over the last three items of each sequence for the last 15 sessions of testing for each bird to evaluate performance. Among the pigeons, we observed three basic outcomes.

First, two pigeons learned very little over the course of training. Pigeon #L4 showed no significant differences for either absolute, $F(1, 2) = 0.21$, $p = .69$, or relational control, $F(1, 2) = 0.65$, $p = .50$, with no interaction, $F(1, 2) = 1.3$, $p = .37$, as there was no difference in peck rate among the four conditions. Pigeon #B2 showed a small, but significant, degree of control by the absolute component, $F(1, 2) = 61.4$. Nevertheless, as can be seen, any difference was quite small and not much larger than that observed for #L4. This bird showed no significant difference based on relational control, $F(1, 2) = 0.68$, $p = .50$, and no interaction, $F(1, 2) = 0.58$, $p = .52$. Pigeon #B1 showed good evidence of learning among the conditions but only as significantly controlled by the absolute features of the discrimination, $F(1, 2) = 355.2$; there was no main effect of relational features, $F(1, 2) = 2.8$, $p = .24$, and no interaction effect, $F(1, 2) = 0.0$, $p = 1.00$. Finally, pigeon #B3 showed good evidence of learning about both types of information, as demonstrated a higher response rate to the AD+ condition relative to the other three S− conditions (BD, BS, and AS). There was no significant differentiation between these three conditions. For this pigeon, there was significant control exhibited by both the absolute, $F(1, 2) = 27.5$, and relational, $F(1, 2) = 36.8$, components of the discrimination. The interaction term for this pigeon was also significant, $F(1, 2) = 35.6$, reflecting the smaller difference between AD and AS in comparison to AD's separation from both BD and BS, even though there is still no difference between AS, BD, or BS.

6.1. Discussion

The results of Experiment 2 strongly reflected our success in making the absolute component more difficult. Overall, discrimination in general was not as good as that observed in Experiment 1. Two birds showed little or no success in learning the discrimination. Nevertheless, three of the four birds continued to make reliable distinctions based on absolute factors, albeit one quite weakly in terms of peck rate. Despite the attempt to heighten the salience of the relational component by increasing the difficulty of the absolute discrimination, however, this was only seen in one pigeon. This same bird had demonstrated relational control in Experiment 1 as well.

The increased difficulty of the absolute discrimination manifested itself in several ways. First, two birds showed little or no success in the overall discrimination. This is consistent with the idea that these pigeons persisted in attending to the absolute factors that they had used successfully in Experiment 1, but which apparently proved too difficult to discriminate here. Despite its availability, the redundant and relevant relational cues were not employed by these birds, even at the cost of losing stimulus control entirely. The two other pigeons, however, were more successful with the small 6% frequency separations that separated the different pitches of set A and set B. The psychophysical literature on frequency discrimination in pigeons suggests that this degree of difference is within their ability to detect a change of this magnitude (Dooling et al., 2000; Sinnott et al., 1980). Why then is there a difference between our animals in their ability to use the absolute pitch in this discrimination? This difference was not related to age, as one older and one young pigeon each failed or succeeded with these absolute values. One key factor may be that studies of difference thresholds typically involve successively played tones, and the subjects' task is to report a difference or change. While this taps the requirements needed for detecting our *different* sequences, our absolute discrimination also requires that the pigeons memorize the specific frequencies involved over trials and sessions. A memory for frequency differences is different than the perceptual detection of immediate frequency change, and it may be in the former capacity that our pigeons differed. For example, humans can easily tell when a song modulates key while it is playing, but it is very difficult to detect if a song is being played in the same key, for example, across days (Snyder, 2000). The latter is much more like what the pigeons had to do here.

Experiment 2 manifested little increase in the salience of the relational component. Pigeon #B3 showed the best evidence of relational control in Experiment 1 and continued to show the same pattern of control in this experiment. Perhaps due to the increased difficulty of discrimination of the absolute factor, the degree of control exhibited by both factors now seemed more equivalent for this bird. Nevertheless, the original goal of the experiment was not achieved, as none of the other pigeons showed any increased control by the relational component as a function of the change in the difficulty of the absolute component.

7. Experiment 3

Experiment 3 examined the consequences of reducing the difficulty of the relational discrimination while continuing to make the absolute component relatively difficult in comparison with the original discrimination in Experiment 1. To make the relational discrimination easier, the frequency range of each set was spread out over two octaves rather than one as done in the first two experiments. This change made detecting successive relational changes in the *different* sequences easier. To maintain the difficulty of the absolute discrimination at the same time, we continued to alternate the membership of each pitch to each set and also keep them within a half-step of a member of the other set, as done in Experiment 2 (see keyboard legend in Fig. 6 for arrangement). In Experiment 3, the pigeons were again trained for 50 sessions. Because they were showing good evidence of relational learning at this time, training was extended for 20 sessions using a slightly altered procedure.

8. Methods

8.1. Animals and apparatus

The same pigeons and apparatus used in Experiment 1 were used in Experiment 3.

8.2. Procedure

Six notes again comprised each stimulus set, but this time with an expanded pitch range. One set was composed of the C4, E4, G#4, D5, F#5, and Bb5 notes from across two octaves (262–932 Hz), and the other set was composed of the Db4, F4, A4, Eb5, G5, and B5 notes from across the same two octaves (277–988 Hz). For pigeons #B1 and #L4, set A stimuli were composed of pitches from the first set of stimuli, and set B stimuli were composed of pitches from the second set of stimuli. For pigeons #B2 and #B3, set A stimuli were composed of pitches from the second set of stimuli, and set B stimuli were composed of pitches from the first set of stimuli.

The procedure was otherwise identical to Experiments 1 and 2 for the first 50 sessions except for the stimulus sets described above. Following this training, the pigeons were tested for 20 sessions using an altered procedure. In this procedure, S− sequences (AS, BD, and BS) continued to play after the initial 12-item sequence until 15 s had passed since the last peck to the screen. This was designed to help to emphasize the three negative conditions. No pecks after the twelfth item were included in any analyses of these data in order to make everything comparable. Finally, it should be noted that #B3 began to consistently fail to finish many sessions during the latter part of this experiment due to a developed ability to eat directly from the hopper.

9. Results

Shown in Fig. 5 are the acquisition results for Experiment 3 as measured by mean peck rate over the last three items for each 12-item sequence over the 70 sessions. As can be seen, both absolute and relational properties of the discrimination came to control peck rates, as there was a clear separation between the set A conditions (AD and AS) and the set B conditions (BD and BS) and a separation between the *different* conditions (AD and BD) and the *same* conditions (AS and BS) based on the relational properties.

As in the previous experiments, however, understanding the individual results is important. The results for the individual pigeons are shown in Fig. 6. Each panel again shows mean peck rate during each of the 12 items comprising a sequence within a

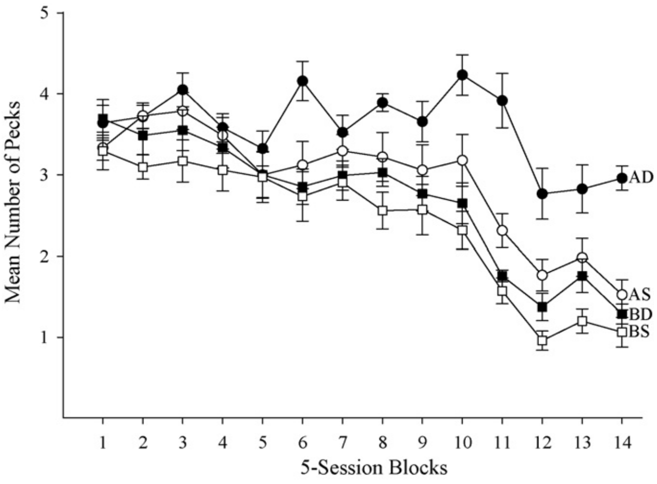

Fig. 5. Mean number of pecks over the last three serial position intervals across five-session blocks for the four conditions tested during training in Experiment 3. The last four blocks represent training with a slightly altered procedure (see text for details). The error bars represent the standard error of the mean.

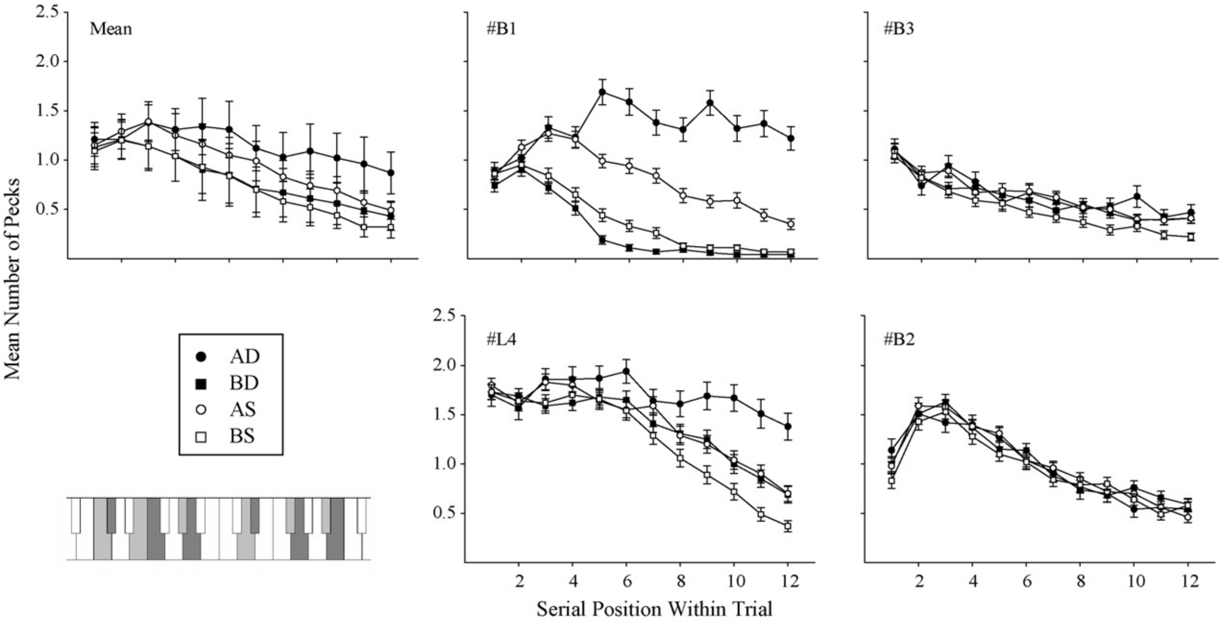

Fig. 6. These graphs show peck rate for all four conditions tested during training in Experiment 3 across 12 items serially presented within a trial for the last 15 sessions for all four birds and for each bird individually. The error bars represent the standard error of the mean. The keyboard depicts the relations of the stimuli within each stimulus set tested in Experiment 3, with one set consisting of six notes from both the fourth and fifth octaves, and the other set consisting of six alternate notes from both octaves.

trial over the last 15 sessions of testing. We conducted two-way repeated measures (absolute [set A versus set B] × relational [*same* versus *different*]) ANOVAs on the mean peck rate over the last three items of each sequence for the last 15 sessions of testing for each bird to evaluate performance.

Three of the four birds (#B1, #B3, and #L4) showed patterns of significant control by both absolute and relational properties. These three birds exhibited a significant main effect as a function of a sequence's absolute properties, #B1–$F(1, 2) = 319.2$; #B3–$F(1, 2) = 43.7$; #L4–$F(1, 2) = 527.0$, and a sequence's relational properties, #B1–$F(1, 2) = 126.4$; #B3–$F(1, 2) = 63.82$; #L4–$F(1, 2) = 344.5$. Finally, the interaction of these two factors showed significant asymmetries in the degree of control exhibited among the four conditions for two birds, #B1–$F(1, 2) = 401.29$; #L4–$F(1, 2) = 59.26$; this was not significant for #B3, $F(1, 2) = 0.10$, $p = .78$. Pigeon # B1 showed relational separation only between conditions AD and AS. Pigeon #L4 showed relational discrimination both between AD and AS and between BD and BS, although this separation was larger between AD and AS. As in Experiment 1, using a criterion of a 15% difference in peck rate between conditions, absolute control for these pigeons emerged after one to three items in the sequence, while relational difference emerged after four or more items. Finally, as in Experiment 2, pigeon #B2 failed to learn the discrimination, even after 70 sessions of testing; there was no absolute main effect, $F(1, 2) = 7.5$, $p = .11$, relational main effect, $F(1, 2) = 1.5$, $p = .34$, or interaction effect, $F(1, 2) = 1.3$, $p = .37$.

9.1. Discussion

The outcomes of Experiment 3 revealed that decreasing the difficulty of the relational discrimination, while maintaining the increased difficulty of the absolute discrimination, caused the pigeons to show a greater reliance on using the relational cues in the sequences. Two birds that had previously shown only control by absolute factors now employed both absolute and relational factors in performing the discrimination. The one pigeon who had consistently shown relational control in the prior experiments continued to show this pattern, although much less strongly due to motivational issues related to its direct and unauthorized eating from the hopper. The form of the absolute discrimination used in Experiment 3 continued to be too difficult for one pigeon, who continued to show no auditory stimulus control. The remaining three birds, however, could and did use both the absolute pitch and relational S/D information in each set to discriminate between the conditions.

Thus, the relative saliency of the absolute and relational factors is an important determinant of their use. If absolute information is readily available, such as in the frequency content of these stimuli, the pigeons can quickly lock on to this component. This is likely at the expense of relational control. Only when this is prevented by making the absolute discrimination very difficult, as done here, or by eliminating it entirely as done by design in S/D experiments (Cook and Brooks, in press), does relational information come to control behavior. Nevertheless, under the right circumstances, the pigeons in the current experiment did eventually and spontaneously use relational information in these sequences.

The latter finding suggests that special training is not needed to get pigeons to process S/D information in the auditory modality. Previously, Cook and Brooks (in press) found that it was initially difficult to train pigeons in their S/D auditory discrimination task. They eventually used an asymmetrical training procedure to establish a reliable discrimination. In their procedure, 12 individual items were mixed together to form *different* trials, and then individual items were slowly introduced one at time on *same* trials over a period of sessions until a complete S/D discrimination had been constructed. This suggested that learning S/D relations in the auditory domain might be more difficult than in the visual modality, where this type of complication had not been encountered in successive discriminations (Cook et al., 2003). The results of the current experiment suggest that such special procedures are not a necessary condition for the development of relational auditory control.

After Experiment 3, we collected two more sets of observations with these pigeons that are worthy of mention. The first involved returning the pigeons to conditions identical to those in Experiment 1, except for the reversal of the octaves assigned to set A and set B. Despite the return to a much easier absolute discrimination, all three pigeons that had shown mixed absolute and relational control in Experiment 3 continued to do so in this unreported experiment, although only one of those birds had shown relational control in Experiment 1. This outcome suggests that once relational control is established, it can be maintained in situations that had previously been dominated by absolute cues. In addition, the one bird that had failed to discriminate in Experiments 2 and 3 returned to showing control by the absolute component of the discrimination. This suggests that it was indeed the range and arrangement of the pitches in those experiments that had interfered with learning rather than any perceptual deficits in this bird. Finally, all pigeons were eventually transferred to conditions similar to those used in Cook and Brooks (in press), where only relational information was differentially reinforced, and absolute cues were eliminated by design. In these observations, all birds eventually learned to discriminate *same* and *different* sequences based exclusively on relational cues.

10. General discussion

Together, these experiments reveal that both absolute and relational properties can concurrently control a sequential auditory discrimination by pigeons. Overall, we saw either one of two basic patterns of control emerge, with a pigeon either being controlled exclusively by absolute properties or showing a mixed degree of simultaneous control by both absolute and relational properties. In none of the experiments did a pigeon show exclusive control by only the relational components of the sequences. In all of the experiments, the pigeons readily learned to discriminate the absolute fundamental pitch of the notes differentiating our two sets. This was true whether the set difference was characterized by different octave ranges or smaller 6% differences between alternating adjacent tones (although the latter organization proved too difficult for one bird). In general, these results fit well with the recent results on the discrimination of absolute pitch of pure tones by pigeons (Friedrich et al., 2007).

Relational control was also instituted but seemed more difficult to establish, at least with the values we employed. One pigeon consistently demonstrated relational control from the start with relational differences occurring over a one octave range, but two other birds only learned this when we used an easier relational discrimination built over a two octave range. The one remaining pigeon briefly showed evidence of relational control in Experiment 1, but never after that point. These relational results are consistent with the S/D findings of Cook and Brooks (in press) and indicate that relational control can emerge without special training procedures or without explicitly being differentially reinforced as done in S/D studies.

In general, control by absolute factors was more dominant than control by relational factors. Within our parameters, more of the pigeons over more of the time were controlled by the absolute properties than compared to the relational properties. In addition, control by absolute factors consistently emerged earlier during training. We also observed that absolute control emerged earlier within a trial sequence. Based on absolute pitch, the conditions separated within the first or second items of a sequence. When the birds did express relational control, it tended to emerge only after four or more items of a sequence had been presented. This slower relational processing of auditory sequences was also observed by Cook and Brooks (in press). In both of these cases, the emergence of relational auditory control was slower than what we had observed for successive visual S/D tasks (Cook et al., 2003). One advantage of absolute properties is that they can provide immediate recognition based on a single item, whereas relational control requires that at least two items to have been processed before it can be determined. Although absolute properties generally seemed more salient, these experiments also importantly demonstrate that the interaction between relational and absolute factors is determined in part by the relative discriminability of these properties. Absolute control was more difficult to establish, for instance, after we had made this discrimination harder for Experiment 2, and relational control was easier to establish after we had made it more salient for Experiment 3. Thus, any conclusion or generalization about the relative saliency of these factors within and across modalities or species needs to be calibrated and examined within the context of basic discriminability.

These auditory results mirror what has been found in similar discriminations involving simultaneous visual discriminations by pigeons (Gibson and Wasserman, 2003, 2004). Gibson and Wasserman found that pigeons learn about absolute and relational factors when both are redundant and relevant cues in an icon-based visual discrimination. One area of discrepancy is that Gibson and Wasserman found both types of control seemed to emerge at the same point in training, whereas in the current study, absolute control emerged to a greater degree and more quickly than did control by the relational component. In this sense, our results are more like the results of Wasserman et al. (2002) in which stronger absolute control was present. Despite this point, the major conclusion is that pigeons are capable of attending and processing to both types of information in either modality when both are relevant.

One important question that remains to be addressed involves the representations of these different types of stimulus control across the two modalities. Clearly, the absolute features of our auditory stimuli share no overlap with the visual icons of Wasserman et al. (2002) and Gibson and Wasserman (2003, 2004), for example. As a result, the item representations involved must have been modality specific and independent of one another. This is potentially not the case with relational information. This type of higher-order information has the possibility of being more abstract and modality independent. It is for this powerful reason that relational encoding can contribute directly to the development of generalized intelligence. Thus, abstract descriptors such as *same* and *different* can be understood and applied regardless of source modality. Now that procedures for creating relational auditory and visual discriminations have been established, it will be important to determine whether relational control in these modalities shares any form of common representation. Evidence for this type of common higher-order representation could come from pigeons showing cross modal transfer between visual and auditory S/D discriminations, for example.

A potential issue is that the pigeons may have memorized the specific sequences involved, instead of using more generalized S/D responding. Because there are 1,440 possible *different* sequences and only six possible *same* sequences in any given experiment, sequence memorization could have played a role in some our results. Pigeons are certainly capable of remembering large number of pictures, for example (Cook et al., 2005; Fagot and Cook, 2006; Wasserman et al., 2002). Previous research with S/D tasks, however, has suggested that such memorization is not an important factor as the birds readily transfer to new items with which they have no past experience (Cook, 2002; Cook and Brooks, in press; Cook et al., 1997, 2003).

As mentioned previously, Weisman et al. (2004) suggested several comparative hypotheses regarding the processing of absolute pitch among animals. Among bird species, songbirds have been found to have better absolute pitch discrimination than either rats or humans, suggesting that songbirds may be generally better at processing this auditory feature than mammals. In a recent attempt to examine this possibility for birds as a class, Friedrich et al. (2007) tested a non-songbird, pigeons. They found pigeons were more sensitive to absolute pitch than mammals, but not to the degree found in songbirds. While it is difficult to compare our procedures directly, our results are certainly consistent with this conclusion. Our pigeons were strongly predisposed to process this absolute feature in all of our experiments, even under the highly demanding conditions tested in Experiments 2 and 3. Thus, our results are consistent with comparative idea that absolute pitch is a readily available auditory feature to birds as a class.

We would also like to suggest that the processing and memorization of absolute or stimulus-specific features may represent a fundamental and general adaptation of the avian nervous system more generally. This capacity can be seen in the pigeon's remarkable ability to memorize pictures (Chase and Heinemann, 2001; Cook et al., 2005; Fagot and Cook, 2006; Vaughan and Greene, 1984), pictorial details (Edwards and Honig, 1987; Greene, 1983), object orientations (Peissig et al., 2000; Spetch and Friedman, 2003), and stimulus relations (Carter and Werner, 1978; Wright, 1997). Various species of other birds have been found to have durable long-term memories for specific foraging (Henderson et al., 2001) and migratory (Mettke-Hoffman and Gwinner, 2003) experiences. Further evidence from the auditory modality indicates that some birds can distinguish among relatively large numbers (<64) of conspecific songs (Chew et al., 1996; Stoddard et al., 1992) and that mockingbirds have learned repertoires of 150 or more heterospecific songs (Derrickson, 1987). Similarly, the Clark's Nutcracker has been found to have a large capacity memory for spatially related caching experiences (Balda and Kamil, 1992; Tomback, 1980). Such findings suggest that birds in general may rely on the learning and retention of large amounts of highly specific information to guide their behavior in a variety of areas. This may even represent their primary or preferred strategy for acquiring information, much as observed in the current study.

These pigeon results contribute to the general study of auditory processing in birds (Baptista and Gaunt, 1994; Doupe and Kuhl, 1999). Pigeons have a reputation for being difficult to train and test with auditory stimuli. Our recent experience has not confirmed this characterization, as we have found them relatively accommodating to learning auditory discriminations of different types. By examining auditory processing in a non-songbird without complex vocal capabilities, this kind of research helps to cast a new light on the specialized and common features of auditory processing in birds. Such comparisons contribute to our understanding of how evolution may have shaped cognition in different modalities and species and the nature of avian auditory processing outside of the more specialized domain of bird song and communication.

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References

Balda, R.P., Kamil, A.C., 1992. Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. Animal Behaviour 44, 761–769.

Baptista, L.F., Gaunt, S.L.L., 1994. Advances in studies of avian sound communications. Condor 96, 817–830.

Berryman, R., Cumming, W.W., Cohen, L.R., Johnson, D.F., 1965. Acquisition and transfer of simultaneous oddity. Psychological Reports 17, 767–775.

Blaisdell, A.P., Cook, R.G., 2005. Two-item same-different concept learning in pigeons. Learning & Behavior 33, 67–77.

Bovet, D., Vauclair, J., 2000. Picture recognition in animals and humans. Behavioural Brain Research 109, 143–165.

Carter, D.E., Werner, J.T., 1978. Complex learning and information processing in pigeons: a critical analysis. Journal of the Experimental Analysis of Behavior 29, 565–601.

Chase, S., Heinemann, E.G., 2001. Exemplar memory and discrimination. In: Cook, R.G. (Ed.), Avian Visual Cognition http://www.pigeon.psy.tufts.edu/avc/chase/.

Chew, S.J., Vicario, D.S., Notebohm, F., 1996. A large-capacity memory system that recognizes the calls and songs of individual birds. Proceedings of the National Academy of Sciences 93, 1950–1955.

Cook, R.G., 2002. The structure of pigeon multiple-class same-different learning. Journal of the Experimental Analysis of Behavior 78, 345–364.

Cook, R.G., Brooks, D.I., in press. Generalized auditory same-different discrimination by pigeons. Journal of Experimental Psychology: Animal Behavior Processes.

Cook, R.G., Roberts, S., 2007. The role of video coherence on object-based motion discriminations by pigeons. Journal of Experimental Psychology: Animal Behavior Processes 33 (3), 287–298.

Cook, R.G., Smith, J.D., 2006. Stages of abstraction and exemplar memorization in pigeon category learning. Psychological Science 17, 1059–1067.

Cook, R.G., Wasserman, E.A., 2006. Relational learning in pigeons. In: Wasserman, E.A., Zentall, T. (Eds.), Comparative Cognition: Experimental Explorations of Animal Intelligence. Oxford University Press, London, pp. 307–324.

Cook, R.G., Katz, J.S., Cavoto, B.R., 1997. Pigeon same-different concept learning with multiple stimulus classes. Journal of Experimental Psychology: Animal Behavior Processes 23, 417–433.

Cook, R.G., Kelly, D.M., Katz, J.S., 2003. Successive two-item same-different discrimination and concept learning by pigeons. Behavioural Processes 62, 125–144.

Cook, R.G., Levison, D.G., Gillett, S.R., Blaisdell, A.P., 2005. Capacity and limits of associative memory in pigeons. Psychonomic Bulletin & Review 12, 350–358.

Cumming, W.W., Berryman, R., Cohen, L.R., 1965. Acquisition and transfer of zero delay matching. Psychological Reports 17, 435–445.

Cynx, J., 1995. Similarities in absolute and relative pitch perception in song birds (starling and zebra finch) and a non-song bird (pigeon). Journal of Comparative Psychology 109, 261–267.

Delius, J.D., Tarpy, R.M., 1974. Stimulus control of heart rate by auditory frequency and auditory pattern in pigeons. Journal of the Experimental Analysis of Behavior 21, 297–306.

Derrickson, K.C., 1987. Yearly and situational changes in the estimate of repertoire size in Northern Mockingbirds (*Mimus polyglottos*). Auk 104, 198–207.

Dooling, R.J., Brown, S.D., Park, T.J., Okanoya, K., Soli, S.D., 1987. Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*). I. Pure tones. Journal of Comparative Psychology 101, 139–149.

Dooling, R.J., Lohr, B., Dent, M.L., 2000. Hearing in birds and reptiles. In: Dooling, R.J., Fay, R.R., Popper, A.N. (Eds.), Comparative Hearing: Birds and Reptiles. Springer, New York, NY, pp. 3081–3359.

Doupe, A.J., Kuhl, P.K., 1999. Birdsong and human speech. Annual Review of Neuroscience 22, 567–631.

Edwards, C.A., Honig, W.K., 1987. Memorization and "feature selection" in the acquisition of natural concepts in pigeons. Learning and Motivation 18, 235–260.

Fagot, J., Cook, R.G., 2006. Evidence for large long-term memory capacities in baboons and pigeons and its implication for learning and the evolution of cognition. Proceedings of the National Academy of Science 103, 17564–17567.

Fagot, J., Wasserman, E.A., Young, M.E., 2001. Discriminating the relation between relations: the role of entropy in abstract conceptualization by baboons (*Papio papio*) and humans (*Homo sapiens*). Journal of Experimental Psychology: Animal Behavior Processes 27, 316–328.

Fersen, L.V., Delius, J.D., 1989. Long-term retention of many visual patterns by pigeons. Ethology 82, 141–155.

Friedrich, A., Zentall, T.R., Weisman, R.G., 2007. Absolute pitch: frequency-range discriminations in pigeons (*Columba livia*)—comparisons with zebra finches (*Taeniopygia guttata*) and humans (*Homo sapiens*). Journal of Comparative Psychology 121, 95–105.

Gibson, B.M., Wasserman, E.A., 2003. Pigeons learn stimulus identity and stimulus relations when both serve as redundant, relevant cues during same-different discrimination training. Journal of Experimental Psychology: Animal Behavior Processes 29, 84–91.

Gibson, B.M., Wasserman, E.A., 2004. Time-course of control by specific stimulus features and relational cues during same-different discrimination training. Learning & Behavior 32, 183–189.

Greene, S.L., 1983. Feature memorization in pigeon concept formation. In: Commons, M.L., Herrnstein, R.J., Wagner, A.R. (Eds.), Quantitative Analyses of Behavior: Discrimination Processes, 4. Ballinger, Cambridge, MA, pp. 209–229.

Henderson, J., Hurly, T.A., Healy, S.D., 2001. Rufous hummingbirds' memory for flower location. Animal Behaviour 61, 981–986.

Herman, L.M., Pack, A.A., Wood, A.M., 1994. Bottlenose dolphins can generalize rules and develop abstract concepts. Marine Mammal Science 10, 70–80.

Holmes, P.W., 1979. Transfer of matching performance in pigeons. Journal of the Experimental Analysis of Behavior 31, 103–114.

Hurly, T.A., Ratcliffe, L., Weisman, R.G., 1990. Relative pitch recognition in white-throated sparrows, *Zonotrichia albicollis*. Animal Behaviour 40, 176–181.

Katz, J.S., Wright, A.A., 2006. Same/different abstract-concept learning by pigeons. Journal of Experimental Psychology: Animal Behavior Processes 32, 80–86.

Lohr, B., Dooling, R.J., 1998. Detection of changes in timbre and harmonicity in complex sounds by zebra finches (*Taeniopygia guttata*) and budgerigars (*Melopsittacus undulatus*). Journal of Comparative Psychology 112, 36–47.

Mercado III, E., Killebrew, D.A., Pack, A.A., Macha, I.V.B., Herman, L.M., 2000. Generalization of 'same-different' classification abilities in bottlenosed dolphins. Behavioural Processes 50, 79–94.

Mettke-Hoffman, C., Gwinner, E., 2003. Long-term memory for a life on the move. Proceedings of the National Academy of Sciences 100, 5863–5866.

Page, S.C., Hulse, S.H., Cynx, J., 1989. Relative pitch perception in the European starling (*Sturnus vulgaris*): Further evidence for an elusive phenomenon. Journal of Experimental Psychology: Animal Behavior Processes 15, 137–146.

Peissig, J.J., Young, M.E., Wasserman, E.A., Biederman, I., 2000. Seeing things from a different angle: The pigeon's recognition of single geons rotated in depth. Journal of Experimental Psychology: Animal Behavior Processes 26, 115–132.

Pepperberg, I.M., 1987. Acquisition of the same/different concept by an African Grey parrot (*Psittacus erithacus*): learning with respect to categories of color, shape, and material. Animal Learning & Behavior 15 (4), 423–432.

Price, L.L., Dalton, L.W., Smith, J.C., 1967. Frequency DLs in the pigeon as determined by conditioned suppression. Journal of Auditory Research 7, 229–239.

Riley, D.A., 1968. Discrimination Learning. Allyn and Bacon Inc., Boston, MA.

Sinnott, J.M., Sachs, M.B., Hienz, R.D., 1980. Aspects of frequency discrimination in passerine birds and pigeons. Journal of Comparative & Physiological Psychology 94, 401–415.

Snyder, B., 2000. Music and Memory: An Introduction. MIT Press, Cambridge, MA.

Spence, K.W., 1937. The differential response in animals to stimuli varying within a single dimension. Psychological Review 44, 430–444.

Spetch, M.L., Friedman, A., 2003. Recognizing rotated views of objects: interpolation versus generalization by humans and pigeons. Psychonomic Bulletin & Review 10, 135–140.

Stoddard, P.K., Beecher, M.D., Loesche, P., Campbell, S.E., 1992. Memory does not constrain individual recognition in a bird with song repertoires. Behaviour 122, 274–287.

Thompson, R.K.R., Oden, D.L., Boysen, S.T., 1997. Language-naive chimpanzees (*Pan troglodytes*) judge relations between relations in a conceptual matching-to-sample task. Journal of Experimental Psychology: Animal Behavior Processes 23, 31–43.

Tomback, D.F., 1980. How nutcrackers find their seed stores. Condor 82, 10–19.

Vaughan, W., Greene, S.L., 1984. Pigeon visual memory capacity. Journal of Experimental Psychology: Animal Behavior Processes 10, 256–271.

Wasserman, E.A., Young, M.E., Dalrymple, R.M., 1997. Memory-based same-different conceptualization by pigeons. Psychonomic Bulletin & Review 4, 552–558.

Wasserman, E.A., Frank, A.J., Young, M.E., 2002. Stimulus control by same-versus-different relations among multiple visual stimuli. Journal of Experimental Psychology: Animal Behavior Processes 28, 347–357.

Weisman, R.G., Ratcliffe, L., Johnsrude, I.S., Hurly, T.A., 1990. Absolute and relative pitch production in the song of the black-capped chickadee. Condor 92, 118–124.

Weisman, R.G., Njegovan, M.G., Williams, M.T., Cohen, J.S., Sturdy, C.B., 2004. A behavior analyses of absolute pitch: sex, experience and species. Behavioural Processes 66, 289–307.

Wright, A.A., 1997. Concept learning and learning strategies. Psychological Science 8, 119–123.

Wright, A.A., 1998. Auditory list memory in rhesus monkeys. Psychological Science 9, 91–98.

Wright, A.A., Santiago, H.C., Sands, S.F., 1984. Monkey memory: same/different concept learning, serial probe acquisition, and probe delay effects. Journal of Experimental Psychology: Animal Behavior Processes 10, 513–529.

Wright, A.A., Shyan, M.R., Jitsumori, M., 1990. Auditory same/different concept learning by monkeys. Animal Learning & Behavior 18, 287–294.

Young, M.E., Wasserman, E.A., 2001. Stimulus control in complex arrays. In: Cook, R.G. (Ed.), Avian Visual Cognition http://www.pigeon.psy.tufts.edu/avc/young/.