Research Report

DETECTION OF GLASS PATTERNS BY PIGEONS AND HUMANS:
Implications for Differences in Higher-Level Processing

Debbie M. Kelly, Walter F. Bischof, Douglas R. Wong-Wylie, and Marcia L. Spetch

University of Alberta, Edmonton, Alberta, Canada

Abstract—*Glass patterns have been used to examine mechanisms underlying form perception. The current investigation compared detection of Glass patterns by pigeons and humans and provides evidence for substantial species differences in global form perception. Subjects were required to discriminate, on a simultaneous display, a random dot pattern from a Glass pattern. Four different randomly presented Glass patterns were used (concentric, radial, parallel-vertical, and parallel-horizontal). Detection thresholds were measured by degrading the Glass patterns through the addition of random noise. For both humans and pigeons, discrimination decreased systematically with the addition of noise. Humans showed detection differences among the four patterns, with lowest thresholds to radial and concentric patterns and highest thresholds to the parallel-horizontal pattern. Pigeons did not show a detection difference across the four patterns. Implications for differences in neural processing of complex forms are discussed.*

Although investigations of neurons in the visual cortex have demonstrated neuronal sensitivity to specific line and edge orientations (Hubel & Wiesel, 1962, 1968), it is less understood how this information is formulated into the ability to recognize global patterns. H.R. Wilson and his colleagues (Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Asaad, 1997) addressed this issue using Glass patterns (Glass, 1969; Glass & Pérez, 1973). Glass patterns are composed of random dot pairs positioned, within a specified field, in such a way that a larger global pattern is perceived (see Fig. 1). Wilson and his colleagues measured detection thresholds for different Glass patterns embedded in noise, and found that human observers showed lower thresholds for concentric and radial patterns than for parallel patterns. Wilson et al. concluded that there is global pooling of orientation information for the processing of concentric and radial patterns, but only local processing for the detection of parallel patterns. Further, they suggested that this type of global pooling occurs in V4 and that V4 is an important level for form recognition in the pathway between V1 and the inferior temporal cortex (IT). Similar studies using grating stimuli have shown V4 to be important in form perception in the nonhuman primate visual system (Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996).

Electrophysiological studies have shown that there are orientation-sensitive units in the pigeon visual system (e.g., P. Wilson, 1980), and behavioral studies have shown that pigeons are capable of discriminating complex stimuli and global patterns (e.g., Cook, Katz, & Cavoto, 1997; Kirkpatrick-Steger, Wasserman, & Biederman, 1998; Watanabe & Ito, 1991). For this reason, we were interested in examining form perception by pigeons. If pigeons show differential sensitivity to patterns, as has been shown with Glass patterns in humans (H.R. Wilson

& Wilkinson, 1998; H.R. Wilson et al., 1997) and with similar grating stimuli in nonhuman primates (Gallant et al., 1993, 1996), then one might conclude that similar processing is involved in form perception by these species. Conversely, if pigeons do not show differential sensitivity, one might conclude that form perception is organized differently in avian and primate species. Interestingly, honeybees have been shown to prefer radial over other patterns (Lehrer, Horridge, Zhang, & Gadagkar, 1995), presumably because radial patterns are important for flower recognition. Thus, the existence of differential sensitivity to patterns such as Glass patterns may reveal fundamental species-specific differences in the architecture of the form-processing system. In the current study, we compared humans' and pigeons' sensitivity to Glass patterns to see if pigeons, like humans, show differential sensitivity to Glass patterns.

METHOD

Subjects

Pigeons

Eleven Silver King pigeons with previous unrelated touch-screen experience served as subjects. Four pigeons failed to learn the task and were removed from the study, leaving 7 birds. The birds were housed in individual cages under a 12-hr light:dark cycle (light onset at 6:00 a.m.). All birds were maintained at approximately 85% of their free-feeding weights by mixed grain during experimental sessions and supplemental feedings of Kay Tee pigeon pellets after sessions. Water and grit were available *ad lib* in the home cages.

Humans

Nine subjects participated in the study. Seven were experimentally naive, and 2 were informed regarding likely experimental outcomes. All subjects had normal or corrected-to-normal vision. The subjects ranged in age from 23 to 35 years.

Apparatus

Pigeons

The experiment was conducted in touch-screen operant chambers. The chamber dimensions ($h \times d \times w$) were either $36 \times 34 \times 50$ cm or $42 \times 32 \times 73$ cm. A Zenith 1492 color monitor with attached infrared touch frame (Carroll Touch, 1492 Smart Frame) was placed against an opening centered in the back wall of each chamber. The touch-screen was recessed from the opening by 3 cm and was spaced 1.6 cm from the monitor. Each chamber contained two Gerbrands pigeon feeders, one on each side of the monitor on the back wall of the larger chamber or on the side walls of the smaller chamber. A lamp illuminated a feeder when it was made available to the pigeon, and the feeder was retracted 2 s after the head entry into it. Microcomputers, located in an

Address correspondence to Debbie M. Kelly, BSP 220 Biological Sciences Bldg., University of Alberta, Edmonton, AB T6G 2E9, Canada; e-mail: wfb@ualberta.ca.
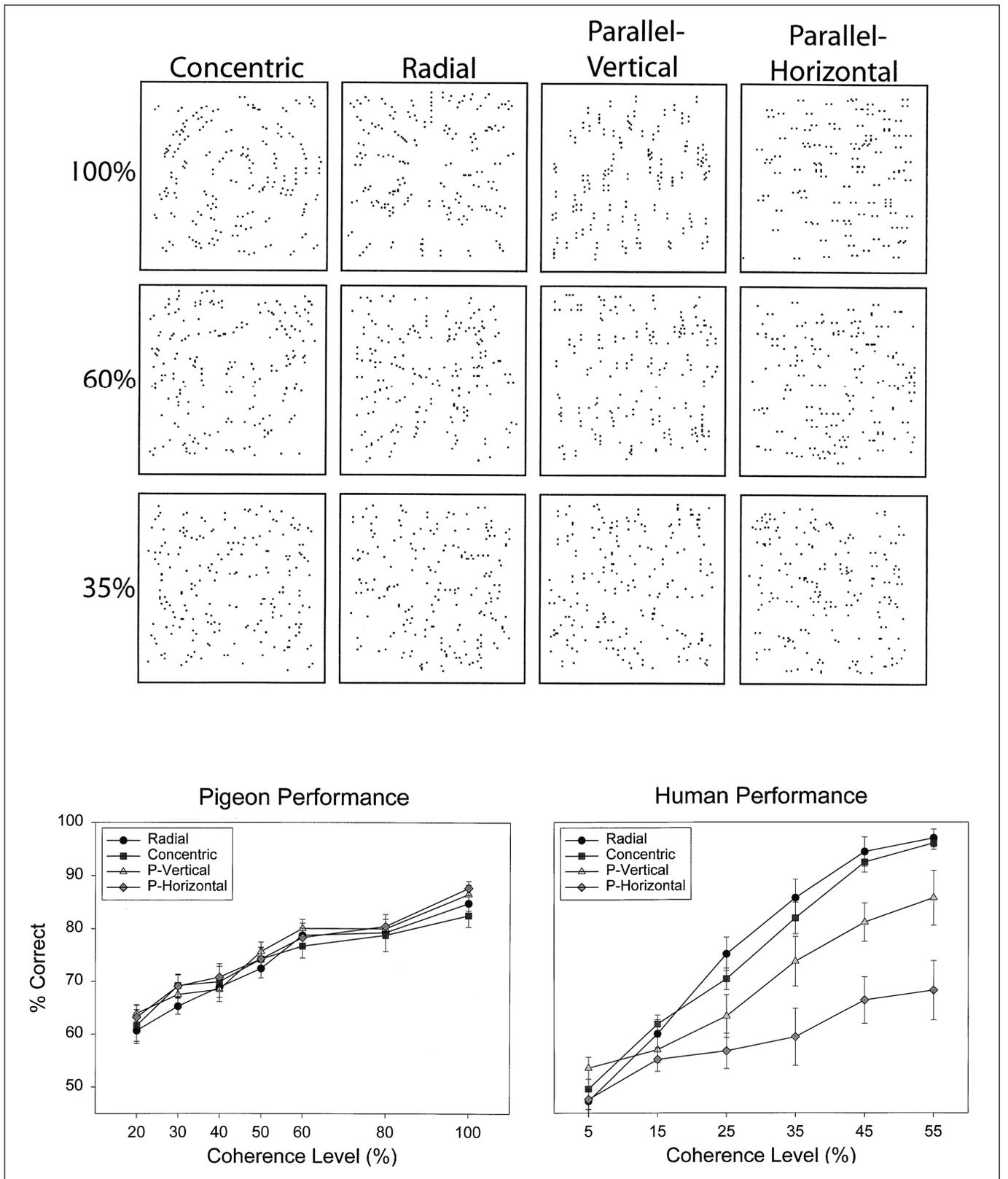
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Fig. 1. Examples of stimuli and results. The four Glass patterns at coherence levels of 100%, 60%, and 35% are shown at the top. The graphs at the bottom show pigeons' (left) and humans' (right) accuracy in discriminating the Glass patterns from random dot patterns as a function of coherence level.

adjacent room, controlled experimental contingencies and recorded responses. The touch frame was programmed to detect individual responses (i.e., it detected beam breaks; after a break, subsequent return to an unbroken state had to be detected before another response could be detected). Although the pigeons were free to view the monitor display from any position within the chamber, previous reports (Bischof, Reid, Wylie, & Spetch, 1999) and our observations indicated that the birds typically maintained a viewing distance of 9 cm or less.

Humans

Stimuli were presented on a Hitachi Superscan Elite 21 monitor under the control of a VGA display card. Viewing distance was 14 cm, and stimuli were sized so that the visual angle was as similar as possible for pigeons and humans. A keyboard to make responses was within easy reach of the subjects.

Stimuli

The stimuli consisted of four Glass patterns (concentric, radial, parallel-vertical, and parallel-horizontal; refer to Fig. 1) as the positive stimuli and a random dot pattern as the negative stimulus. On each trial, a positive pattern and a negative pattern were presented side by side, separated by a gap of 29.9°. Each stimulus measured 47.9° × 47.9° (the patterns were substantially larger than those used by H.R. Wilson et al., 1997, and H.R. Wilson & Wilkinson, 1998). The right/left position of the positive stimulus was counterbalanced across trials in each session. Each stimulus consisted of 200 black dots (luminance of approximately 5 cd/m^2) on a white background (luminance of 98 cd/m^2). Dot size was 0.5° × 0.5°. For the positive stimulus, a proportion of the dots was shown in pairs (dot separation of 1.4°) aligned tangentially to the Glass pattern, and any remaining dots were positioned randomly within the display window. For pigeons, 20 to 100 dot pairs were aligned according to the Glass pattern (coherence level of 20% to 100%); for humans, 5 to 55 dot pairs were aligned according to the Glass pattern (coherence level of 5% to 55%). For the negative stimulus, all dots were positioned randomly.

The dot patterns were presented in a simultaneous forced-choice procedure. Responses to the Glass pattern were considered correct, and responses to the random pattern were considered incorrect. For pigeons, each display was presented until two responses were made to one of the display areas of the screen (typically between 1 and 3 s). For humans, each display was presented for a total duration of 1 s.

Procedure for Pigeons

All sessions began with 10 warm-up trials not included in analysis. Each trial began with the presentation of a 6-cm yellow square, which served as a warning stimulus indicating the beginning of a new trial. The pigeon was required to peck the warning stimulus once to begin the stimulus presentation. During training trials, if the positive stimulus received two pecks first, the stimulus display was terminated, and 2 s of access to a randomly selected food hopper followed. However, if the negative stimulus received two pecks first, the stimulus display was terminated without access to a food hopper. Trials were separated by a 2-s intertrial interval (ITI). Following the ITI on an incorrect trial, a correction procedure was instituted. During a correction procedure, the patterns previously shown were redisplayed until the correct response was made. Correction trials were not used in the data analysis.

Initial training procedure

During initial training sessions, on each trial the pigeon was presented with a Glass pattern, at 100% coherence, on one half of the screen; the other half of the screen remained blank. Pecks to the stimulus side of the screen resulted in access to the food hopper for 10 s. Pecks to the nonstimulus side of the screen were inconsequential. Once the pigeon completed 60 trials for 3 consecutive days, the next stage of training was initiated.

Blocked-pattern training procedures

During blocked-pattern training sessions, each trial consisted of the simultaneous presentation of a Glass pattern, at 100% coherence, and a random dot pattern (0% coherence). Each daily session included 100 trials. Four of the pigeons were initially trained with two of the four Glass patterns (counterbalanced across birds), which were alternated across sessions. Because only 2 of these birds acquired the task within 35 sessions with this two-pattern training procedure, the other 2 pigeons and all remaining pigeons were trained to criterion with only a single pattern at a time, with order of exposure to patterns varied across birds. Once performance reached an accuracy level of 80% or greater for 3 consecutive sessions, the bird received coherence-level testing with the trained pattern.

Blocked-pattern testing procedures

During blocked-pattern testing, the trained Glass pattern (or patterns) was presented at coherence levels of 20%, 30%, 40%, 50%, 60%, 80%, and 100%. The coherence levels were presented in a quasi-random fashion, with each coherence level presented a maximum of 18 times per session. Daily sessions were increased to 120 trials. Following a minimum of 12 test sessions, each bird was then trained and tested with the remaining patterns.

Mixed-pattern testing procedures

Once the birds finished the blocked testing procedures, they were tested with all four patterns presented in a quasi-random fashion within each session. Again, each pattern was presented at the seven coherence levels. Mixed-pattern testing continued for a total of 25 sessions.

Procedure for Humans

Four of the 9 subjects received six mixed-pattern sessions and eight blocked-pattern sessions (two sessions for each pattern). The remaining 5 subjects received only the six mixed-pattern sessions. The mixed-pattern sessions began with 24 warm-up trials including all four patterns at six coherence levels (5%, 15%, 25%, 35%, 45%, and 55%). The warm-up trials were followed by four blocks of 96 trials, with each block consisting of four presentations of each of the four patterns at six coherence levels. Each blocked-pattern session also began with 24 warm-up trials, with the pattern to be tested in that block being presented four times at six coherence levels. The warm-up trials were followed by three blocks of 96 trials, with each block consisting of one pattern presented 16 times at six coherence levels. Of the subjects who participated in both the mixed- and the blocked-pattern sessions, 2 received all of the random sessions before the blocked sessions, and the other 2 received all of the blocked sessions initially, followed by the random sessions.

A trial began with presentation of the stimulus display for 1 s. Subjects were instructed to determine which stimulus was the Glass pattern and press the arrow key on the keyboard that corresponded to the side of the screen (left or right) on which the Glass pattern was located. The subjects were not provided with feedback regarding accuracy of their choices. The ITI was 1 s. After each block of trials, subjects were prompted to take a brief self-timed break.

RESULTS

For all statistical tests, the alpha level was set at .05 unless otherwise noted. Figure 1 shows the pigeons' and humans' accuracy for each pattern at each coherence level.

Pigeons

Only data from the mixed-pattern testing sessions were used in the analysis. A repeated measures analysis of variance (ANOVA) on accuracy scores showed a significant effect of coherence, $F(6, 36) = 54.22$, but no significant effect of pattern, $F(3, 18) = 2.06$. Performance with each pattern increased linearly with coherence (linear regression, $r^2 = .939$, .910, .926, and .970 for the radial, concentric, parallel-vertical, and parallel-horizontal patterns, respectively).

Humans

Only data from the mixed-pattern sessions were used in the analysis. A repeated measures ANOVA on accuracy scores showed significant main effects for both pattern, $F(3, 24) = 16.26$, and coherence, $F(5, 40) = 156.55$. A significant interaction of pattern with coherence was also present, $F(15, 120) = 9.33$. Performance with each pattern increased linearly with coherence, but because of a ceiling effect, the data for patterns with 55% coherence were not included in the regression analysis ($r^2 = .990$, .998, .973, and .943 for the radial, concentric, parallel-vertical, and parallel-horizontal patterns, respectively). Newman Keuls multiple comparisons revealed that performance was significantly better for both the radial and the concentric patterns than for the parallel-vertical and parallel-horizontal patterns, and was better for the parallel-vertical pattern than for the parallel-horizontal pattern.

DISCUSSION

Our results replicate those of H.R. Wilson and his colleagues (Wilson & Wilkinson, 1998; Wilson et al., 1997) in that the human observers in our study showed highest detection accuracy with the radial and concentric Glass patterns. We also found lower accuracy for the horizontal pattern than for the vertical pattern, suggesting that horizontal patterns may engage only local processing.

Pigeons did not show differential sensitivity to the four Glass patterns. Thus, according to the logic of H.R. Wilson and his colleagues (Wilson & Wilkinson, 1998; Wilson et al., 1997), whereas humans show global pooling of orientation units for construction of concentric and radial patterns, pigeons do not. The pigeons' accuracy with all patterns at 100% coherence was comparable to the humans' performance with the vertical pattern (argued by Wilson and his colleagues to be processed at a local level) at 55% coherence, thus suggesting that the pigeons processed all patterns at a local level. Overall, the lack of differential pattern sensitivity by the pigeons shows that form-perception processes are organized differently in pigeons than in humans or nonhuman primates.

Recent anatomical and physiological studies have highlighted numerous similarities in the organization of avian and mammalian visual pathways presumed to be important for form analysis. The mammalian primary visual cortex (V1) is thought to be equivalent to the visual Wulst in birds (e.g., Karten & Shimizu, 1989; Shimizu & Karten, 1993), although Shimizu, Cox, and Karten (1995) cautioned against a simplistic comparison of the two structures. An electrophysiological study of the Wulst in chicks found that most cells showed orientation sensitivity (P. Wilson, 1980), as is the case in V1 (e.g., Hubel & Wiesel, 1968).

Neurons in primate extrastriate areas such as IT encode more complex stimuli (e.g., Tanaka, 1996), including faces (e.g., Perret, Rolls, & Caan, 1982). H.R. Wilson and his colleagues (Wilson & Wilkinson, 1998; Wilson et al., 1997) suggested that the global pooling of orientation units for the detection of concentric patterns represents an intermediate step for face processing, and that it occurs in V4. If they are correct, then superior detection of concentric patterns by humans but not pigeons may reflect differences in the evolution of specialized mechanisms for processing faces. The pigeon equivalent to mammalian extrastriate cortices is the ectostriatum (Ec; Karten & Shimizu, 1989). Watanabe (1992) reported that Ec lesions disrupted pigeons' discrimination of conspecifics, but not their discrimination of different species. However, in contrast to humans and at least some nonhuman primates (Pascalis, Petit, Kim, & Campbell, 1999), pigeons may not use a specialized face-processing mechanism to recognize individuals. Instead, pigeons' recognition of individuals may depend on a combination of several visual features (Ryan & Lea, 1994), as well as on motion (Shimizu, 1998) and behavioral cues during social interaction (Watanabe, 1992). Further, primates and pigeons appear to process faces differently. In a working memory task, Phelps and Roberts (1994) found that humans and monkeys were affected by facial inversion, whereas pigeons were not.

Our findings suggest that the processes underlying complex form perception are organized differently in pigeons than in humans. Perhaps pigeons do not show superior detection of concentric Glass patterns, as do humans, because discrimination of individual pigeons involves numerous cues other than facial structure.

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