2006

Altered features of female pigeons (Columba livia) elicit preference behavior in male pigeons

Tadd B. Patton
University of South Florida

Scholar Commons Citation

Patton, Tadd B., "Altered features of female pigeons (Columba livia) elicit preference behavior in male pigeons" (2006). *USF Tampa Graduate Theses and Dissertations.*
https://digitalcommons.usf.edu/etd/2657

Altered Features of Female Pigeons (*Columba livia*) Elicit Preference Behavior in Male Pigeons

by

Tadd B. Patton

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Arts
Department of Psychology
College of Arts and Sciences
University of South Florida

Major Professor: Toru Shimizu, Ph.D.
Michael Brannick, Ph.D.
Sarah Partan, Ph.D.
Thomas Sanocki, Ph.D.

Date of Approval:
May 19, 2006

Keywords: Bird, Face Recognition, Conspecific Recognition, Vision, Mate Selection

Acknowledgements

The author would like to thank the following individuals for their invaluable assistance with the completion of this study and thoughtful review of previous drafts of this manuscript: Toru Shimizu, Gabrielle Szafranski, Justine VandenBosche, Sophia Delgado, and Joshua Nadeau.

Dedication

This thesis is dedicated to my friends and family that have been behind me every step of the way. A special dedication goes to Melinda Patton who encouraged me to finish what I started.

Table of Contents

List of Tables iii

List of Figures iii

Abstract v

Introduction 1

Importance of Head and Face for Recognition and Selection 2

Importance of Local Components vs. Global Configuration for Recognition 4

Methods

Subjects 10

Apparatus 10

Stimuli 11

Procedure 15

Data Analysis 16

Results 17

Qualitative Movement Observation 17

Position Preference Analysis 19

Time Spent Near Altered vs. Original Stimuli 20

Vocalizations Near Altered vs. Original Stimuli 23

Circling Displays Near Altered vs. Original Stimuli 25

Discussion 27

Critical and Non-Critical Features 27

  - Contour 29
  - Global Configuration 29
  - Methodological Considerations 31
  - Concluding Remarks 31

- References 33
- Appendices 37
  - Appendix A Summary of Cumulative Results 38

List of Tables

Table 1. Preference for one side over the other side 19

Table 2. Preference for altered stimuli over original stimuli 21

List of Figures

Figure 1. Schematic illustration of testing apparatus 11

Figure 2. Sample photographic images of each stimulus group..................................14

Figure 3. Subject movement patterns 18

Figure 4. Boxplot of position preference scores..20

Figure 5. Boxplot of time spent near altered stimuli..21

Figure 6. Boxplot of vocalizations toward altered stimuli 22

Figure 7. Boxplot of bowing displays toward altered stimuli 23

Altered Features of Female Pigeons (*Columba livia*) Elicit Preference Behavior in Males

Tadd B. Patton

ABSTRACT

Previous research has shown that male pigeons (*Columba livia*) respond with courtship displays to video playbacks of a female pigeon indicating that they ‘recognize’ the female as a potential mate. Courtship displays significantly decline when the head region of the female is occluded (Shimizu, 1998) suggesting that features located within the head are important for species recognition and mate selection. However, little is known about the exact visual features necessary to elicit displays. The current study examined the preference behavior of male pigeons when given a choice between photographic images of normal looking or altered female pigeon faces. The altered-face categories included: 1) enlarged or removed facial features such as the eyes or beak; 2) the eyes and beak reconfigured within the head; and 3) removed contour (outline). The results showed that subjects responded preferentially toward females with enlarged features (eyes or beak). However, subjects responded preferentially toward normal females when the alternative stimuli were faces that were missing the eyes and/or beak. Preference for normal females was also observed when females with “incorrect” configuration were shown. Finally, subjects responded significantly less to females lacking contour, even when the eyes and beak were visible. The overall findings suggest local facial components are important, although this effect diminishes if the contour of the female is not visible. These findings also suggest that pigeons attend to both local

components and global configuration when they detect conspecifics and identify potential mates.

Introduction

Bird vision is equal to, or better than, human vision, in terms of acuity, color discrimination, and motion detection ability (Hodos, 1993; Frost & Sun, 1997; Shimizu, Patton, & Szafranski, In press). Birds use these superb abilities to navigate their environment, forage for food, and watch for predators from a safe distance. For instance, pigeons are able to identify members of their own species (conspecific recognition) and choose potential mates (mate selection) based solely on visual cues (Shimizu, 1998). The goal of the proposed study was to extend our understanding of how birds accomplish complex visual discrimination tasks, such as the recognition of conspecifics and the selection of mates. The main question was: When a bird recognizes a stimulus as a conspecific or a potential mate, does it rely on specific local components of the stimulus (e.g., eyes, beak) or a global configuration of these components (e.g., the position of eyes in relation to beak), or both? In addition, the importance of stimulus contour (outline) was investigated. The hypothesis was that pigeons depend, to some degree, on both local and global features – in the head and/or face and on the contour of the stimulus – to accomplish conspecific recognition and mate selection. The results of this study extended our understanding of the perceptual and cognitive processes birds use to accomplish such complex tasks. Furthermore, these findings can be used to draw comparisons between avian and mammalian visual processing.

Importance of the Head and Face for Recognition and Selection.

For many animals, characteristics of the head or face convey biologically relevant and salient information to individuals that allow them to detect members of the same species, identify potential mates and rivals, and recognize specific individuals within a group. This is perhaps most evident for humans. Studies have shown that we are capable of recalling the names of individuals when given photographs of only the head and face (Bahrick, Bahrick, & Whittlinger, 1975). This is somewhat remarkable considering that faces within a given species are relatively homogenous (i.e., all faces have eyes, nose, and mouth with the same spatial configuration). Therefore, face recognition requires a sophisticated level of visual discrimination. Studies have shown that information in the head and face is important to non human primates for recognition of individuals within a group. A study by Parr, Winslow, Hopkins, and de Waal (2000) demonstrated that the chimpanzee (*Pan troglodytes*) and rhesus monkey (*Macaca mulatta)* could identify individuals of their own species based solely on information in the head and/or face region. In this study, subjects were required to discriminate between pairs of photographs that were either of the same individual conspecific or of different individuals. After reaching a level proficiency, features in some of the stimulus photographs were masked so that only the head and/or face region were visible. The results suggest that both species were capable of discriminating individuals without information about the rest of the body (de Waal et al., 2000).

Species recognition has been studied in many bird species as well. Previous studies have shown that birds, such as budgerigars (*Melopsittacus undulatus*), also use the head and/or face for conspecific and individual recognition. The head and face region of the budgerigar is characterized by several noticeable markings on the cheeks and around the eyes that presumably convey information such as age, sex, and willingness to mate (Brown & Dooling, 1993). A study by Trillmich (1976) demonstrated the ability of budgerigars to discriminate conspecific individuals based solely on visual cues. In this study, budgerigars were trained to discriminate between two live conspecific individuals and between color slides (photographs) of them. When portions of the stimuli were masked so that the head was not visible, budgerigars performed less accurately than when the whole head was visible. This indicates that information in the head and/or face is important for individual discrimination for this species.

In the studies discussed above, animals were successfully trained to discriminate images of conspecific heads/faces using appetitive operant conditioning procedures. The assumption is that animals in natural settings recognize conspecific individuals using the same discrimination ability. However, because discrimination can be accomplished without ‘recognition,’ it is not clear if these animals were actually ‘recognizing’ the objects in the photographs as conspecifics. An alternative to operant training procedures is to study naturally occurring responses to biologically relevant stimuli. For instance, courtship displays by male birds in the presence of females can be used as a measure of conspecific recognition and mate selection (Ryan & Lea, 1994).

This ethological approach has been extensively used in studies of Japanese quail (*Coturnix coturnix japonica*). In an experiment by Domjan and Nash (1988), male subjects placed in a test cage could see taxidermically prepared females or males through a window. The experimenters measured the proximity of subjects to the window during the presentation of different stimuli. When the stimulus was the whole female model or only the head portion, male subjects showed an increased proximity to the window, suggesting that the subjects were ‘interested’ in these stimuli. However, the proximity was significantly lower when the stimulus was a male model, inverted female model, or the body of the female model without the head.

Shimizu (1998) studied the visual recognition capability of male pigeons by presenting video playbacks of various female pigeon stimuli. The natural response of a male pigeon toward a female conspecific is to display characteristic courtship behaviors such as bowing, tail dragging, and vocalizations (Levi, 1974; Stokes, 1979). In the study, male pigeons were sometimes presented with video playbacks of an obstructed view of a female pigeon to study the significance of different physical components (i.e., head or body) for conspecific recognition. Subjects’ responses were significantly lower when only the body of a female pigeon was presented. However, when only the head region was presented, males reacted to the stimuli as rigorously as in the unobstructed view of the whole female pigeon. Both of these studies, using ethological approaches, provide additional evidence that visual components in the head and/or face are important for conspecific recognition and mate selection.

Importance of Local Components vs. Global Configuration for Recognition

What remains unknown is which specific information in the face birds use for recognition and mate selection. Do they use local components, global configuration of the components, or both? There are examples, in which relatively simple local components can elicit distinct behaviors. In a classic ethological study investigating herring gull behavior, Tinbergen and Perdeck (1950) showed that herring gull chicks would peck at a red spot on their mother’s beak to elicit regurgitation of food. It was subsequently determined that the red spot located on the mother’s beak was the key stimulus that acted as a releaser for this behavior. In another example, some birds (e.g., jays) are acutely sensitive to the brightly colored designs on the forewings of various moths that appear to be large eyes. The eyespot patterns on the moth serve as effective deterrents to small insectivorous passerines presumably because they mimic the eyes of large avian predators, such as owls (McFarland, 1985). Eyespot mimicry has been extensively and systematically investigated in laboratory studies. In a study conducted by Blest (1957), birds were first trained to eat mealworms off of a specially designed box. Then, different stimulus shapes would be illuminated near the mealworm in the box as birds approached. The stimuli ranged from simple lines to more complex eyelike shapes. The findings showed that the more eyelike the stimuli, the more effective they were in eliciting avoidance behavior from the birds.

The releasers used in these examples above are not directly involved in conspecific recognition or mate selection. In social communications between conspecifics, the relative importance of local components and global configuration is still in debate. Research in human face perception has shown that humans use different strategies for recognition depending on conditions, such as familiarity and orientation (Schwaninger, Lobmaier, & Collishaw, 2002). Specifically, when the face is familiar or in its normal, upright position, we rely on a global configuration of diverse components for recognition. That is, successful face recognition does not necessarily depend on any particular local components within the face (e.g., shape, size, or color of eyes), but on the Gestalt of all the parts (Farah, Tanaka, & Drain, 1995; Sergent, 1984). However, when the face is unfamiliar or inverted (upside-down), subjects attend to local components for recognition (Thompson, 1980).

Similar results have been found in non-human primates suggesting they use similar processes for face recognition. For instance, one study showed that chimpanzees exhibit the face inversion effect for humans and chimpanzees, but not for capuchins (*Cebus apella*) or automobiles (Parr, Dove, & Hopkins, 1998). However, there is some evidence that when a face is unfamiliar or partially masked, specific components are important for recognition. For instance, when chimpanzees and rhesus monkeys were forced to rely on local components of the face, they appear to pay attention to eyes rather than other components. In a previously discussed study by Parr et al., (2000), investigators masked portions of chimpanzee and rhesus monkey face photographs (e.g., eyes and/or mouth), and found that both species had more difficulty when the eyes of these photographs were masked than when mouths were masked. The results suggest that eyes are particularly salient local components used for individual and conspecific recognition, and are consistent with other primate studies of individual recognition (McKelvie, 1976; Keating & Keating, 1993). As in primates, previous studies of avian visual behaviors suggest that birds can also use both local components and global configuration in order to discriminate conspecific individuals. Using appetitive operant conditioning procedures, Brown and Dooling (1992; 1993) conducted a series of studies using budgerigars to study this issue. In one study (Brown & Dooling, 1992), they trained budgerigars to discriminate whether two color photographs of conspecific faces belonged to the same bird or not. It was determined that subjects successfully discriminated them based solely on local components within the face. By analyzing the reaction time to these stimuli using multi-dimensional scaling, the researchers identified which specific local components acted as salient cues for accomplishing this task. The results showed that birds could discriminate individuals, using local components including face color and pattern of markings in the head region. The results also showed that specific features of their eyes, such as darkness of the iris and size of pupil, provide important information for identifying individuals.

Global configuration is also important according to a subsequent series of experiments by Brown and Dooling (1993). In the study, budgerigars were presented with synthetic (computerized) conspecific faces that had been modeled after real budgerigars. When some local components of the stimulus faces were scrambled so that all components remained in the stimuli, but were not in their correct location, reaction times for scrambled faces were significantly longer compared to non-scrambled (normal) stimuli. The results demonstrated the importance of global configuration and correct orientation of specific components.

Unlike budgerigars, pigeons do not have many noticeable facial components. Nevertheless, there is evidence that both local components and global configuration are important for conspecific recognition and mate selection in pigeons. Watanabe and Ito (1991) investigated the ability of pigeons to discriminate photographs of the head regions of other pigeons, in which they arbitrarily assigned some as positive stimuli (S+) and others as punishment (S-). Using appetitive operant conditioning procedures, once subjects were trained to discriminate between the S+ and S- birds, some face components were altered and subjects were tested for their responses to the new stimuli. Pigeons showed a significant reduction in pecking at S+ birds when eyes or beak were completely removed. The results suggest that eyes and beak are important for discrimination of individuals.

The importance of global configuration was also tested in this study. When subjects were shown a silhouette (no visible local component) of the S+ pigeon, they responded to this stimulus almost as strongly as when all components of the S+ were visible. In addition, when the stimuli were scrambled so that the local components were visible, but not in the correct locations (e.g., eyes were positioned below the beak; the beak and eyes were positioned away from the head), responses to these stimuli were greatly reduced. These results suggest that global configuration, such as the contour, or outline of the face and the correct orientations of these components, were critical as well.

These findings indicate that pigeons use both individual components (especially eyes) and global configuration of these components for conspecific recognition. However, these studies used operant conditioning procedures to force birds to choose one or the other stimulus with food as reward. The relative importance of these components may change in natural settings. In order to understand the function and evolution of the visual discrimination ability in birds, it is essential to study how birds use diverse visual components in natural settings for conspecific recognition and mate selection.

The goal of the proposed study was to identify: 1) the specific local facial features important for species recognition and mate selection; 2) the importance of configuration of these local facial features; and 3) the importance of the contour (outline) of the stimulus. It was hypothesized that pigeons differentially rely on each these features attributes in order to accomplish conspecific recognition and mate selection.

In the present study, we used face pictures of female pigeons as stimuli to test which facial components of females were critical for triggering male courtship behavior. Male subjects were forced to choose between photographic images of normal female faces and those that had been digitally altered along a specific dimension (e.g., faces with enlarged eyes or removed eyes). In particular, we manipulated the size of local components (eyes and beak), as well as spatial configuration of these components and contour (outline) of a female stimulus. We analyzed their preference for an altered stimulus over the original stimulus by measuring stereotyped courtship behaviors toward each stimulus, as described elsewhere (Shimizu, 1998; Partan, Yelda, Price, & Shimizu, 2005).

In the present study, it was necessary to use static images instead of video playback because the stimulus manipulations would require frame-by-frame alteration, a procedure which was deemed inefficient early in the stimulus production process. Although a previous study showed the importance of biological motion (Shimizu, 1998), we reduced the potential for “boredom” by successively presenting static images from different view angles every five seconds during a trial. The procedure was successful enough that birds reacted vigorously to these stationary stimuli.

Methods

Subjects

Twelve (12) male white Carneaux pigeons (*Columba livia*) obtained from Palmetto Pigeon Plant, South Carolina, were used in this experiment. Bird weights ranged from 500 to 600 g, and they were sexually matured. The sex of each bird was confirmed before the experiment, by observing its response to a live female pigeon. All birds were housed individually in cages, separated by opaque partitions to limit visual and physical interaction with other birds for the entire duration of the experiment. The vivarium was maintained on a constant 12 h light/12 h dark cycle. All the procedures were reviewed and approved by the Institutional Animal Care and Use Committee at the University of South Florida.

Apparatus

The present study used a testing apparatus large enough for a pigeon to move freely (90 x 90 x 60 cm) (see Figure 1). The walls of the apparatus were made of clear Plexiglas covered with water-resistant contact paper (Tuff-Ware, Inc. almond-90.9983). A wire-mesh was placed over the top to keep subjects from flying away during the trials. Two opposing sides of the testing apparatus had openings (30 x 35 cm) to accommodate a liquid crystal display (LCD) monitor (17" color flat panel, Dell UltraSharp 1702FP) or a clear Plexiglas chamber (41 x 41 x 30 cm) used for presenting live-bird stimuli. An observation video camera (Panasonic wv-BP134) was positioned above the testing apparatus to record all movements of the subjects. A microphone (Audio Technica Omnidirectional ATR35s) was attached to the wire-mesh covering the testing apparatus to record all vocalizations.

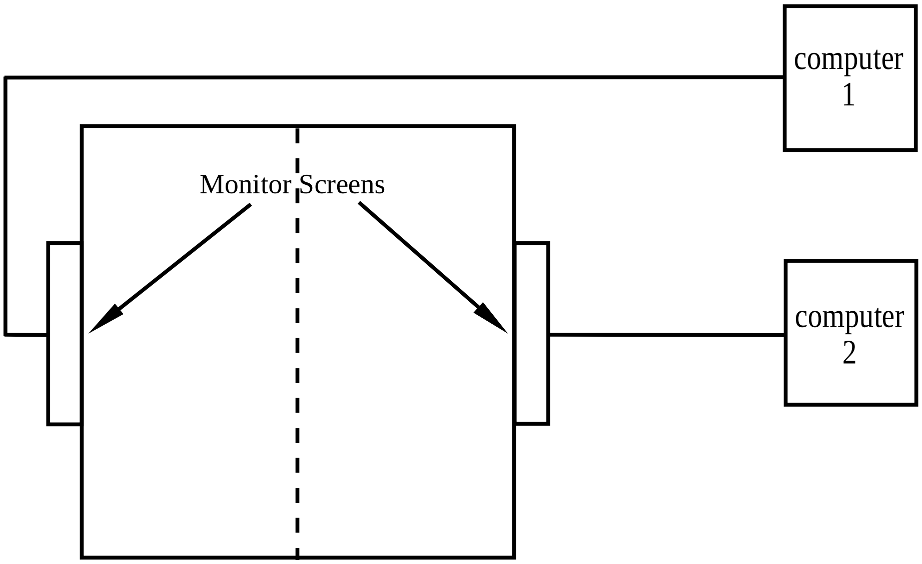

Figure 1. Schematic representation of the testing apparatus (view from above). Dashed line represents the midline. Stimulus presentations were controlled via two personal computers located in an adjacent room.

Stimuli

Two female white Carneaux pigeons were individually photographed using a digital camera (Nikon Coolpix 4800) while a male pigeon in a clear cage was presented to each of them. The presence of the male increased the female's activity, which, in turn, increased the likelihood of obtaining a variety of female stimulus viewpoints.

Twelve color photographs of each female stimulus bird were selected. These comprised of four images from three different camera angles (0, 45, and 90 degrees). All photographs were cropped just below the female's breastbone and applied to a black background. These images were then copied and horizontally flipped to make a complete set of 24 images from each stimulus bird. This procedure was followed for each of the eight stimulus conditions tested in this experiment. Thus, there were a total of 192 original stimulus photos (24 original photos x 8 stimulus conditions) from each stimulus bird.

To make altered stimulus images, the 24 original stimuli were digitally manipulated with photo editing software (Adobe Photoshop v. 8.0). The following eight stimulus conditions were prepared for each original stimulus:

1. Enlarged Eyes (LE) - original female with eye size enlarged by 180%. The increment scale was selected to contain the enlarged eyes inside the head;
2. Enlarged Beak (LB) - original female with beak size enlarged by 180%. The increment scale was selected to be consistent with the eye enlargement;
3. Removed Eyes (NE) - original female with eyes removed;
4. Removed Beak (NB) - original female with beak removed;
5. Removed Eyes and Beak (NEB) - original female with eyes and beak removed;
6. Shifted Feature Configuration (SEB) - original female with shifted eyes and beak position. Using photo editing software, the eyes and beak were selected as one object and rotated approximately 180 degrees so that the beak was at eye level and eyes were at beak position.

7. No Contour, with visible facial features (NC+EB) - original female with Gaussian blur applied to the entire image except for the eyes and beak; and

8. No Contour (NC) - original female with Gaussian blur applied to the entire image including the eyes and beak.

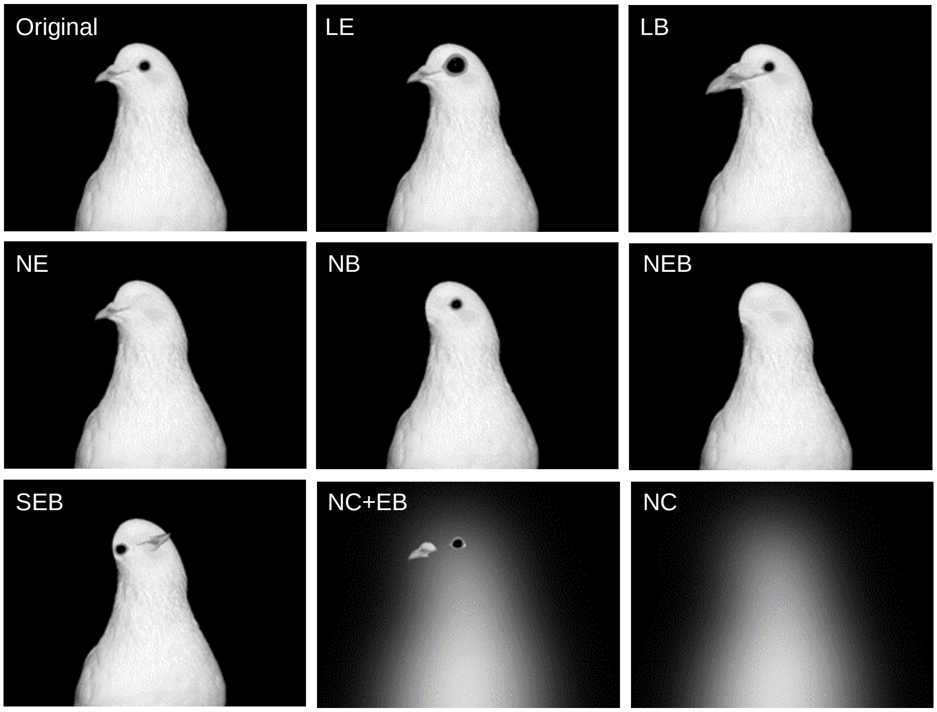

Figure 2. Sample photographs from each stimulus type. See above for abbreviations.

Figure 2 shows examples of an original stimulus female face and its eight altered stimulus faces. During each trial, one of the eight altered stimulus conditions was presented with their matching original female face images. In total, each subject was exposed to 384 (24 originals x 8 stimulus conditions x 2 female exemplars) stimulus pairs in the experiment. Each trial lasted two minutes, during which 24 stimulus pairs were consecutively presented for five seconds each. The slide show presentations were rendered using visual-effects software (Adobe After Effects 5.5), and played back on Windows Media Player (v. 9).

Procedure

Birds used in the experiment were acclimated to the testing apparatus for at least 20 minutes per day for five consecutive days or until they walked freely within the apparatus. Following acclimation, testing trials began. During the testing trials, to eliminate the possibility of position/monitor preference, each stimulus condition was presented twice by alternating presentation positions (i.e., left and right monitor). Therefore, there were 32 trials in total (8 stimulus conditions x 2 exemplars x 2 positions). The presentation order of the 32 trials was counterbalanced between subjects. Only one trial per day was conducted every other day.

In each trial, a subject was placed in the testing apparatus and allowed to acclimate for at least five minutes. After the acclimation was accomplished, and before the testing trial began, the subject was exposed to alternating "preview" on both monitors for 30 seconds each. This was a preview of the upcoming stimulus (i.e., original or altered) to be presented on the monitor screen. Once a trial started, stimuli were presented only on the monitor that was on the side where a subject was located. The other monitor was dark and the corresponding stimulus category was not visible unless a subject crossed the midline of the testing apparatus. The center of the head of the subject was used as a reference point for the bird's location. A two-minute trial was followed by two minutes of a post-trial phase, during which no stimulus was presented on either monitor. Subjects were returned to their home cage following a post-trial phase. Subjects were exposed to a live female white Carneaux pigeon in a Plexiglas stimulus chamber periodically (once a week) throughout the experiment. This procedure was used to reduce stimulus habituation and served to rekindle the courtship displays for the remaining conditions.

Data Analysis

Video and audio-recordings of each trial were analyzed for two well-documented courtship behaviors (Shimizu, 1998; Partan et al., 2005). One measurement was circling display frequency, which was the number of times a subject turned in full circles with its neck feathers ruffled and its head lowered. The other measurement was vocalization frequency, which was the number of times a subject made a *coo* sound. These courtship displays were chosen as dependent measures because they are robust stereotypical behaviors easily observed during courtship (Levi, 1974; Stokes, 1979). The amount of time subjects spent on each half of the testing apparatus was also measured.

Preference scores, (‘altered’) / (‘altered’ + ‘original’), were obtained for each stimulus condition. In preference calculations, ‘altered’ and ‘original’ were the averaged measurements (i.e., time, frequency) expressed near the altered or original stimuli. The preference scores became 1.0 when a subject showed behavior exclusively near the altered stimuli, whereas the scores became zero when a subject preferred the original completely. The overall effect of the stimulus conditions on preference score was evaluated by one way repeated measure analysis of variance (ANOVA). For each of the stimulus conditions, the preference score was analyzed using single sample t-tests with a hypothetical mean of 0.5. The binomial exact probability was also calculated to determine whether significantly more subjects prefer the altered stimuli over the original stimuli.

Results

Eleven out of the 12 subjects showed some courtship behaviors (i.e., ‘coo’s and circling) when presented with the described stimuli on the monitor screens. Data from the subject that exhibited no courtship behavior was excluded from further analysis.

Qualitative Movement Observation

Figure 3 shows the path of a subject as observed during three separate trials. Figure 3A shows a pattern in which the subject did not exhibit much movement. The pattern in Figure 3B shows a subject that paced back and forth with no indication of stimulus preference. The pattern in Figure 3C shows that the subject spent time on both sides of the testing apparatus, yet showed a preference for the stimulus displayed on the left side by circling more often on the left side. During tests, most subjects exhibited clear courtship displays as exemplified in Figure 3C rather than staying still (Fig. 3A) or pacing back in forth between the two sides (Fig. 3B).

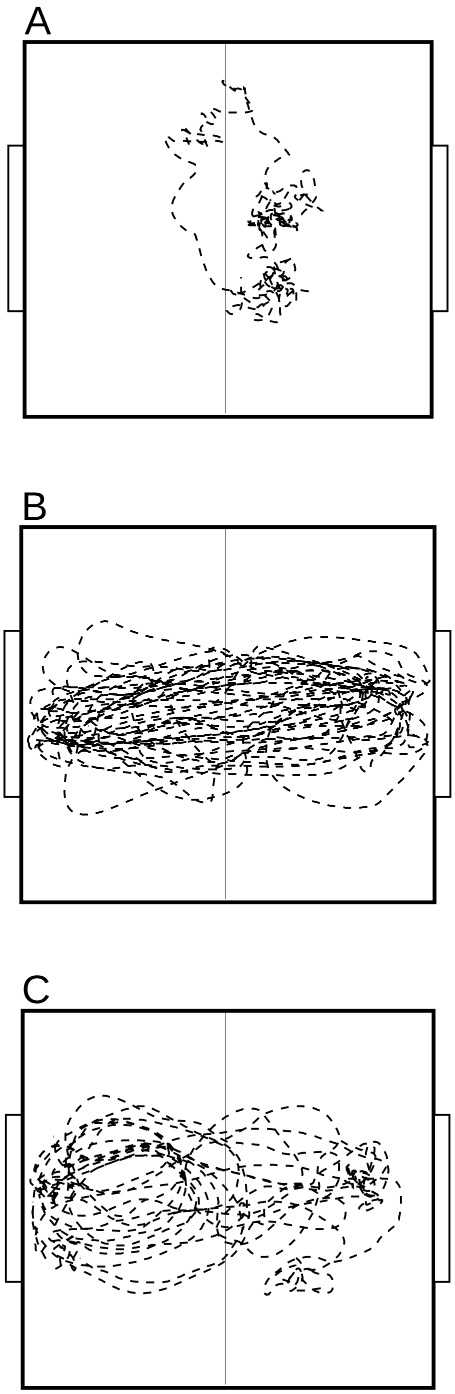

Figure 3. Three distinct patterns of subject's movement observed during testing: A) low activity level and no courtship; B) high activity level with no stimulus preference; and C) high activity level with clear stimulus preference.

Position Preference Analysis

The mean preference score for time spent on one half of the apparatus versus the other half was 0.48, with scores ranging between 0.44 and 0.50. A one way repeated measure ANOVA showed that there was no significant overall difference among stimulus conditions [$F(7,70) = 0.56$, $p = 0.79$]. Table 1 shows the number of animals that preferred the left side to the right side of the testing apparatus (i.e., preference score > 0.5). There were no significant differences in the number of subjects preferring one side to the other for any stimulus conditions (i.e., binomial $p > 0.05$). These results confirmed that the subjects did not show any position/monitor preference during the experiment.

Table 1

Number of male subjects that preferred the one side over the other side (N=11)

Measure	Stimulus Type							
	LE	LB	NE	NB	NEB	SEB	NC+EB	NC
Position	5	5	6	3	5	5	4	5

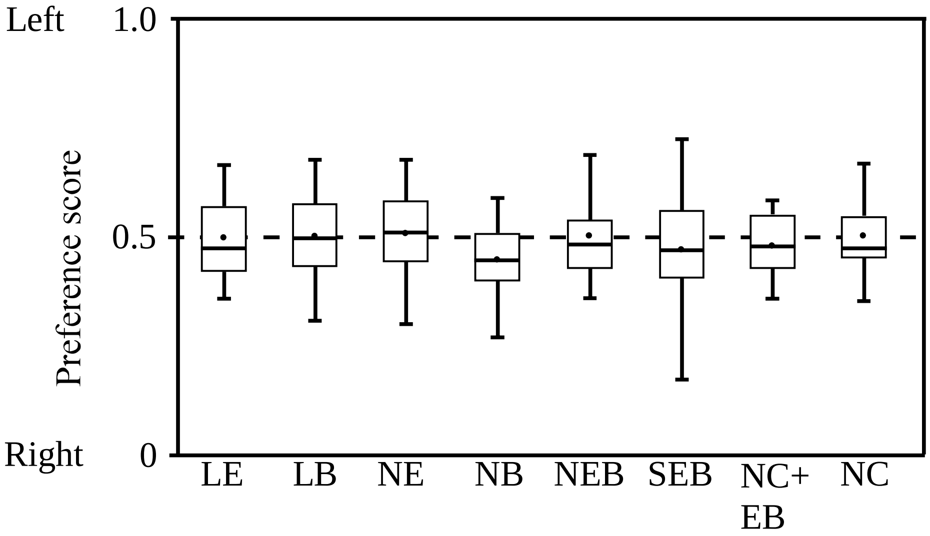

Figure 4. Boxplot showing the position preference scores between the original and altered stimuli based on time duration spent on each side of the testing apparatus. Boxes represent the interquartile range between the 25th and 75th percentiles. Horizontal lines represent medians and circles represent means. Vertical lines represent the entire range of scores. See the Method section for abbreviations.

Time Spent Near Altered vs. Original Stimuli

Figure 5A is a boxplot showing the preference scores based on time spent near altered stimuli relative to time spent near original stimuli. The mean preference score was 0.47, with scores ranging between 0.40 and 0.54. A one-way ANOVA showed that different stimulus conditions have differential effects [$F(7,70) = 2.58$, $p < 0.05$]. Birds spent more time near altered faces with large beaks (LB) than near original unaltered faces [$t_{(11)} = 1.95$, $p < 0.05$]. In contrast, birds spent less time near the faces without beaks (NB) [$t_{(11)} = 1.95$, $p < 0.05$] and those without contour, but with eyes and beak intact (NC+EB) [$t_{(11)} = 2.15$, $p < 0.05$]. No other comparisons of time spent near altered faces compared to normal faces were significant. However, the number of subjects that spent more time near altered faces compared to normal faces was also evaluated (see Table 2) Binomial tests showed that significantly more birds preferred the original intact faces than altered faces without eyes and beak (NEB, p< 0.05), or faces without contour (NC, p< 0.01).

Table 2

Number of male subjects that preferred the altered stimuli to the original stimuli (N=11)

Measures	Stimulus Type							
	LE	LB	NE	NB	NEB	SEB	NC+EB	NC
Time Spent	5	7	5	3	2*	7	3	1**
Vocals	10**	10**	5	3	0**	3	0**	1**
Bowing	4	9*	3	1**	1**	3	0**	0**

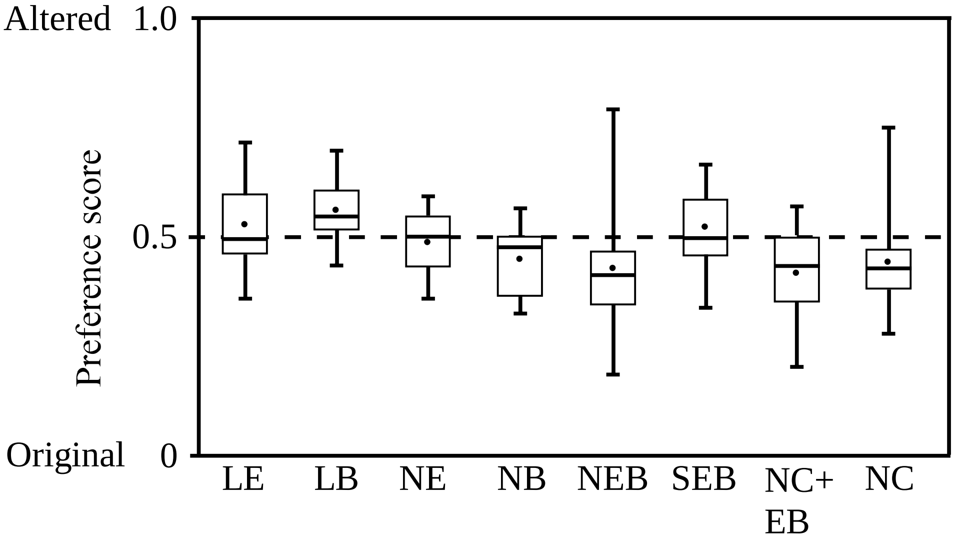

Figure 5A. Boxplot showing the preference scores of time spent near the altered stimulus for each stimulus pair. Data points represent the median durations. Boxes represent the interquartile range between the 25th and 75th percentiles. Horizontal lines represent medians and circles represent means. Vertical lines represent the entire range of scores. See the Method section for abbreviations.

Vocalizations Near Altered vs. Original Stimuli

Figure 5B shows the preference scores based on the number of coo vocalizations subjects produced near altered faces, relative to the number made near original faces. The scores (mean = 0.42, with scores ranging between 0.26 and 0.57) showed rather a large variance among conditions. A one-way ANOVA confirmed that subjects reacted differentially depending on stimulus conditions [$F(7,70) = 5.67$, $p < 0.01$].

Single sample t-tests showed that birds vocalized more near LB faces than near faces [$t_{(11)} = 4.28$, $p < 0.01$]. In contrast, the birds vocalized more near original faces than near NB faces [$t_{(11)} = 2.05$, $p < 0.05$], NEB face [$t_{(11)} = 5.11$, $p < 0.01$], SEB faces [$t_{(11)} = 1.91$, $p < 0.05$], NC+EB faces [$t_{(11)} = 3.75$, $p < 0.01$] and NC faces [$t_{(11)} = 5.51$, $p < 0.01$]. As seen in Table 2, significantly more birds vocalized near LE faces (binomial $p < 0.01$) and LB faces (binomial $p < 0.01$) than near original faces. In contrast, subjects produced fewer vocalizations near NEB faces (binomial $p < 0.01$), or NC+EB and NC faces (binomial $p < 0.01$).

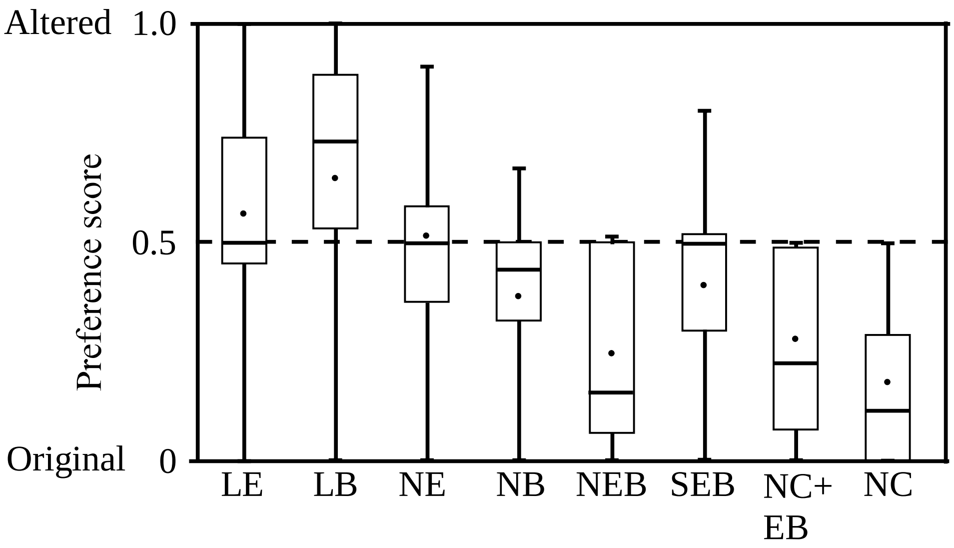

Figure 5B. Boxplot showing the preference scores of vocalizations near the altered stimulus for each stimulus pair. Data points represent the median durations. Boxes represent the interquartile range between the 25th and 75th percentiles. Horizontal lines represent medians and circles represent means. Vertical lines represent the entire range of scores. See the Method section for abbreviations.

Circling Display Near Altered vs. Original Stimuli

Figure 5C shows the preference scores based on the number of circling displays near the altered stimuli, relative to the original stimuli. The mean score was 0.40, ranging between 0.17 and 0.64, suggesting even a wider variance than the vocalization measure. A one-way ANOVA showed that different stimulus conditions had differential effects [$F(7,70) = 4.36$, $p < 0.01$]. Birds tended to circle more often near original faces than near NB faces [$t_{(11)} = 1.82$, $p < 0.05$], NEB faces [$t_{(11)} = 3.93$, $p < 0.01$], or NC+EB faces [$t_{(11)} = 4.07$, $p < 0.01$] and NC faces [$t_{(11)} = 5.86$, $p < 0.01$]. As seen in Table 2, significantly more birds circled near LB faces (binomial $p < 0.05$) than original facef. In contrast, fewer circled near NB and NEB faces (binomial $p < 0.01$), or NC+EB faces and NC faces (binomial $p < 0.01$).

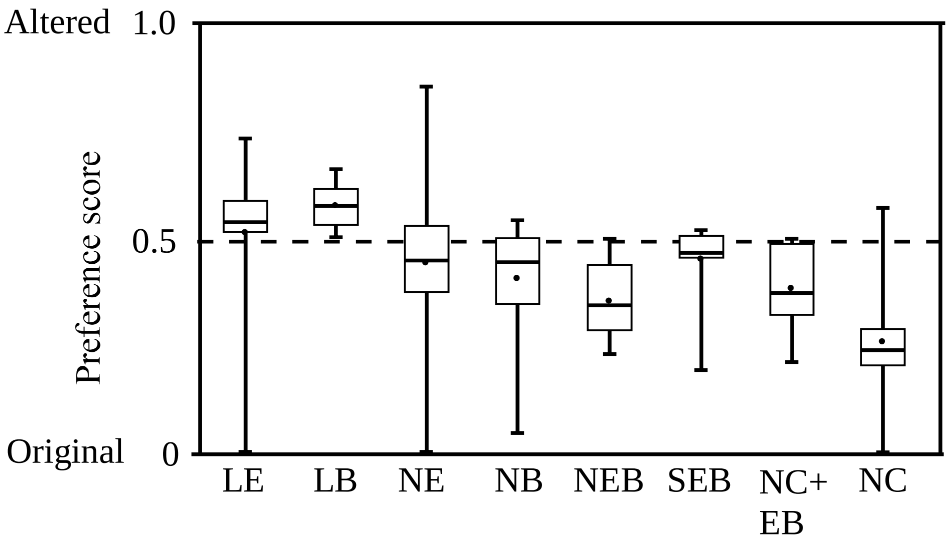

Figure 5C. Boxplot showing the preference scores of circling displays near the altered stimulus for each stimulus pair. Data points represent the median durations. Boxes represent the interquartile range between the 25th and 75th percentiles. Horizontal lines represent medians and circles represent means. Vertical lines represent the entire range of scores. See the Method section for abbreviations.

Discussion

The results showed that male subjects responded differentially to the various stimulus types. Overall, the present study clarified the importance of the presence of local facial features in visual discrimination and species recognition. Furthermore, the present study revealed that the global configuration of facial features was not as crucial as it is in other species, such as humans, but the contour was. The following discussion will focus on several issues related to the significance of 1) local facial features, 2) global configuration, and 3) contour.

Critical and Non-Critical Features

In general, more subject birds preferred female pictures with unnaturally large local components to the original pictures with normal size features. The results suggest that these local components provide important information that facilitates conspecific recognition and mate selection in the natural setting. The finding that unnaturally large features can initiate strong preference behavior is reminiscent of the well-established notion of supernormal stimuli introduced by early ethologists. Their studies showed that, when certain dimensions of a releasing stimulus (e.g., size or color) are exaggerated, such supernormal stimuli initiate more vigorous behavior than the normal stimuli (Baerends & Drent, 1982; Tinbergen & Perdeck, 1951; Basolo, 1990). In the present study, the enlarged local components within the face might have functioned as supernormal stimuli.

The importance of local components was confirmed by the effect of removal of them. More subjects preferred the original stimuli to those stimuli in which facial features were removed (NEB and NB, but not NE stimuli). This finding is consistent with other research on the subject. In a study on visual discrimination of individual pigeons, Watanabe and Ito (1991) rained pigeons to peck at photographs of certain pigeons (S+) and not at other pigeons (S-). Then, the eyes and beak of the S+ pigeons were removed, which resulted in significantly decreased pecking accuracy, suggesting that these local facial components served as critical discriminative stimuli in their task. Similarly, the present study suggests that birds use these local facial components as critical signals for eliciting courtship display.

While local features are clearly important, it is difficult to determine which of the two local face components (eyes or beak) is more crucial for species recognition based on this study. There are two reasons why this comparison is impossible. First, although the eyes and beak differ naturally along many physical dimensions such as shape, size, and color, only their physical size was altered in the present study. Little is known about the salience of these various physical attributes for eliciting courtship. It is most likely that there were differential effects of such alteration on the salience of eyes and beak, and thus the results of the size alteration cannot be compared directly. Second, as discussed below, the present study showed that the contour itself played an important role in eliciting courtship display and the alteration of eyes and beak affected the contour differently. When the eyes were enlarged or removed, the contour as a whole was not affected. Alterations of beak size changed the overall contour of the stimuli, making it difficult to isolate the importance of the beak as a specific local component. That is, were birds influenced caused by changes to the beak itself or to the altered contour? Thus, the relative influence manipulations (enlargement and/or removal) have on the eyes compared to the beak is not possible based on the current data.

Contour

Most birds showed a strong preference for the original stimuli to those stimuli in which the contour was removed (NC condition). This is, perhaps, unsurprising, since there were no ‘bird-like’ global, or local, facial components visible in this altered stimulus condition. However, the preference for original faces persisted even when the eyes and beak were visible (NC + EB condition). This finding is in agreement with the results presented by Watanabe and Ito (1991), in which pigeons showed a significant decrease in pecks toward S+ photographs when only the eyes and beak were visible (i.e., contour had been removed), suggesting that the eyes and beak alone were not sufficient for visual discrimination of individual pigeons. Together, these results suggest that the ‘bird-like’ contour of the stimulus is essential for species recognition, and that, without the contour, specific facial features such as the eyes and beak are ineffective (or not sufficient to elicit courtship).

Global Configuration

Birds produced more coo vocalizations near the original face than near the SEB face. Although this was not statistically significant, this pattern of preference for the original face was supported by the fact that eight of the eleven subjects produced more coo vocalizations and circles near the original face than near the SEB face (Table 2). It is possible that the preference for the original faces over SEB faces might have been even stronger if we used more extreme violations of global configuration (i.e., local components positioned outside of the head region) in the SEB condition. Thus, although there were numerous possibilities for configural alteration, we used only one stimulus condition (SEB).

With this caveat in mind, the present finding of the effect of configural alteration is in contrast to other observations about visual discrimination behavior of pigeons (Cavoto & Cook, 2001; Cerella, 1980; Delius & Hollard, 1995; Hollard & Delius, 1982). For example, experiments conducted by Hollard and Delius (1982, 1995) showed that, unlike humans, pigeons could recognize visual stimuli presented at various orientations without significant response decrement. Cerella (1980) showed similar results, suggesting that configuration is not necessarily an important cue for visual discrimination, as pigeons responded to local elements regardless of spatial configuration. These previous studies suggest that, in visual discrimination tasks which used artificial geometrical stimuli, pigeons tend to attend to local features, rather than global configuration or orientation of local features. However, the present results are consistent with previous studies using more naturalistic, biologically relevant stimuli, such as color photographs of the head of pigeons used by Watanabe and Ito (1991), who showed that pigeons responded to global configuration, as well as local features, in order to perform the visual discrimination task. Similarly, Johnson and Horn (1988) reported that newly hatched chicks, which are known to show a natural predisposition to approach a conspecific adult (hen) rather than less naturalistic objects preferred a stuffed hen, when features of their head and neck were in their correct arrangement.

Methodological Considerations

The present study used simultaneous presentation of two visual stimuli and analyzed the preference behavior, instead of sequential presentation of different stimuli. The simultaneous presentation procedure successfully revealed differential responses to various stimulus types. This procedure of presenting two stimuli at the same time was in contrast to previous studies conducted in the same laboratory (Shimizu, 1998; Partan, et al., 2005), which used sequential presentation procedures. Subjects in these previous experiments were exposed to one stimulus type during a given trial. Although this is an effective procedure for systematically evaluating the importance of specific features, there were always concerns about potential ceiling effects. When only one stimulus is presented during a trial, the subject may respond constantly and vigorously at asymptote. In such a case, it is difficult to determine preference for particular stimuli. By using simultaneous procedure, this potential problem was avoided in the present study. In this sense, the present procedure was effective and useful for future studies with similar interests.

Concluding Remarks

In the present study, pigeons showed a predisposition to attend local components, but also global configuration. In contrast, in many visual discrimination tasks using operant conditioning techniques, pigeons tended to pay attention to local features rather than global features of complex stimuli. Pigeons appear to have the predisposition to attend to local elements and not to group these features in order to perceive the global aspect of visual stimuli in these tasks. These findings could be related to the fact that these tasks often required pigeons to discriminate artificial, unnaturalistic stimuli, which may not be biologically salient enough to facilitate their ability to perceive global features. Pigeons and chicks appear to attend to global configuration when biologically-relevant visual stimuli, such as faces of conspecific animals, were used in a discrimination task (Watanabe & Ito, 1991) and also in a preference test (Johnson & Horn, 1988; the present study). Although pigeons appear to show a natural predisposition toward local elements over global elements in many discrimination tasks, this does not mean that pigeons have a general deficiency in perceiving global features. Rather, such a "deficiency" may be contingent on the type of visual stimuli presented (i.e., artificial, biologically less relevant, geometrical figures vs. naturalistic). Future research with more systematic analysis on this issue is clearly warranted.

References

Baerends, G.P. & Drent, R.H. (1982). The herring gull and its egg: II. The responsiveness to egg-features. Behaviour, 82(1-4), 416.

Bahrick, H.P., Bahrick, P.O., & Wittlinger, R.P. (1975). Fifty years of memory for names and faces: A cross-sectional approach. *Journal of Experimental Psychology: General*, 104, 54-75.

Basolo, A.L. (1990). The female preference for male sword length in the green swordtail, Xiphophorus helleri (Pisces: Poeciliidae). *Animal Behaviour*, 40, 332-338.

Blest, A.D. (1957). The function of eyespot patterns in the Lepidoptera. *Behaviour*, 11, 209-256.

Brown, S.D. & Dooling, R.J. (1992). Perception of conspecific faces by budgerigars (*Melopsittacus undulatus*): I. natural faces. *Journal of Comparative Psychology*, 106, 203-216.

Brown, S.D. & Dooling, R.J. (1993). Perception of conspecific faces by budgerigars (*Melopsittacus undulatus*): II. Synthetic models. *Journal of Comparative Psychology*, 107, 48-60.

Cavato, K. & Cook, R.G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 3-16.

Cerella, J. (1980). The pigeons' analysis of pictures. *Pattern Recognition*, 9, 1-6.

Cook, R.G. (2000). The comparative psychology of avian visual cognition. *Current Directions in Psychological Science*, 1, 83-89.

Delius, J.D. & Hollard, V.D. (1995). Orientation invariant pattern recognition by pigeons (Columba livia) and humans (Homo sapiens). *Journal of Comparative Psychology*, 109(3), 278-290.

Domjan, M., & Nash, S. (1988). Stimulus control of social behavior in male Japanese quail, *Coturnix coturnix japonica, Animal Behaviour*, 36, 1006-1015.

Farah, M.J., Tanaka, J.W. & Drain, M.H. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance*, 21, 628-634.

Frost, B.J. & Sun, H. (1997). Visual motion processing for figure/ground segregation, collision avoidance, and optic flow analysis in the pigeon. In M.V. Srinivasan, & S. Venkatesh (Eds.), *From living eyes to seeing machines* (pp. 80-103). New York: Oxford University Press.

Hodos, W. (1993). The visual capabilities of birds. In H.P. Zeigler & H.-J. Bischof (Eds.), *Vision, brain, and behavior in birds* (pp. 77-98). Cambridge, MA: MIT Press.

Hollard, V.D. & Delius, J.D. (1982). Rotation invariance in visual pattern recognition by pigeons and humans. *Science*, 218, 4574.

Johnson, M.H. & Horn, G. (1988). Development of filial preferences in dark-reared chicks. Animal Behaviour, 36, 675-683.

Keating, C.F. & Keating, E.G. (1993). Monkeys and mug shots: Cues used by rhesus monkeys (*Macaca mulatta*) to recognize a human face. *Journal of Comparative Psychology*, 107, 131-139.

Levi, W.M. (1974). *The pigeon*. Sumter, SC: Levi.

McFarland, D. (1985). *Animal behavior.* Reading, MA: The Benjamin/Cummings.

McKelvie, S.J. (1976). The role of eyes and mouth in the memory of a face. *American Journal of Psychology*, 89, 311-323.

Parr, L.A., Dove, T., & Hopkins, W.D. (1998). Why faces may be special: Evidence of the inversion effect in chimpanzees. *Journal of Cognitive Neuroscience*, 10, 615-622.

Parr, L.A., Winslow, J.T., Hopkins, W.D., & de Waal, F.B.M. (2000). Recognizing facial cues: Individual discrimination by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 114, 47-60.

Partan, S., Yelda, S., Price, V, & Shimizu, T. (2005). Female pigeons, Columba livia, respond to multisensory audio/video playbacks of male courtship behavior. *Animal Behaviour*, 70(4), 957-966.

Ryan, C.M.E. & Lea, S.E.G. (1994). Images of conspecifics as categories to be discriminated by pigeons and chickens: Slides, video tapes, stuffed birds and live birds. *Behavioural Processes*, 33, 155-176.

Schwaninger, A., Lobmaier, J.S., & Collishaw, S.M. (2002). Role of featural and configural information in familiar and unfamiliar face recognition. *Lecture notes in computer science*, 2525, 643-650.

Sergent, J. (1984). An investigation into component and configural processes underlying face perception. *British Journal of Psychology*, 75, 221-242.

Shimizu, T. (1998). Conspecific recognition in pigeons (*Columba livia*) using dynamic video images. *Behaviour*, 133, 43-53.

Shimizu T, Patton T B, Szafranski G (In Press) Evolution of the visual system in birds. In M. D. Binder, N. Hirokawa, U. Windhorst, & M. C. Hirsch (Eds.), Encyclopedic Reference of Neuroscience, Heidelberg, Germany: Springer.

Stokes, D.W. (1979). *A guide to bird behavior*. Boston, MA: Little, Brown.

Thompson, P. (1980). Margaret Thatcher: A new illusion. *Perception*, 9, 483-484.

Tinbergen, N., & Perdeck, A.C. (1950). On the response situation releasing the begging response in the newly hatched Herring Gull chick (*larus argentatus agrentatus Pont.*). *Behaviour*, 3, 1-39.

Trillmich, F. (1976). Learning experiments on individual recognition in budgerigars (*Melopsittacus undulates*). *Zeitschrift für Tierpsychologie*, 41, 372-395.

Watanabe, S. & Ito, Y. (1991). Discrimination of individuals in pigeons. *Bird Behaviour*, 9, 20-29.

Watanabe, S., Lea, S.E.G., & Dittrich, W.H. (1993). What can we learn from experiments on pigeon concept discrimination? In H.P. Zeigler & H.-J. Bischof (Eds.), *Vision, brain, and behavior in birds* (pp. 351-376). Cambridge, MA: MIT Press.

Appendices

Appendix A Summary of Cumulative Results

Summary of Cumulative Results

Subject	Monitor	LE	Original	LB	Original	NE	Original	NB	Original	NEB	Original	SEB	Original	NC+EB	Original
246	178 L	88.00	32.00	79.00	41.00	88.00	32.00	90.00	30.00	58.00	62.00	61.00	59.00	51.00	69.00
	178 R	46.00	74.00	62.00	58.00	64.00	56.00	35.00	85.00	46.00	74.00	36.00	84.00	49.00	71.00
	170 L	86.00	34.00	67.00	53.00	49.00	71.00	53.00	67.00	36.00	84.00	68.00	52.00	55.00	65.00
	170 R	75.00	45.00	61.00	59.00	63.00	57.00	68.00	54.00	58.00	62.00	48.00	72.00	22.00	98.00
	Mean	73.75	46.25	67.25	52.75	66.00	54.00	61.50	59.00	49.50	70.50	53.25	66.75	44.25	75.75
250	178 L	39.00	81.00	69.00	51.00	66.00	54.00	53.00	67.00	60.00	60.00	69.00	51.00	41.00	79.00
	178 R	56.00	64.00	47.00	71.00	90.00	30.00	67.00	53.00	60.00	60.00	59.00	61.00	47.00	73.00
	170 L	70.00	50.00	79.00	41.00	50.00	70.00	51.00	69.00	33.00	87.00	46.00	74.00	58.00	62.00
	170 R	67.00	53.00	66.00	54.00	64.00	56.00	65.00	55.00	60.00	60.00	74.00	46.00	71.00	49.00
	Mean	58.00	62.00	65.25	54.25	67.50	52.50	59.00	61.00	53.25	66.75	62.00	58.00	54.25	65.75
254	178 L	78.00	42.00	90.00	30.00	57.00	63.00	60.00	60.00	56.00	64.00	58.00	62.00	78.00	42.00
	178 R	42.00	78.00	99.00	21.00	53.00	67.00	61.00	59.00	1.00	119.00	68.00	52.00	64.00	56.00
	170 L	73.00	47.00	58.00	62.00	60.00	60.00	48.00	72.00	34.00	86.00	35.00	85.00	35.00	85.00
	170 R	31.00	89.00	104.00	16.00	70.00	50.00	59.00	61.00	74.00	46.00	60.00	60.00	0.00	0.00
	Mean	56.00	64.00	87.75	32.25	60.00	60.00	57.00	63.00	41.25	78.75	55.25	64.75	44.25	45.75
255	178 L	64.00	56.00	84.00	36.00	53.00	67.00	56.00	64.00	31.00	89.00	59.00	61.00	38.00	82.00
	178 R	45.00	75.00	41.00	79.00	47.00	73.00	57.00	63.00	58.00	62.00	43.00	77.00	24.00	96.00
	170 L	80.00	40.00	65.00	55.00	56.00	64.00	62.00	58.00	21.00	99.00	53.00	67.00	64.00	56.00
	170 R	82.00	38.00	66.00	54.00	59.00	61.00	62.00	58.00	28.00	92.00	60.00	60.00	82.00	38.00
	Mean	67.75	52.25	64.00	56.00	53.75	66.25	59.25	60.75	34.50	85.50	53.75	66.25	52.00	68.00
256	178 L	57.00	63.00	30.00	90.00	56.00	64.00	38.00	82.00	38.00	82.00	15.00	105.00	58.00	62.00
	178 R	120.00	0.00	71.00	49.00	19.00	101.00	120.00	0.00	98.00	22.00	120.00	0.00	61.00	59.00
	170 L	56.00	64.00	56.00	64.00	50.00	70.00	30.00	90.00	56.00	64.00	53.00	67.00	62.00	58.00
	170 R	64.00	56.00	59.00	61.00	47.00	73.00	61.00	59.00	37.00	83.00	108.00	12.00	92.00	28.00
	Mean	74.25	45.75	54.00	66.00	43.00	77.00	62.25	57.75	57.25	62.75	74.00	46.00	68.25	51.75
257	178 L	104.00	16.00	90.00	30.00	45.00	75.00	51.00	69.00	50.00	70.00	98.00	22.00	51.00	69.00
	178 R	98.00	22.00	58.00	62.00	58.00	62.00	26.00	94.00	48.00	72.00	54.00	66.00	53.00	67.00
	170 L	69.00	51.00	62.00	58.00	42.00	78.00	40.00	80.00	36.00	84.00	61.00	59.00	26.00	94.00
	170 R	72.00	48.00	50.00	70.00	51.00	69.00	55.00	65.00	28.00	92.00	53.00	67.00	36.00	84.00
	Mean	85.75	34.25	65.00	55.00	49.00	71.00	43.00	77.00	40.50	79.50	66.50	53.50	41.50	78.50
258	178 L	101.00	19.00	52.00	68.00	120.00	0.00	85.00	35.00	116.00	4.00	84.00	36.00	38.00	82.00
	178 R	102.00	18.00	106.00	14.00	22.00	98.00	87.00	33.00	112.00	8.00	92.00	28.00	40.00	80.00
	170 L	26.00	94.00	38.00	82.00	20.00	100.00	34.00	86.00	117.00	3.00	46.00	74.00	105.00	15.00
	170 R	50.00	70.00	11.00	109.00	62.00	58.00	65.00	55.00	35.00	88.00	25.00	95.00	65.00	55.00
	Mean	69.75	50.25	51.75	68.25	56.00	64.00	67.75	52.25	95.00	25.75	61.75	58.25	62.00	58.00
259	178 L	49.00	71.00	2.00	118.00	105.00	15.00	15.00	105.00	48.00	72.00	103.00	17.00	28.00	92.00
	178 R	24.00	96.00	100.00	20.00	33.00	87.00	34.00	86.00	57.00	63.00	91.00	29.00	20.00	100.00
	170 L	80.00	40.00	68.00	52.00	66.00	54.00	46.00	74.00	72.00	48.00	110.00	10.00	40.00	80.00
	170 R	55.00	65.00	65.00	55.00	53.00	67.00	71.00	49.00	44.00	76.00	14.00	106.00	9.00	111.00
	Mean	52.00	68.00	58.75	61.25	64.25	55.75	41.50	78.50	55.25	64.75	79.50	40.50	24.25	95.75
260	178 L	25.00	95.00	114.00	6.00	69.00	51.00	60.00	60.00	24.00	96.00	36.00	84.00	34.00	86.00
	178 R	19.00	101.00	15.00	105.00	105.00	15.00	82.00	38.00	108.00	12.00	80.00	40.00	51.00	69.00
	170 L	43.00	77.00	64.00	56.00	38.00	82.00	13.00	107.00	34.00	86.00	14.00	106.00	56.00	64.00
	170 R	84.00	36.00	79.00	41.00	52.00	68.00	70.00	50.00	21.00	99.00	33.00	87.00	28.00	92.00
	Mean	42.75	77.25	68.00	52.00	66.00	54.00	56.25	63.75	46.75	73.25	40.75	79.25	42.25	77.75
261	178 L	54.00	66.00	76.00	44.00	56.00	64.00	70.00	50.00	88.00	32.00	48.00	72.00	50.00	70.00
	178 R	67.00	53.00	90.00	30.00	60.00	60.00	45.00	75.00	42.00	78.00	93.00	27.00	103.00	17.00
	170 L	33.00	87.00	89.00	31.00	105.00	15.00	21.00	99.00	90.00	30.00	70.00	50.00	52.00	68.00
	170 R	64.00	56.00	79.00	41.00	62.00	58.00	38.00	82.00	59.00	61.00	46.00	74.00	64.00	56.00
	Mean	54.50	65.50	83.50	36.50	70.75	49.25	43.50	76.50	69.75	50.25	64.25	55.75	67.25	52.75
263	178 L	58.00	62.00	93.00	27.00	1.00	119.00	24.00	96.00	14.00	106.00	56.00	64.00	18.00	102.00
	178 R	64.00	59.00	96.00	27.00	47.00	73.00	47.00	73.00	26.00	94.00	103.00	17.00	6.00	114.00
	170 L	38.00	82.00	60.00	60.00	35.00	85.00	24.00	96.00	5.00	115.00	36.00	84.00	24.00	96.00
	170 R	79.00	41.00	82.00	38.00	88.00	32.00	60.00	60.00	43.00	77.00	117.00	3.00	79.00	41.00
	Mean	59.75	61.00	82.75	38.00	42.75	77.25	38.75	81.25	22.00	98.00	78.00	42.00	31.75	88.25
	Grand Mean	63.11	56.95	68.00	52.02	58.09	61.91	53.61	66.43	51.36	68.70	62.64	57.36	48.36	68.91
	S.D.	12.31	12.33	11.94	11.84	9.92	9.92	9.99	9.95	19.20	19.03	11.70	11.70	14.01	15.92
	S.E.M.	3.71	3.72	3.60	3.57	2.99	2.99	3.01	3.00	5.79	5.74	3.53	3.53	4.22	4.80

Explanation of Table (From left to right):

Subject number; Location of stimulus presentation (left or right monitor);

Amount of time subject spent near altered and original stimuli for all stimulus pairs.

Appendix A (Continued)

Summary of Cumulative Results

Subject	Monitor	LE	Original	LB	Original	NE	Original	NB	Original	NEB	Original	SEB	Original	NC+EB	Original	NC	Original
246	178 L	12.00	0.00	8.00	1.00	0.00	0.00	0.00	0.00	1.00	2.00	0.00	0.00	0.00	6.00	5.00	0.00
	178 R	2.00	1.00	8.00	1.00	3.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00
	170 L	14.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	8.00	0.00	0.00	0.00	6.00	0.00	16.00
	170 R	5.00	0.00	4.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00	2.00	5.00
	Mean	8.25	0.25	5.00	0.50	0.75	0.00	0.50	0.50	0.25	2.75	0.00	0.25	0.00	3.00	1.75	6.25
250	178 L	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00
	178 R	0.00	0.00	2.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	170 L	0.00	0.00	3.00	1.00	0.00	1.00	0.00	2.00	0.00	0.00	2.00	1.00	0.00	0.00	0.00	5.00
	170 R	0.00	0.00	6.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00
	Mean	0.00	0.00	3.00	0.50	0.25	0.25	0.00	0.75	0.00	0.00	1.00	0.25	0.00	0.75	0.00	1.25
254	178 L	2.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	178 R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	170 L	0.00	0.00	0.00	1.00	0.00	0.00	0.00	4.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
	170 R	0.00	0.00	4.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mean	0.50	0.75	1.00	0.25	0.50	0.00	0.00	1.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.25
255	178 L	1.00	2.00	3.00	1.00	2.00	4.00	0.00	3.00	0.00	5.00	1.00	1.00	0.00	2.00	0.00	4.00
	178 R	0.00	2.00	0.00	2.00	3.00	2.00	1.00	0.00	0.00	2.00	0.00	3.00	0.00	0.00	0.00	5.00
	170 L	4.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	12.00	1.00	3.00	0.00	0.00	0.00	0.00
	170 R	0.00	0.00	2.00	0.00	0.00	0.00	2.00	2.00	1.00	9.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mean	1.25	1.25	2.00	0.75	1.25	1.50	0.75	1.25	0.25	7.00	0.50	1.75	0.00	0.50	0.00	2.25
256	178 L	2.00	0.00	1.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	178 R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00
	170 L	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00
	170 R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	1.00	0.00
	Mean	0.50	0.00	0.25	0.00	0.25	0.50	0.00	0.00	0.00	0.00	0.00	0.25	1.00	1.25	0.25	0.25
257	178 L	3.00	0.00	2.00	0.00	0.00	0.00	2.00	3.00	0.00	0.00	6.00	2.00	1.00	0.00	0.00	0.00
	178 R	0.00	0.00	1.00	1.00	0.00	0.00	8.00	2.00	0.00	0.00	2.00	0.00	1.00	3.00	2.00	0.00
	170 L	4.00	1.00	4.00	3.00	1.00	7.00	0.00	4.00	2.00	8.00	3.00	4.00	0.00	7.00	0.00	9.00
	170 R	4.00	0.00	2.00	4.00	5.00	7.00	0.00	4.00	1.00	10.00	2.00	5.00	1.00	8.00	0.00	7.00
	Mean	2.75	0.25	2.25	2.00	1.50	3.50	2.50	3.25	0.75	4.50	3.25	2.75	0.75	4.50	0.50	4.00
258	178 L	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	178 R	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	170 L	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	170 R	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mean	0.00	0.00	0.00	0.25	0.00	0.00	0.50	0.25	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
259	178 L	2.00	4.00	2.00	0.00	0.00	0.00	0.00	0.00	4.00	6.00	1.00	0.00	0.00	9.00	0.00	0.00
	178 R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	3.00	2.00	0.00	3.00	8.00	4.00	6.00
	170 L	5.00	2.00	6.00	3.00	7.00	3.00	4.00	4.00	10.00	3.00	0.00	0.00	5.00	5.00	1.00	5.00
	170 R	3.00	4.00	3.00	7.00	2.00	6.00	3.00	3.00	2.00	8.00	0.00	5.00	0.00	6.00	3.00	12.00
	Mean	2.50	2.50	2.75	2.50	2.25	2.25	1.75	1.75	5.25	5.00	0.75	1.25	2.00	7.00	2.00	5.75
260	178 L	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	178 R	0.00	0.00	0.00	2.00	0.00	0.00	1.00	3.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00
	170 L	0.00	2.00	0.00	0.00	0.00	4.00	0.00	2.00	2.00	4.00	0.00	3.00	0.00	0.00	0.00	3.00
	170 R	1.00	0.00	0.00	1.00	0.00	5.00	3.00	2.00	0.00	7.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mean	0.25	0.50	0.00	0.75	0.00	2.25	1.00	1.75	0.50	2.75	1.00	0.75	0.00	0.00	0.00	0.75
261	178 L	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.00	0.00	7.00
	178 R	4.00	3.00	3.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00
	170 L	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	170 R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mean	1.00	0.75	0.75	0.00	0.50	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.50	2.00	0.00	1.75
263	178 L	1.00	2.00	6.00	2.00	0.00	11.00	2.00	11.00	1.00	10.00	6.00	7.00	3.00	2.00	0.00	0.00
	178 R	2.00	0.00	5.00	1.00	9.00	7.00	5.00	7.00	5.00	7.00	5.00	3.00	6.00	1.00	4.00	0.00
	170 L	3.00	9.00	5.00	4.00	4.00	10.00	0.00	12.00	0.00	2.00	2.00	12.00	0.00	10.00	0.00	10.00
	170 R	7.00	2.00	8.00	3.00	5.00	0.00	6.00	4.00	3.00	9.00	0.00	0.00	4.00	1.00	4.00	7.00
	Mean	3.25	3.25	6.00	2.50	4.50	7.00	3.25	8.50	2.25	7.00	3.25	5.50	3.25	3.50	2.00	4.25
	Grand Mean	1.84	0.86	2.09	0.91	1.07	1.59	0.93	1.73	0.84	2.70	0.89	1.16	0.68	2.05	0.59	2.43
	S.D.	2.41	1.08	2.00	0.96	1.33	2.15	1.11	2.44	1.61	2.80	1.24	1.69	1.06	2.26	0.87	2.27
	S.E.M.	0.73	0.33	0.60	0.29	0.40	0.65	0.34	0.74	0.48	0.84	0.37	0.51	0.32	0.68	0.26	0.68

Explanation of Table (From left to right):
Subject number; Location of stimulus presentation (left or right monitor);

Number of circling displays near altered and original stimuli for all stimulus pairs.

Summary of Cumulative Results

Subject	Monitor	LE	Original	LB	Original	NE	Original	NB	Original	NEB	Original	SEB	Original	NC+EB	Original	NC	Original
246	178 L	43.00	6.00	34.00	18.00	0.00	0.00	0.00	0.00	11.00	18.00	3.00	4.00	8.00	25.00	7.00	30.00
	178 R	18.00	16.00	18.00	9.00	5.00	3.00	4.00	2.00	10.00	16.00	3.00	5.00	12.00	42.00	11.00	28.00
	170 L	48.00	13.00	9.00	10.00	4.00	5.00	21.00	28.00	9.00	36.00	11.00	11.00	9.00	20.00	7.00	46.00
	170 R	23.00	14.00	18.00	4.00	18.00	17.00	22.00	25.00	0.00	4.00	4.00	0.00	0.00	0.00	11.00	20.00
	Mean	33.00	12.25	19.75	10.25	6.75	6.25	11.75	13.75	7.50	18.50	5.25	5.00	7.25	21.75	9.00	31.00
250	178 L	16.00	12.00	34.00	18.00	29.00	22.00	23.00	27.00	15.00	15.00	9.00	13.00	4.00	22.00	16.00	27.00
	178 R	23.00	24.00	14.00	7.00	17.00	16.00	23.00	32.00	21.00	22.00	23.00	23.00	13.00	23.00	7.00	13.00
	170 L	0.00	0.00	25.00	20.00	19.00	28.00	18.00	30.00	19.00	28.00	8.00	25.00	1.00	18.00	4.00	35.00
	170 R	13.00	13.00	27.00	18.00	23.00	10.00	27.00	19.00	20.00	19.00	26.00	15.00	1.00	8.00	11.00	16.00
	Mean	13.00	12.25	25.00	15.75	22.00	19.00	22.75	27.00	18.75	21.00	16.50	19.00	4.75	17.75	9.50	22.75
254	178 L	22.00	15.00	0.00	0.00	0.00	0.00	32.00	38.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.00
	178 R	0.00	0.00	0.00	0.00	0.00	0.00	34.00	38.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	19.00
	170 L	0.00	0.00	17.00	26.00	0.00	0.00	26.00	41.00	14.00	27.00	0.00	0.00	5.00	10.00	18.00	25.00
	170 R	0.00	0.00	42.00	10.00	42.00	31.00	0.00	0.00	0.00	0.00	10.00	12.00	0.00	0.00	5.00	8.00
	Mean	5.50	3.75	14.75	9.00	10.50	7.75	23.00	29.25	3.50	6.75	2.50	3.00	1.25	2.50	6.25	15.25
255	178 L	36.00	26.00	38.00	22.00	27.00	42.00	26.00	36.00	3.00	46.00	44.00	34.00	23.00	45.00	10.00	53.00
	178 R	28.00	42.00	18.00	30.00	29.00	42.00	12.00	33.00	35.00	47.00	24.00	46.00	13.00	59.00	5.00	50.00
	170 L	49.00	25.00	50.00	42.00	22.00	37.00	7.00	12.00	10.00	61.00	26.00	34.00	31.00	37.00	14.00	53.00
	170 R	45.00	21.00	52.00	45.00	17.00	10.00	39.00	39.00	15.00	55.00	44.00	46.00	40.00	39.00	30.00	49.00
	Mean	39.50	28.50	39.50	34.75	23.75	32.75	21.00	30.00	15.75	52.25	34.50	40.00	26.75	45.00	14.75	51.25
256	178 L	25.00	30.00	10.00	5.00	21.00	28.00	4.00	4.00	0.00	0.00	0.00	0.00	14.00	22.00	0.00	0.00
	178 R	0.00	0.00	20.00	16.00	0.00	0.00	0.00	0.00	0.00	8.00	0.00	0.00	13.00	26.00	0.00	0.00
	170 L	23.00	20.00	31.00	32.00	16.00	25.00	4.00	4.00	13.00	19.00	20.00	27.00	22.00	25.00	12.00	15.00
	170 R	30.00	25.00	24.00	28.00	15.00	12.00	29.00	24.00	5.00	7.00	9.00	9.00	37.00	18.00	29.00	16.00
	Mean	19.50	18.75	21.25	20.25	13.00	16.25	9.25	8.00	4.50	8.50	7.25	9.00	21.50	22.75	10.25	7.75
257	178 L	34.00	18.00	33.00	17.00	23.00	26.00	24.00	28.00	15.00	27.00	38.00	20.00	17.00	24.00	12.00	29.00
	178 R	27.00	23.00	26.00	23.00	16.00	36.00	13.00	42.00	19.00	29.00	24.00	17.00	21.00	28.00	7.00	36.00
	170 L	35.00	18.00	24.00	25.00	22.00	30.00	4.00	27.00	14.00	40.00	23.00	25.00	9.00	46.00	3.00	42.00
	170 R	28.00	11.00	21.00	30.00	13.00	30.00	13.00	28.00	8.00	45.00	9.00	26.00	15.00	40.00	10.00	37.00
	Mean	31.00	17.50	26.00	23.75	18.50	30.50	13.50	31.25	14.00	35.25	23.50	22.00	15.50	34.50	8.00	36.00
258	178 L	0.00	0.00	5.00	8.00	0.00	0.00	0.00	0.00	7.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00
	178 R	0.00	0.00	9.00	3.00	0.00	3.00	0.00	11.00	0.00	2.00	8.00	11.00	0.00	0.00	5.00	7.00
	170 L	0.00	0.00	2.00	0.00	0.00	0.00	1.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	170 R	0.00	2.00	4.00	9.00	0.00	5.00	0.00	0.00	12.00	13.00	8.00	6.00	0.00	0.00	2.00	12.00
	Mean	0.00	0.50	5.00	5.00	0.00	2.00	0.25	5.25	4.75	6.25	4.00	4.25	0.00	0.00	1.75	4.75
259	178 L	12.00	9.00	31.00	18.00	1.00	4.00	1.00	0.00	16.00	21.00	10.00	8.00	1.00	25.00	0.00	0.00
	178 R	0.00	0.00	0.00	3.00	2.00	0.00	14.00	10.00	16.00	28.00	17.00	28.00	27.00	19.00	18.00	27.00
	170 L	28.00	12.00	26.00	24.00	21.00	15.00	22.00	22.00	27.00	16.00	1.00	1.00	18.00	30.00	19.00	33.00
	170 R	16.00	28.00	21.00	22.00	13.00	15.00	27.00	23.00	15.00	26.00	3.00	18.00	2.00	23.00	16.00	23.00
	Mean	14.00	12.25	19.50	16.75	9.25	8.50	16.00	13.75	18.50	22.75	7.75	13.75	12.00	24.25	13.25	20.75
260	178 L	0.00	0.00	33.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.00	0.00	0.00	0.00	0.00
	178 R	0.00	0.00	0.00	0.00	0.00	0.00	3.00	22.00	0.00	0.00	9.00	43.00	0.00	0.00	0.00	0.00
	170 L	21.00	38.00	26.00	24.00	20.00	35.00	2.00	12.00	17.00	42.00	8.00	17.00	0.00	0.00	3.00	20.00
	170 R	32.00	13.00	12.00	24.00	25.00	33.00	30.00	22.00	11.00	41.00	0.00	3.00	0.00	0.00	0.00	0.00
	Mean	13.25	12.75	17.75	12.50	11.25	17.00	8.75	14.00	7.00	20.75	4.25	18.00	0.00	0.00	0.75	5.00
261	178 L	0.00	0.00	2.00	9.00	3.00	5.00	5.00	5.00	0.00	0.00	0.00	0.00	5.00	29.00	0.00	25.00
	178 R	19.00	15.00	31.00	9.00	7.00	2.00	8.00	6.00	0.00	0.00	0.00	0.00	18.00	6.00	0.00	7.00
	170 L	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	170 R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Mean	4.75	3.75	8.25	4.50	2.50	1.75	3.25	2.75	0.00	0.00	0.00	0.00	5.75	8.75	0.00	8.00
263	178 L	21.00	25.00	25.00	22.00	0.00	35.00	6.00	39.00	7.00	41.00	25.00	23.00	24.00	26.00	0.00	0.00
	178 R	26.00	18.00	30.00	18.00	20.00	18.00	20.00	26.00	21.00	25.00	33.00	16.00	36.00	13.00	3.00	32.00
	170 L	19.00	24.00	27.00	18.00	14.00	34.00	7.00	43.00	3.00	9.00	16.00	31.00	11.00	37.00	10.00	36.00
	170 R	30.00	23.00	27.00	23.00	21.00	10.00	24.00	24.00	12.00	35.00	0.00	0.00	17.00	14.00	16.00	23.00
	Mean	24.00	22.50	27.25	20.25	13.75	24.25	14.25	33.00	10.75	27.50	18.50	17.50	22.00	22.50	7.25	22.75
	Grand Mean	17.95	13.16	20.36	15.70	11.93	15.09	13.07	18.91	9.55	19.95	11.27	13.77	10.61	18.16	7.34	20.48
	S.D.	12.70	8.44	9.43	8.92	7.46	10.85	7.49	11.36	6.41	14.96	10.68	11.45	9.57	14.39	4.86	14.63
	S.E.M.	3.83	2.55	2.84	2.69	2.25	3.27	2.26	3.42	1.93	4.51	3.22	3.45	2.89	4.34	1.46	4.41

Explanation of Table (From left to right):
Subject number; Location of stimulus presentation (left or right monitor);

Number of vocalizations near altered and original stimuli for all stimulus pairs.